Center for Biological Diversity • Conservation Law Foundation
Defenders of Wildlife

August 2, 2021

Colleen Coogan
Marine Mammal & Sea Turtle Branch Chief
National Marine Fisheries Service
Northeast Regional Office
55 Great Republic Drive
Gloucester, MA 01930

Jennifer Anderson
Assistant Regional Administrator for Protected Resources
National Marine Fisheries Service
Northeast Regional Office
55 Great Republic Drive
Gloucester, MA 01930

Submitted electronically via regulations.gov

Re: Final Environmental Impact Statement, Regulatory Impact Review, and Final Regulatory Flexibility Analysis for Amending the Atlantic Large Whale Take Reduction Plan: Risk Reduction Rule; NOAA-NMFS-2020-0031

Dear Ms. Coogan and Ms. Anderson,

On behalf of the Center for Biological Diversity, Conservation Law Foundation, Defenders of Wildlife, and our millions of members and supporters, we submit these comments on the final environmental impact statement (FEIS) for the rule amending the Atlantic Large Whale Take Reduction Plan (Plan or ALWTRP) and intended to reduce the risk of serious injury and mortality (SI/M) caused by entanglements in vertical buoy lines used by Northeast American lobster and Jonah crab trap/pot fisheries.

Signatories to this letter are conservation members on the Atlantic Large Whale Take Reduction Team (Team) and have zealously advocated for the National Marine Fisheries Service (NMFS) to fulfill its obligations under the Marine Mammal Protection Act[1] (MMPA) and Endangered Species Act[2] (ESA) to protect large whales covered by the Plan, especially the critically imperiled North Atlantic right whale. As we noted in prior comments, this rulemaking cannot satisfy the MMPA's requirement to immediately bring SI/M below the right whale's potential biological removal (PBR) level and impermissibly puts off that goal for a full decade longer under the agency's "Conservation Framework." We further noted that the agency's approach is particularly egregious considering that under the plain language of the MMPA, NMFS should

---

[1] 16 U.S.C. §§ 1361–1389.
[2] *Id.* §§ 1531–1544.

have already adopted measures to reduce SI/M to "insignificant levels approaching a zero mortality and serious injury rate" (i.e., ZMRG) *two decades ago*.[3]

The FEIS does nothing to allay our concerns. While the right whale crisis demands immediate and substantial reductions in entanglements, the measures in the FEIS that compose the preferred alternative (FEIS Alternative 2) will accomplish neither.

While NMFS made certain modifications to the risk reduction measures in Alternative 2, including an expansion of the size of the seasonal restricted area south of Cape Cod,[4] these measures still fail to meet the mandatory and non-discretionary legal requirements of the ESA and MMPA. Among other things, they are aimed at a risk reduction target that NMFS recognizes cannot get SI/M below PBR (let alone ZMRG) and is egregiously low given recent information on population status and estimates of cryptic mortalities that NMFS acknowledges in the FEIS; they rely on unproven technologies such as weak line and inserts as well as flawed assumptions regarding the ability of these measures to sufficiently reduce risk; and they are not based on the best available scientific information on the sub-lethal effects of chronic entanglements and on right whale distribution.[5]

The rule and this accompanying FEIS should be withdrawn. Further, while supplementing its analysis and revising the rule, the agency should act on our December 2, 2020 petition for emergency rulemaking under MMPA section 118(g) by: (1) making a finding that the incidental mortality and serious injury of right whales from commercial fisheries is having an immediate and significant impact on the species; and (2) prescribing emergency regulations, including temporary closures, to protect right whales in the interim.[6] In addition to new concerns raised here, please incorporate by reference prior concerns raised in comment letters submitted on March 1, 2021 (regarding the proposed rule and its associated draft environmental impact statement);[7] and June 29, 2021 (regarding the efficacy of so-called weak line) by our organizations.[8] Moreover, because NMFS must meet its obligation to ensure its actions do not jeopardize the right whale's continued existence or adversely modify the species' designated critical habitat, please also incorporate our February 19, 2021 comments on NMFS's draft biological opinion to the extent those concerns—especially the concerns we raised regarding the Conservation Framework—apply.[9]

---

[3] *See id.* § 1387(b)(1).

[4] *See* FEIS Vol. I at p. 34.

[5] To the extent that provisions in the final rule offer fishing opportunities in current ALWTRP closures without vertical buoy lines, those provisions should be segmented and implemented as soon as possible.

[6] *See* https://www.biologicaldiversity.org/species/mammals/North_Atlantic_right_whale/pdfs/2020-12-02-Center-et-al-NARW-MMPA-Emergency-Petition.pdf.

[7] Comments submitted by the Center for Biological Diversity, Conservation Law Foundation, Defenders of Wildlife, Humane Society of the United States, and Humane Society Legislative Fund to NMFS on March 1 regarding the Proposed Rule to amend the ALWTRP Regulations and Draft Environmental Impact Statement (DEIS) are attached to this letter as Attachment A.

[8] Comments submitted by the Center for Biological Diversity, Conservation Law Foundation, and Defenders of Wildlife to NMFS on June 29, 2021 regarding new scientific information on the efficacy of weak rope are attached to this letter as Attachment B.

[9] Comments submitted by the Center for Biological Diversity, Conservation Law Foundation, Defenders of Wildlife, Humane Society of the United States, Humane Society Legislative Fund, and Natural

A. The Preferred Alternative Is Not Aimed at the Appropriate Risk Reduction Target

The FEIS states that the suite of measures in the preferred alternative (Alternative 2), "which includes broad trawling up requirements and two new seasonal restricted areas closed to lobster and Jonah crab buoy lines," will achieve "at least the 60 percent minimum risk reduction target. As discussed in prior comment letters, this 60 percent risk reduction target is wholly inadequate based on the most recent data, new population estimates, a new PBR, and new cryptic mortality estimates.

Nearly two years ago, NMFS provided the Team with a 60–80% risk reduction goal based on 2016 population estimates and a PBR of 0.9. At the time, NMFS indicated that, if cryptic mortalities were included in its analysis, the average annual rate of serious injuries and mortalities from entanglement in U.S. fisheries was 4.3 and "would have to be reduced by about 80% in U.S. fisheries to get below the stock's PBR of 0.9."[10] Moving forward into scoping for the rulemaking, however, NMFS lowered this target to 60% without an adequate explanation of why it aimed for the lower bound that did not account for cryptic mortality.

Since then, NMFS has revised its population estimates, its average annual rate of serious injuries and mortalities resulting from incidental entanglements in U.S. fishing gear, and its estimates of cryptic mortality.[11] **Using NMFS's own methodology and updated data, the FEIS acknowledges that PBR is 0.8 and the risk reduction target required to reduce M/SI in US fisheries may exceed 90%.**[12]

Resources Defense Council to NMFS on February 19, 2021 regarding its Draft Endangered Species Act Section 7 Consultation on the: (a) Authorization of the American Lobster, Atlantic Bluefish, Atlantic Deep-Sea Red Crab, Mackerel/Squid/Butterfish, Monkfish, Northeast Multispecies, Northeast Skate Complex, Spiny Dogfish, Summer Flounder/Scup/Black Sea Bass, and Jonah Crab Fisheries and (b) Implementation of the New England Fisheries Management Council's Omnibus Essential Fish Habitat Amendment 2, Consultation No. GARFO-2017-00031, are attached to this letter as Attachment C.

[10] Take Reduction Target Letter from Colleen Coogan, NMFS, to the Atlantic Large Whale Take Reduction Team (April 5, 2019).

[11] FEIS Vol I at 10, 14.

[12] *Id.* at 59 ("according to data from the model from Pace et al. (2021) and NMFS right whale incident data, there was an annual average of 2.2 incidents with an undetermined cause of death and an estimated 12.3 unobserved mortalities from 2010 through 2018, for a total of 14.5 incidents that were not accounted for in the calculations for minimum risk reduction target. If we assume half of these incidents occurred in the U.S as described above, then 7.25 additional incidents likely occurred in the U.S. According to incident data, 77 percent of all incidents (from 2010-2019) are a result of entanglement mortality and serious injury so we then assume 77 percent of 7.25 unknown or unobserved incidents were the result of an entanglement, or 5.6 per year. Adding this to the known entanglement data yields an annual average of 7.96 entanglements causing serious injury or mortality in U.S. waters every year between 2010 and 2018. This number would require a 90 percent reduction in mortality and serious injury (equation: 1-(0.8/7.96)). Under those assumptions, mortality and serious injury of right whales in U.S. fishing gear would need to be reduced by at least 60 percent according to documented mortality but may require up to 92 percent, depending on the year range and cause assumptions used, to reduce actual estimated mortality and serious injury below PBR.").

At a minimum, the final rule must get SI/M to below PBR. That is especially true considering new information noted in the FEIS, including an updated paper from Pace et al. (2021) that determined based on data from 2010–2017 that the observed mortality detection rate was only 29% of total mortality, leaving 71% of mortalities undetected.[13] Notably, the paper found that "the disparity in observed rates of serious injury by cause suggests that cryptic deaths due to entanglements significantly outnumbers cryptic deaths from vessel collisions or other causes."[14] The estimate from the New England Aquarium that the number of right whales alive at the end of 2019 was only 356 individuals, as few as 70 of which were breeding females, also emphasizes why NMFS must ensure the final rule drives right whale SI/M to below PBR.[15]

Even if 60% were the appropriate risk reduction target (it is not), and weak line/inserts could be relied upon to appropriately reduce risk (they cannot), the measures in FEIS Alternative 2 would still be highly unlikely to meet that target because of revisions related to measures analyzed in the Draft Environmental Impact Statement (DEIS). For example:

- Not all of the line reductions analyzed in the DEIS Alternative 2 were included in the FEIS Alternative 2;
- It appears that conservation equivalencies proposed in public comment will allow for the increased trawl length requirements analyzed in the DEIS to be exchanged for more expansive weak insert requirements in LMA2 (Vol I at p. 34);
- It appears that requirements for a weak link at the buoy were removed from FEIS Alternative 2 (Vol I at p. 34); and
- It appears that conservation equivalencies proposed in public comment for the Maine Exempted Area, all areas 3-12 nm from shore, and LMA3 will allow for a reduction in the number of weak inserts required (Vol I at p. 34).

B. The Preferred Alternative Relies on Flawed Assumptions about the Efficacy of Weak Rope

Our organizations do not support the weak line or insert measures analyzed in the FEIS[16] because they do not reduce encounter rates thus cannot eliminate sublethal effects. Moreover, the weak line and insert measures analyzed in the FEIS are unproven to reduce SI/M in use, and thus cannot guarantee any risk reduction target. In our comments on the proposed rule, we stated that key assumptions about the efficacy of weak line and inserts for reducing serious injuries and mortalities in these unproven measures were "largely theoretical." Newly available science discussed below, however, casts significant and new doubts on those assumptions and must be fully considered before NMFS makes any final decisions.

On June 29, 2021, we notified NMFS that it must reinitiate consultation on its recently-issued biological opinion and urged it to reconsider certain aspects of the forthcoming rule associated

---

[13] Pace, R. M. III et al. 2021. Cryptic mortality of North Atlantic right whales. Conservation Science and Practice. e346.

[14] *Id.*

[15] New England Aquarium, Right Whale Consortium Releases 2020 Report Card Update, Nov. 9, 2020, https://www.andersoncabotcenterforoceanlife.org/blog/2020-narwc-report-card/.

[16] *See* FEIS Vol I at 8-9, 14-16.

with this FEIS to address new evidence on the efficacy of these measures to mitigate the impacts of entanglements on the critically endangered North Atlantic right whale. That letter is attached as Exhibit B and the concerns raised are incorporated by reference here.

C. NMFS Has Legal Obligations to Use the Best Available Science in this Rulemaking and Must Supplement its Analysis

NMFS's decisions under the MMPA and ESA and its environmental analysis under the National Environmental Policy Act (NEPA) must be based on the best available scientific information (also termed evidence or data) to meet statutory requirements and to pass judicial muster under the Administrative Procedure Act (APA).[17]

There are several recent and relevant scientific studies that were not considered in the FEIS and have direct bearing on decisions related to the survival and recovery of North Atlantic right whales. NMFS must therefore prepare a supplemental EIS that incorporates the following scientific studies, at a minimum, into the analysis:

1. Stewart et al., Decreasing body lengths in North Atlantic right whales, *Current Biology* (2021), available at https://doi.org/10.1016/j.cub.2021.04.067.

This recently-published paper by NMFS scientist Joshua Stewart and co-authors indicates that the sub-lethal effects of entanglements may decrease the reproductive success of North Atlantic right whales and increase the risk of lethal entanglements. Their research compares length measurements of 129 individual whales born between 1981 and 2019 for which age and length data were collected in two periods, from 2000–2002 and from 2016–2019. It demonstrates that right whales "born in recent years have experienced stunted growth, and over the same period that we have detected this effect they have experienced increasing rates of entanglement."

2. Fortune et al., Body growth of North Atlantic right whales (Eubalaena glacialis) revisited, *Marine Mammal Science* (2020), available at https://doi.org/10.1111/mms.12753.

This paper demonstrates that healthy right whales are considerably heavier than previously estimated and that previously estimated energy requirements have been underestimated for some age-classes. Specifically, "sexually mature right whales require more energy per unit body mass than previously thought because their estimated body mass exceeds the upper limits of previous estimates." In the Atlantic, where North Atlantic right whales are significantly less healthy than their southern and North Pacific counterparts, knowing the size-at-age is important for determining prey requirements and making inferences about the nutritional status of individuals as well as their population.

3. Graham et al., Stress and reproductive events detected in North Atlantic right whale blubber using a simplified hormone extraction protocol, *Conservation Physiology* (2021), available at https://doi.org/10.1093/conphys/coaa133.

---

[17] *See, e.g.*, *Conner v. Burford*, 848 F.2d 1441, 1454 (9th Cir. 1988) (ESA); *Brower v. Evans*, 257 F.3d 1058, 1070–71 (9th Cir. 2001) (MMPA).

This paper confirms that the highest detected levels of stress hormones from biopsy or necropsy samples of right whales with known life history states came from whales with active entanglements or that died from acute entanglements. This paper is relevant to the high energetic and stress costs of sublethal entanglements to individual females.

4. Quintanna-Rizzo et al, Residency, demographics, and movement patterns of North Atlantic right whales Eubalaena glacialis in an offshore wind energy development in southern New England, USA, *Endangered Species Research* (2021), available at https://doi.org/10.3354/esr01137.

This paper confirms that North Atlantic right whales are increasingly using the area south of Nantucket and Martha's Vineyard and that since 2017 whales have been sighted in this area in nearly every month of the year. Models suggest that nearly one quarter of the population is present between December and May and that it is "an important destination for right whales, including conceptive and reproductive females, and qualitative observations included animals feeding and socializing." This information is directly relevant to the new South Island Restrict Area in Alternative 2 that only prohibits trap/pot fishing with vertical buoy lines between February 1 and April 30.[18]

5. Moore et al, Assessing North Atlantic right whale health: threats, and development of tools critical for conservation of the species, *Diseases of Aquatic Organisms* (2021), available at https://doi.org/10.3354/dao03578.

Among other issues related to North Atlantic right whale conservation, this paper looks at the energetic costs of entanglements and concludes that "to enable species recovery, reduction in mortalities have to be accompanied by substantial reduction of sub-lethal trauma as well." It also examines the role of the weak line and inserts proposed in the FEIS and states: "The role of sub-lethal entanglement drag in reducing NARW health and fecundity should be a major consideration in comparing the efficacy of potential mitigation measures. Thus, while 1700 lb (~773 kg) breaking strength rope may reduce mortality and severe injury, it will continue to be a source of morbidity. Ultimately, removal of rope from the water column will better enable species recovery."

6. Pace, R.M., Revisions and further evaluations of the right whale abundance model: Improvements for hypothesis testing. NOAA Technical Memorandum NMFS-NE-269. April 2021. Available at: https://apps-nefsc.fisheries.noaa.gov/rcb/publications/tm269.pdf.

In this paper, NMFS scientist Richard Pace modified the model NMFS uses to characterize annual estimates of age-specific survival. He found that the regime change in 2011 has influenced right whale area-use patterns, and the model modification will allow for better representations of population demography over time going forward.

All of these papers except the NOAA Technical Memorandum are attached to this letter behind the 3 public comment letters as Attachment D.

---

[18] FEIS Vol I at 7.

D. NMFS Has Not Responded to the CBD et al. MMPA Emergency Petition by Making a Discrete Finding as Required by the MMPA

NMFS has not responded to, let alone denied, the CBD et al. Petition for emergency action in the FEIS or in any other context. The FEIS lists it an alternative that was considered but rejected,[19] and appears to respond to comments made in the Petition regarding proposed closures rather than comments on the DEIS, however this does not constitute a denial under the MMPA or APA.

Section 118 of the MMPA requires NMFS to take emergency action to protect marine mammals in certain situations. Specifically, under Section 118, for species for which take reductions plans are in place,

> [i]f [NMFS] finds that the incidental mortality and serious injury of marine mammals from commercial fisheries is having, or is likely to have, an immediate and significant adverse impact on a stock or species, [NMFS] shall. . .
>
> (i) prescribe emergency regulations that, consistent with such plan to the maximum extent practicable, reduce incidental mortality and serious injury in that fishery; and
> (ii) approve and implement, on an expedited basis, any amendments to such plan that are recommended by the take reduction team to address such adverse impact.[20]

Despite the fact that there is no doubt that the incidental mortality and serious injury of right whales is having a significant adverse impact on the species, NMFS has refused to respond to the Petition by making the requisite "finding."

Instead, the FEIS provides the agency position that an onerous NEPA process would take longer than the current rulemaking:

> Emergency rulemaking does not exempt NMFS from the NEPA process. Initiating a new EIS for an emergency rulemaking suspend this rulemaking and restart the lengthy rulemaking clock. It would also dismiss the TRT process as well as the public input requirements of the APA. It would also be difficult to assess the effect of the rule given it is highly dependent on when it is implemented. For example, if NMFs implemented an emergency rule closing the Massachusetts South Island Restricted Area as requested starting in July, the first month would only reduce 0.3 percent to 1.9 percent of risk within a given month. Broader line reduction is needed to reduce overall risk.[21]

However long this rulemaking may take does not circumvent NMFS's legal obligations under the MMPA to find, under the circumstances, that an emergency exists. Further, we proposed alternatives in our emergency petition that the agency should consider once it gets past the

---

[19] *See* Vol I at 117-119 and Vol II at 41.

[20] 16 U.S.C. § 1387(g)(1)(A).

[21] FEIS Vol I at 19.

finding, but the agency is obligated to make the finding first, and then consider how to meet the statutory goal via interim measures.

Regardless, under current regulations it appears that NMFS has adequate authority to take emergency action without the NEPA analysis:

> Where emergency circumstances make it necessary to take an action with significant environmental impact without observing the provisions of the regulations in this subchapter, the Federal agency taking the action should consult with the Council about alternative arrangements for compliance with section 102(2)(C) of NEPA. Agencies and the Council will limit such arrangements to actions necessary to control the immediate impacts of the emergency. Other actions remain subject to NEPA review.[22]

V. CONCLUSION

NMFS's rule and its associated FEIS are fundamentally flawed and fail to comply with the agency's legal obligations under the MMPA, ESA, and NEPA in numerous ways. NMFS must revise its risk reduction target, the rule and associated documents; reissue them for public notice and comment; and implement emergency measures to significantly reduce entanglement risk in the interim. Failure to do so would be a gross dereliction of the agency's duties and condemn the right whale to suffer yet more of the entanglements in commercial fishing that are not only impeding the species recovery, but actively driving it closer to the brink of extinction.

Sincerely,

/s/ *Erica Fuller*
Erica Fuller
Senior Attorney
Conservation Law Foundation
efuller@clf.org

/s/ *Kristen Monsell*
Kristen Monsell
Oceans Legal Director & Senior Attorney
Center for Biological Diversity
kmonsell@biologicaldiversity.org

/s/ *Jane Davenport*
Jane Davenport
Senior Attorney
Defenders of Wildlife
jdavenport@defenders.org

---

[22] 40 C.F.R. § 1506.12 Emergencies.

Attachment A

• Center for Biological Diversity • Conservation Law Foundation •
• Defenders of Wildlife • Humane Society of the United States •
• Humane Society Legislative Fund •

Colleen Coogan
National Marine Fisheries Service
Northeast Regional Office
55 Great Republic Drive
Gloucester, MA 01930

March 1, 2021

via regulations.gov

Re: Proposed Rule to Amend Atlantic Large Whale Take Reduction Plan Regulations, 85 Fed. Reg. 86,878 (Dec. 31, 2020), and Draft Environmental Impact Statement NOAA-NMFS-2020-0031

Dear Ms. Coogan,

On behalf of the Center for Biological Diversity, Conservation Law Foundation, Defenders of Wildlife, the Humane Society of the United States, Humane Society Legislative Fund, and our millions of members and supporters, we submit these comments to the National Marine Fisheries Service (NMFS) on its proposed rule to amend the regulations implementing the Atlantic Large Whale Take Reduction Plan (Plan or ALWTRP) and associated Draft Environmental Impact Statement (DEIS).

As conservation members and alternates on the Atlantic Large Whale Take Reduction Team (Team), we have forcefully advocated for NMFS to fulfill its obligations under the Marine Mammal Protection Act[1] (MMPA) and Endangered Species Act[2] (ESA) to protect large whales covered by the Plan, especially the critically imperiled North Atlantic right whale. The history of the Plan is the history of NMFS's failure to meet these statutory mandates. The species—and the fisheries—now face the consequences of twenty-five years of agency denial and delay.

Since NMFS first promulgated the Plan in 1997, it has never complied with its MMPA obligation to bring mortalities and serious injuries (M/SI) in Category I and II fisheries to at or below the right whale's potential biological removal (PBR), to say nothing of the zero mortality rate goal (ZMRG). NMFS has been equally cavalier with its ESA obligations, tacitly allowing unlawful right whale take in both state and federal fisheries without consequences. On NMFS's watch, right whales don't die of old age.

Yet time and again NMFS has dragged its feet in amending and implementing the Plan. It has refused to finalize proposed regulations until compelled to do so by litigation. It has failed to

---

[1] 16 U.S.C. §§ 1361–1389.
[2] *Id.* §§ 1531–1544.

implement proactive, protective measures the right whale's status demands and the law requires. It has acceded to certain industry demands to carve out exemptions and rollbacks from Plan requirements and caved in the face of resistance to basic measures like gear marking.

Now, nearly twenty-five years after the original Plan, the right whale—and the agency—are at a crossroads. In the decade since 2011, the right whale has lost nearly all the hard-won population gains it made the decade previously. From a peak of 483 individuals in 2011, the population has plummeted to 356 animals—only around 56 more than when the Plan was first finalized in 1997. Lethal and sublethal entanglements are killing off right whales and depressing their reproduction. Cryptic mortalities are nearly 2.5 times observed mortalities. Two-thirds of cryptic mortalities are entanglement-related. Mortalities are outpacing births by a significant and growing margin.

In short, the species is on a death march to oblivion that can only be reversed with decisive, large-scale, sweeping federal actions to address the existential threats of fishing gear entanglements and vessel strikes in U.S. and Canadian waters. If there was ever a time for NMFS to answer Congress' clarion calls in the ESA and MMPA to save the right whale from extinction at human hands, that time is now.[3]

But while this crisis necessitates immediate and substantial reductions in entanglements, NMFS has proposed a rule that will accomplish neither. NMFS does not even pretend that this rulemaking will satisfy the MMPA's immediate requirement to bring M/SI below PBR, explicitly putting off that goal for a full decade longer under its Conservation Framework. The proposed measures are highly unlikely to meet even the inadequate 60% risk reduction target NMFS set based on now-outdated data, let alone the much higher risk reduction target that new data on population estimates, PBR, and cryptic mortality necessitate. The DEIS does not satisfy the National Environmental Policy Act's (NEPA) requirements for analyzing a full range of reasonable alternatives that meet the purpose and need of this rulemaking. And as described at length in our recent comments on the draft Biological Opinion (BiOp), NMFS cannot finalize that document as drafted without violating the ESA.

In short, NMFS cannot conclude this rulemaking within the parameters and proposals it has proffered for public comment without violating the MMPA, NEPA, and the ESA. If it proceeds as planned NMFS will inevitably face litigation while subjecting industry to costly, disruptive, and ultimately insufficient regulatory measures and wasting more months and years that the critically endangered right whale does not have to spare.

The only reasonable course of action is for NMFS to withdraw the proposed rule and take it (along with the DEIS and draft BiOp) back to the drawing board to bring them into compliance with the law. In the interim, NMFS must act on our December 2, 2020 petition for emergency rulemaking under MMPA section 118(g) by: (1) finding that the incidental mortality and serious injury of right whales from commercial fisheries is having an immediate and significant impact on the species; and (2) prescribing emergency regulations, including temporary closures, to protect right whales in the interim while developing, approving, and implementing Plan amendments that will satisfy NMFS's legal obligations while setting the right whale and the

---

[3] The United States must also aggressively engage in an open and transparent process with Canada to ensure that appropriate risk reduction measures are implemented bilaterally.

commercial fisheries on a sustainable path forward.

While revising the rule, the agency should clarify for the public and the industry that it must take this action to address long standing legal requirements under the ESA and MMPA, not only the court decision which required the agency to do what the law already required of it. In addition, the agency should clarify that a particular risk reduction target is not equivalent to the same reduction in fishing effort. Regardless, ignoring new scientific data will not adequately protect right whales or the industry which will be told, once again, that despite implementing costly modifications, they were not enough.

I. TIMING OF THE PROPOSED RULE/NEPA ANALYSIS RELATIVE TO THE FINAL BIOLOGICAL OPINION

The agency is well aware that it must complete its new biological opinion by May 31, 2021. Yet NMFS staff have stated several times during the course of informational meetings and public hearings on the proposed rule that the agency expects to complete the final rule and Final Environmental Impact Statement (FEIS) sometime this summer, with the Record of Decision (ROD) to follow after a 30-day minimum waiting period. We are deeply concerned that if NMFS follows through on its plan to complete the biological opinion months earlier than the final rule and FEIS/ROD, it will violate the ESA, the Administrative Procedure Act (APA), or both. This approach would also contradict representations that NMFS made in federal court—representations on which the Court based its decision.

A biological opinion must be coextensive with the agency action it analyzes and must analyze the effects of the entire agency action. *Conner v. Burford*, 848 F.2d 1441, 1453, 1457–58 (9th Cir. 1998); *see also id.* at 1453. We have already detailed the extensive defects in the agency's definition of the proposed action in our comments on the draft BiOp. We need not reiterate those here to state the obvious: if NMFS has not yet decided on the measures to be promulgated in the final rule amending the Plan, it cannot complete a meaningful and lawful biological opinion without the certainty of what the final action—and thus the effects of the entire agency action—will be. *See Ctr. for Biological Diversity v. Ross*, Case No. 18-cv-112 (D.D.C.), ECF No. 111-1 (Fourth Declaration of Jennifer Anderson) at para. 14 ("Completion of the Biological Opinion is linked to completion of the rulemaking process, as the analysis of the effects of the fisheries as modified by the rulemaking necessitates knowing what measures will be in the final rule."). A biological opinion issued when the agency action itself is not final is ipso facto incomplete and unlawful.

As is equally obvious, NMFS must have a valid biological opinion on the state of the world as it exists (i.e., on the ongoing authorization and management of state and federal fisheries as regulated by the Atlantic Coastal Fisheries Cooperative Management Act, the MMPA and the Magnuson-Stevens Fishery Conservation and Management Act), not a biological opinion on future measures not in effect yet. If NMFS issues a final biological opinion that relies on future measures in the final rule and FEIS/ROD, it will continue to be in violation of sections 7 and 9 of the ESA.

NMFS also risks violating the APA's notice and comment requirements if it rushes to finalize its

MMPA decision for purposes of the ESA consultation but then publishes the final rule months later, particularly if it has still not finished analyzing and responding to public comments. The APA obligates NMFS not only to analyze and respond to the public's comments on the proposed rule but to make reasoned choices in its final rule and to alter course where justified. That requires the agency to keep a mind sufficiently open to change based on public comments. *See, e.g.*, *Grand Canyon Air Tour Coal. v. FAA*, 154 F.3d 455, 467–68 (D.C. Cir. 1998) ("An agency is required to provide a meaningful opportunity for comments, which means that the agency's mind must be open to considering them").

If NMFS renders its final decision on what measures to incorporate in the final rule amending the Plan for ESA consultation purposes but still has not completed its FEIS, let alone the ROD, it will have violated NEPA. That statute's twin aims are informing decisionmakers and informing the public both to stimulate public involvement in federal agency decisionmaking and to ensure agency accountability. *See Dep't of Transp. v. Public Citizen*, 541 U.S. 752, 768 (2004) (describing NEPA as intended to "provid[e] a springboard for public comment" (alteration in original)); *New Mexico ex rel. Richardson v. Bureau of Land Mgmt.*, 565 F.3d 683, 703) (10th Cir. 2009) ("By focusing both agency and public attention on the environmental effects of proposed actions, NEPA facilitates informed decisionmaking by agencies and allows the political process to check those decisions."). NMFS must take this hard look "objectively and in good faith, not as an exercise in form over substance, and not as a subterfuge designed to rationalize a decision already made." *Metcalf v. Daley*, 214 F.3d 1135, 1142 (9th Cir. 2000). If NMFS has already decided for ESA consultation purposes what its action will be long before the FEIS and ROD issue, the NEPA process will have been a meaningless exercise.

Additionally, in *Center for Biological Diversity v. Ross*, the Court vacated the previous 2014 biological opinion, but stayed that vacatur until May 31, 2021 based explicitly on NMFS's representations for how much time it would need to complete the *final rule*, not just the new biological opinion. For example, the Court stated: "vacatur of the 2014 BiOp is appropriate, but [] relief shall be stayed until May 31, not January 31, 2021, to give Defendants time to complete *the new rule* and BiOp." 480 F.Supp.3d 236, 240 (D.D.C. 2020) (emphasis added). The Court based its decision on the fact that:

> NMFS currently estimates that it will publish a final amended Take Reduction Plan and implementing regulations by May 31, 2021. *See* Fourth Anderson Decl., ¶¶ 11–13. The agency intends to issue a new BiOp (presumably including an ITS this time, if required) for the lobster fishery simultaneously with publishing the final amended Plan, as the required "analysis of the effects of the fisheries [on the right whale] ... necessitates knowing what measures will be in the final rule." Defs. Remedy Opp. at 10–11.

Id. at 243. Indeed, after finding that NMFS's "timetable for completing the rulemaking process is reasonably consistent with the MMPA," the Court stated: "[a]lthough the Court therefore finds the May 31, 2021, deadline acceptable, it will look with considerable disfavor on any future requests by NMFS for even more time to *complete the new rule* and BiOp." *Id.* at 249 (emphasis added).

A. NMFS Has a Decades-Long History of Failing to Implement Measures Sufficient to Meet PBR

NMFS has lost sight of several critical aspects of section 118 in the nearly twenty-five years it has administered the ALWTRP. First, Congress did not intend to allow NMFS decades to reduce right whale M/SI to below PBR or to give the agency leeway to promulgate a Plan or amendments that admittedly will not meet this target at all. Second, Congress expressly stated that reducing M/SI to below PBR is only an interim goal on the way to ZMRG. Third, Congress explicitly allowed NMFS to take into account economic and other factors in a Plan *only* if M/SI is below PBR and on its way to ZMRG.

Congress amended the MMPA in 1994 to add section 118 to require "*immediate* action to protect . . . marine mammal stocks most affected by interactions with commercial fishing operations." S. Rep. No. 103-220, at 6 (1994) (emphasis added); 16 U.S.C. § 1387. Especially concerned about the incidental take of endangered marine mammals in commercial fisheries, Congress specified that any such take requires authorization under both section 118 and section 101(a)(5)(E). *See* 16 U.S.C. §§ 1371(a)(5)(E), 1387(a)(2).

Section 118 requires NMFS to develop a take reduction plan for Category I and II fisheries that interact with "strategic stocks," including ESA-listed marine mammals. *Id.* §§ 1387(f)(1), 1362(19)(C). The statute specifies that, as a short-term goal, each take reduction plan must contain regulatory measures to reduce fishery-related mortality and serious injury to below the species' PBR *within six months* of the plan's implementation. *Id.* § 1387(f)(2), (f)(5)(A), (f)(7)(F). The true goal of section 118 is not PBR but ZMRG. *Id.* § 1387(b). Therefore, the long-term goal of a take reduction plan must be to reduce, within five years of its implementation, incidental mortality and serious injury "to insignificant levels approaching a zero mortality and serious injury rate."[4] 16 U.S.C. § 1387(f)(2).

Congress did not entrust NMFS with the latitude to interpret a reasonable timeframe for accomplishing section 118's goal for species like the right whale. Rather, it established section 118's "immediate" goal "that the incidental mortality or serious injury of marine mammals occurring in the course of commercial fishing operations be reduced to insignificant levels approaching a zero mortality and serious injury rate within 7 years after April 30, 1994." *Id.* § 1387(a)(1) (emphasis added); *see also id.* § 1387(b)(1) ("Commercial fisheries shall reduce incidental mortality and serious injury of marine mammals to insignificant levels approaching a zero mortality and serious injury rate within 7 years after April 30, 1994").

Congress thus set clear expectations for NMFS to reduce M/SI of right whales in commercial fisheries to below PBR and to ZMRG by dates certain, as NMFS acknowledged in promulgating the original 1997 ALWTRP. *See* 62 Fed. Reg. 39,157, 39,159 (Jul. 22, 1997) (MMPA required Plan to reduce right whale M/SI below PBR of 0.4 animals per year by January 1998 and further reduce M/SI to ZMRG by April 30, 2001 while taking into account fisheries economics, etc.). Yet the Plan not only failed to accomplish these statutory mandates by the congressionally-set deadlines, it has not even managed to keep pace with the increasing rates of M/SI in U.S.

---

[4] NMFS defines "insignificant levels approaching . . . zero" or "ZMRG" to mean 10% of a stock's PBR. 50 C.F.R. § 229.2.

commercial fisheries.

Although NMFS cannot turn back the clock to comply with prior deadlines, it is equally obvious that it may not continue to push substantive compliance with the statute off to some future point one minute longer. Congress did not give NMFS a free hand to determine when a Plan or its amendments will fulfill section 118's mandates, such as NMFS is now purporting to do with the proposed rule and Conservation Framework that optimistically (and unrealistically) project finally achieving M/SI reductions below PBR five to ten years from now.

Nor did Congress give NMFS a free hand to determine whether a Plan or its amendments will meet the statutory mandates at all. The language of section 118 allows no exceptions: any take reduction plan or amendments thereto *shall* include measures to reduce M/SI to below PBR, and, thereafter, shall be amended as necessary to meet section's 118 requirements (i.e., ZMRG). *See, e.g.*, 16 U.S.C. § 1387(f)(7)(C), (F).

B. Economics Only Comes into Play When Analyzing ZMRG

Section 118 does not authorize NMFS to promulgate amendments that yet again attempt merely to reduce the risk of commercial fisheries on right whales, *e.g.*, 85 Fed. Reg. at 86,879; it must promulgate measures that will in fact meet the statutory targets of reducing M/SI to below PBR and ultimately to ZMRG. NMFS knows full well that the proposed rule will not meet PBR; at the very, very best, it will bring down M/SI to more than three times PBR.[5]

From the very outset, NMFS has imputed to itself discretion under section 118 to subsume the requirement to bring right whale M/SI below PBR through the Plan (which it has never succeeded in doing) to its desire to minimize economic impacts to the fisheries. *See* 62 Fed. Reg. at 39,159 (rejecting approach of extensive closures that would guarantee M/SI "but only at a high cost to many fishermen" and instead choosing an approach relying on untested gear modifications, limited closures, and disentanglement efforts); *id.* at 39,182 ("Widespread closures, although they might achieve the goals of the MMPA, would be economically costly. Such huge economic costs would not be necessary if disentanglement efforts and gear modifications are successful in reducing bycatch to MMPA standards."). Yet section 118 itself does not support that exercise of discretion, as illustrated by the very different language Congress used in the two sentences composing section 118(f)(2)'s commands for a strategic stock such as the right whale. The first sentence reads:

> The immediate goal of a take reduction plan for a strategic stock shall be to reduce, within 6 months of its implementation, the incidental mortality or serious injury of marine mammals incidentally taken in the course of commercial fishing operations to levels less than the potential biological

---

[5] *See* NMFS, Draft Endangered Species Act Section 7 Consultation on the: (a) Authorization of the American Lobster, Atlantic Bluefish, Atlantic Deep-Sea Red Crab, Mackerel/Squid/Butterfish, Monkfish, Northeast Multispecies, Northeast Skate Complex, Spiny Dogfish, Summer Flounder/Scup/Black Sea Bass, and Jonah Crab Fisheries and (b) Implementation of the New England Fisheries Management Council's Omnibus Essential Fish Habitat Amendment 2 [Consultation No. GARFO-2017-00031, Jan. 2021, available at https://www.greateratlantic.fisheries.noaa.gov/public/nema/PRD/DraftFisheriesBiOp011421.pdf (Draft BiOp). 230.

> removal level established for that stock under section 1386 of this title.

16 U.S.C. § 1387(f)(2). Only *after* that goal has been accomplished does the second sentence allow the agency to balance how to accomplish the long-term goal, i.e., ZMRG, against the fisheries' interests:

> The long-term goal of the plan shall be to reduce, within 5 years of its implementation, the incidental mortality or serious injury of marine mammals incidentally taken in the course of commercial fishing operations to insignificant levels approaching a zero mortality and serious injury rate, *taking into account the economics of the fishery, the availability of existing technology, and existing State or regional fishery management plans.*

Id (emphasis added). Congress clearly intended NMFS to immediately reduce M/SI below PBR; only after that immediate goal has been achieved may NMFS balance the requirement to further reduce M/SI to ZMRG with fisheries economics and other concerns.

For twenty-four years now, NMFS has administered, and, from time to time, amended, a Plan based on the hope that gear modifications and limited closures will achieve in bringing right whale M/SI down to PBR, falling well short of the six-month deadline and the goal of the statute.

II. NONE OF THE PROPOSED MEASURES ADEQUATELY REDUCE RISK

Our organizations do not support either Alternative 2 (Preferred Alternative) or Alternative 3 in the DEIS for several reasons including: (1) that they cannot adequately reduce risk to right whales as packaged; (2) many of the assumptions upon which they allegedly reduce risk are unfounded; (3) to the extent they incorporate state measures they are not yet added to the TRP; and (4) an admitted lack of enforcement beyond 12 nautical miles makes their effectiveness questionable. Neither do we support Alternative 1, the "No Action Alternative," as action is clearly needed.

According to the proposed rule, the Preferred Alternative will "achieve a greater than 60-percent reduction" in risk by ultimately implementing measures falling into four main categories: (1) gear modifications intended to reduce the number of vertical lines; (2) seasonal restricted areas that would allow ropeless fishing; (3) the replacement of buoy lines with weak rope or weak insertions; and (4) additional gear marking requirements. 85 Fed. Reg. at 86,881, 86,885. In the DEIS, NMFS estimates that the Preferred Alternative could reduce risk by up to 64.3%. DEIS Vol. I at 3-68.

Alternative 3 analyzes similar measures as well as: (1) larger, longer, and additional seasonal restricted areas; (2) a line cap allocation capped at 50 percent of the lines fished in 2017 in federal and non-exempt waters throughout the Northeast except in offshore LMA3; and (3) more robust gear markings. NMFS indicates that Alternative 3 could reduce risk by up to 72.6%. DEIS Vol. I at 3-69.

A. The Risk Reduction Targets are not based on the Best Scientific and Commercial Data Available

Nearly two years ago, NMFS provided the Atlantic Large Whale Take Reduction Team (TRT) with a 60-80% risk reduction goal based on 2016 population estimates and a PBR of 0.9. *Id.* at 3-47, 67. At the time, NMFS indicated that, if cryptic mortalities were included in its analysis, the average annual rate of serious injuries and mortalities from entanglement in U.S. fisheries was 4.3 and "would have to be reduced by about 80% in U.S. fisheries to get below the stock's PBR of 0.9." Since that time, NMFS has revised its population estimates and average annual rate of serious injuries and mortalities resulting from incidental entanglements in U.S. fishing gear. In its recently published draft BiOp , NMFS stated: "Using the methods in Pace et al. (2017), this year's preliminary estimate is 366 (95% credible interval range of 353-377) individuals as of January 2019."[6] Using 366 as the Nmin, PBR is now 0.7.[7] Table 57 of the draft BiOp estimates the annual average M/SI of right whales from U.S. fishery entanglements as 6.724.[8] Thus, **using NMFS's own methodology and updated data, the risk reduction target required to reduce M/SI in US fisheries is closer to 90%.**

The proposed rule needs to be revised to achieve M/SI below PBR (at minimum). That is especially true considering other new information, including an updated paper from Pace et al. (2021) that determined based on data from 2010–2017 that the observed mortality detection rate was only 29% of total mortality, leaving 71% of mortalities undetected,[9] and the estimate from the New England Aquarium that the number of right whales alive at the end of 2019 was only 356 individuals, as few as 70 of which were breeding females.[10]

B. The Gear Modifications Proposed to Reduce the Number of Vertical Lines Cannot Adequately Reduce Risk

The proposed rule describes 2 major gear modifications necessary to reduce the number of vertical lines in the Preferred Alternative: (1) increasing the number of traps on a trawl ("trawling up"); and (2) extending the maximum trawl length (distance between endlines) in LMA3. 85 Fed. Red. at 86,881. NMFS also analyzes capping line allocations at 50 percent of average monthly lines in federal waters in the DEIS for Alternative 3. *See* DEIS Vol. I at 1-7. We address each of these in turn.

1. Trawling Up and Line Caps

Every vertical line in the water increases entanglement risk for right whales. Trawling up is one method to reduce the number of vertical lines and could encourage efficiency. However, trawling up will only be guaranteed to reduce the number of vertical lines in the water (and thus risk) if it is combined with a line cap providing a concrete metric for reductions from the baseline. *See*

---

[6] Draft BiOp.

[7] PBR = Nmin x 0.5 (Rmax) x Fr. In this case, 0.7 = 366 x 0.2 x 0.1.

[8] Draft BiOp.

[9] Pace, R. M. III et al. 2021. Cryptic mortality of North Atlantic right whales. Conservation Science and Practice. e346.

[10] New England Aquarium, Right Whale Consortium Releases 2020 Report Card Update, Nov. 9, 2020, https://www.andersoncabotcenterforoceanlife.org/blog/2020-narwc-report-card/.

DEIS Vol. II at 5-143 (indicating that a 50% line cap reduction would reduce entanglement risk by 45% in federal waters and stating that trawling up alone is insufficient to reduce vertical line numbers). According to a September 18, 2018 TRT presentation, the number of vertical lines in the Northeast region has increased since the 2013 vertical line reduction rule was implemented. Even considering the possibility of a statistical error, there was no significant decrease detected from the implementation of the rule. This combination would hold the fisheries accountable and could prevent latent effort from being realized. *See* DEIS Vol. II at 5-139 (discussing need for a mechanism to prevent latent effort from being activated).

It is not clear, however, that trawling up necessarily reduces risk to right whales (especially to juvenile and calves). Quantitative date on the relationship between gear configurations and the probability of causing serious injuries and mortalities is largely lacking. DEIS Vol. II at 3-12. For example, an inshore fisherman forced to fish 15 rather than 5 traps/trawl may choose heavier line thus increasing risk. On the other hand, an offshore fisherman forced to fish 45 rather than 25 traps/trawl is already using heavy line and probably does not significantly increase risk as a right whale will likely drown under either scenario given the weight of the gear. *See e.g.*, DEIS Vol. II at 3-47-48.

Fishermen have raised safety concerns related to trawling up. It is logical to expect that trawling up could be more difficult on a smaller vessel (where the deck may not be able to accommodate the increased number of traps), or for Captains fishing alone. For those reasons, our organizations do not oppose the conservation equivalency proposed for LMA3, that would increase the maximum length of a trawl from 1.5nm to 1.75 nm to allow a limited number of vessels to fish more than 45 traps per trawl so that smaller vessels can fish less traps/trawl due to safety concerns. 85 Fed. Reg. 86,886.[11]

Although the proposed rule only seeks comment on the Northeast American lobster fishery, it is our view that all fisheries using vertical line, including but not limited to aquaculture, must be considered in this cap. Placing the sole burden of vertical line reduction on the lobster and Jonah crab fishery does little to reduce risk to right whales if risk is increased elsewhere by permitting other fisheries and activities. Data provided in the DEIS, indicate that gillnets pose a disproportionately high risk of entanglement to right whales. *See* DEIS Vol. I at Table 2.2 showing that gillnet/netting represents 47% of known fishery entanglements to right whales, yet gillnets represent only 1.9% of vertical lines in non-exempt waters (Table 2.3 of DEIS Vol. I)).

To reduce the number of serious injuries and mortalities below PBR, NMFS must evaluate the vertical line risk in all fisheries and identify a regulatory mechanism for implementing line caps as soon as possible.

2. NMFS Should Require the Use of One End-Line

The DEIS states that fishing with one end-line was "considered but not analyzed" due to industry concerns about safety, increased gear conflict, and increased gear loss. DEIS Vol. II at 5-138. Given that none of the measures in the proposed rule adequately reduce risk to right whales and

---

[11] Pers. comm. with TRT member David Borden (only a limited number of vessels will want an exemption from the 45 trap/trawl requirement.

that the remaining measures that would adequately reduce risk are not generally attractive to the industry either, NMFS should fully analyze this option as part of its do-over.

To immediately reduce the number of vertical lines outside of closures, NMFS should require all trap/pot fisheries operating in the Northeast to use a single surface end-line in those areas where right whales are known or expected to be (either socializing, transiting, feeding, or breeding). This immediate 50% reduction in endlines would reduce risk. Understanding that additional gear conflicts could occur in the absence of surface markings, agreements about the direction of gear sets should be developed by industry members fishing in specific regions and sharing agreements with the mobile gear fleet should be drafted (as they already are in certain areas).

C. The Seasonal Restrictions to Buoy Lines Proposed Will Not Adequately Reduce Risk

Both the Preferred Alternative and Alternative 3 propose new restricted areas that are inadequate to reduce risk sufficient to meet PBR. It is also difficult to discern how NMFS evaluated risk related to gear displacement for the specifically identified closures. *See* DEIS Vol. II at 3-36 (only analyzing redirected effort generally and modelling redirected effort for the Northeast Canyons and Seamounts National Marine Monument) While it is likely that some portion of gear (traps and lines) will be moved or removed, a risk analysis that looks at the impact of such gear displacement should be considered before assuming the costs or benefits. To the extent that NMFS relies on state measures to reduce risk, it must incorporate those into the Plan.

Our organizations support the following new Restricted Areas:

- The LMA1 Restricted Area in Alternative 3—Offshore ME LMA1/3 border, zones C/D/E—closed from October to February that allows fishing without buoy lines (with appropriate authorizations for exemption from surface gear requirements).
- The "Large Rectangular Area" in Alternative 3 in Southern New England, as modified to be a year-round restricted area closed to buoy lines with allowances for fishing without buoy lines (with appropriate authorizations for exemption from surface gear requirements).

1. The LMA1 Restricted Area in Gulf of Maine

Based on the best commercial and scientific data available in the public domain, including acoustic data, **we support the LMA1 Restricted Area analyzed in Alternative 3 which closes the area to vertical buoy lines October - February**. This area has been identified as a "foraging hotspot" for right whales using the Duke Habitat Model within the Decision Support Tool and poses a higher than average risk based on co-occurrence. DEIS Vol. I at 3-71, 72. It is also our understanding that based on the demographics of the fleet operating within the boundaries denoted and testimony at public hearings, that at least some of the gear will come out of the water minimizing risk due to shifted effort.

We oppose the trigger process described in the Preferred Alternative that allows the Regional Administrator the discretion to make a decision about this closure based on non-identified criteria. Any proposal to close an area to fishing should be based on sound science and demonstrate a tangible risk reduction to right whales, thus it is unclear how a proposed closure would no longer be warranted simply based on public input or whatever conservation equivalencies would be established in place of this closure if it is removed. Ironically, this is contradictory to what the agency has said elsewhere about its ability to do NEPA analysis on dynamic management.

2. The Massachusetts South Island Restricted Area in the Preferred Alternative is Insufficient

Our organizations do not support the Preferred Alternative - "South Island Restricted Area" - that closes an area south of Nantucket from February through April because the area is too small in time and space. A large body of science demonstrates a year-round presence of right whales in Southern New England. Based on this data, as well as the size of previously established restricted areas in the Plan, **we support the "Large South Island Restricted Area" analyzed in Alternative 3**. **However, we urge the agency to make this a year-round closure to vertical buoy lines.** Modifying the Large South Island Restricted Area to restrict vertical buoy lines year-round would be the most protective and fully account for the variable habitat use of this region by right whales.

Right whale distribution and habitat use has shifted since 2010 in response to climate change-driven shifts in prey availability.[12] The best scientific and commercial data available, including aerial surveys,[13] acoustic detections,[14] stranding data,[15] a series of DMAs declared by NMFS pursuant to the ship strike rule,[16] and prey data,[17] all indicate that right whales now heavily rely

---

[12] Record, N., Runge, J., Pendleton, D., Balch, W., Davies, K., Pershing, A., Johnson, C., Stamieszkin, K., Ji, R., Feng, Z. and Kraus, S. 2019. Rapid Climate-Driven Circulation Changes Threaten Conservation of Endangered North Atlantic Right Whales. Oceanography. Vol. 32, pp. 162–169.

[13] Kraus, S.D., Leiter, S., Stone, K., Wikgren, B., Mayo, C., Hughes, P., Kenney, R.D., Clark, C.W., Rice, A.N., Estabrok, B., and Tielens, J. 2016. Northeast large pelagic survey collaborative aerial and acoustic surveys for large whales and sea turtles. Final Report. OCS Study, BOEM 2016-054, pp. 118; Leiter, S.M., Stone, K.M., Thompson, J.L., Accardo, C.M., Wikgren, B.C., Zani, M.A., Cole, T.V.N., Kenney, R.D., Mayo, C.A., and Kraus, S.D. 2017. North Atlantic right whale *Eubalaena glacialis* occurrence in offshore wind energy areas near Massachusetts and Rhode Island, USA. Endangered Species Research. Vol. 34, pp. 45–59; Quintana, E., "Monthly report No. 3: May 2017," Report prepared for the Massachusetts Clean Energy Center by the New England Aquarium, pp. 26 (May 15, 2017).

[14] Kraus, et al. 2016; Davis, G.E., Baumgartner, M.F., Bonnell, J.M., Bell, J., Berchick, C., Bort Thorton, J., Brault, S., Buchanan, G., Charif, R.A., Cholewiak, D., 2017. Long-term passive acoustic recordings track the changing distribution of North Atlantic right whales (*Eubalaena glacialis*) from 2004 to 2014. Scientific Reports. Vol. 7, p. 13460.

[15] Asaro, M.J., Update on US Right Whale Mortalities in 2017, NMFS, November 30, 2017, available at: https://www.greateratlantic.fisheries.noaa.gov/protected/whaletrp/trt/meetings/2017%20Nov/asaro_usstrandings_nov2017.pdf.

[16] NMFS Interactive DMA Analyses: https://www.nefsc.noaa.gov/rcb/interactive-monthly-dma-analyses/.

[17] Pendleton, D.E., Pershing, A., Brown, M.W., Mayo, C.A., Kanney, R.D., Record, N.R., and Cole, T.V.N. 2009. Regional-scale mean copepod concentration indicates relative abundance of North Atlantic right whales. Marine Ecology Progress Series. Vol. 378, pp. 211–225; NOAA Northeast Fisheries Science Center, "Ecology of the

on Southern New England waters.[18] In January 2019, an aggregation representing a quarter of the population—100 whales—was seen in this area[19] engaged in both foraging and social activities, demonstrating that it is clearly more than just a migratory corridor. Southern New England is important to all life history stages.[20] Surface Active Groups have also been documented in this region[21] and, given the gestation period of right whales, this behavior is more likely to result in pregnancy during the winter months.

Large, consistent aggregations of right whales in all four seasons, have led scientists and a NMFS Expert Working Group to describe Southern New England as a year-round foraging "hotspot."[22] Several other scientific data sources demonstrate that right whales use these waters year-round.[23] Further, a recent presentation at the North Atlantic Right Whale Symposium discussed new evidence showing that 11 out of 15 newly catalogued whales identified south of Cape Cod have never been sighted further north in the Bay of Fundy or the Gulf of St. Lawrence,[24] and suggesting this area may represent an end-point of the northern migration for some portion of the population.

In addition to year-round use of the area, the relative abundance in the area has increased. For example, there is -evidence of a broader temporal shift in distribution resulting in greater densities off Rhode Island and Massachusetts later in the year, through May and into the summer months.[25] April appears to be particularly important for females of reproductive age.[26] Inter-annual and inter-seasonal variability in aerial and acoustic detections imply that there are no clear spatial patterns of habitat use across Southern New England and right whales should be expected to be encountered equally across the region.[27]

Northeast US Continental Shelf – Zooplankton," available at https://www.nefsc.noaa.gov/ecosys/ecosystem-ecology/zooplankton.html.

[18] Although there are challenges in the use of opportunistic sightings data (no area systematically surveyed, effort not corrected for, and potential for counting an individual whale more than once), they are a proxy for habitat used by North Atlantic right whales, as validated by NMFS' management actions based on these data, including the implementation of DMAs.

[19] NMFS, Voluntary Vessel Speed Restriction Zone in Effect South of Nantucket to Protect Right Whales (Jan. 28, 2019), https://www.fisheries.noaa.gov/feature-story/voluntary-vessel-speed-restriction-zone-effect-south-nantucket-protect-right-whales.

[20] Leiter et al. 2017, at 52–54.

[21] *Id.*

[22] Oleson, E.M., Baker, J., Barlow, J., Moore, J.E., and Wade, P., 2020. North Atlantic Right Whale Monitoring and Surveillance: Report and Recommendations of the National Marine Fisheries Service's Expert Working Group. NOAA Technical Memorandum NMFS-OPR-64, at Fig. 1.

[23] Kraus, S.D. 2016; Davis, G.E., et al. 2017; NMFS Interactive DMA Analyses.

[24] Hamilton, P., "North Atlantic Right Whale Catalog Update, Recent Genetic Findings and Whale Naming Results," Presentation at the North Atlantic Right Whale Consortium Annual Meeting (Oct. 29, 2020).

[25] Davis, G. E., et al. 2017.

[26] Leiter, S.M., et al., "North Atlantic right whale *Eubalaena glacialis* occurrence in offshore wind energy areas near Massachusetts and Rhode Island, USA." Endang Spec Res Vol. 34: 45–59 (2017).

[27] *Id.*; DMAs; Redfern, J., Pendleton, D., O'Brien, O., Ganley, L., Hodge, B. and McKenna, K., "Tools to identify and minimize risk to marine mammals," Presentation to the Massachusetts Habitat Working Group (Dec. 11, 2020).

Finally, the Preferred Alternative could result in redirected effort into areas of high risk as the Commonwealth of Massachusetts did not close state waters south of the islands after all.[28] Given the potential for this area to be a winter mating ground as well as preferred habitat for at least some calving females, it is essential that it be afforded significant protection from both vessel strikes and entanglements. **We strongly urge NMFS to modify the entire Large South Island Restricted Area as a Seasonal Management Area to simultaneously reduce vessel strike risks**.

3. The Georges Basin Restricted Area

Alternative 3 analyzes a buoy line closure in the "Georges Basin Restricted Area" between May and August. Our organizations support closures that do not cause predictable relocation of lines to areas of high co-occurrence with right whales, inadvertently displacing risk. This particular offshore area in Georges Basin is important to right whales as plankton data demonstrates its importance as foraging habitat[29] and sightings data (albeit rare currently) as well as telemetry data[30] suggest that this may be a transit corridor for whales moving between the Gulf of St. Lawrence and the Gulf of Maine. *See* DEIS Vol. II at 3-62 (showing increased right whale density along the northern edge of Georges Bank from April through September). However, those benefits are only afforded if gear does not shift into areas of increased risk. Given the size and demographic of the fishing effort there, it is our view that these traps/vertical lines are unlikely to come out of the water between May and August and it is more likely than not that they will relocate into equally high risk areas.

For that reason, we have concerns that a full closure of the area proposed could increase risk by shifting effort south and west resulting in even higher densities along the corridor. Given the potential for the northern edge of Georges Bank to be a regular route between the Gulf of St. Lawrence and Gulf of Maine, **we recommend that NMFS only allow trap/pot fishing with one end line along the entire northern edge of Georges Bank from April – September, as an alternative to the Georges Basin Restricted Area proposed.** While it would not entirely remove risk, it would reduce risk to a larger spatial area by 50% without incurring additional costs to the industry. In addition, NMFS should send an enforcement boat to the area on a regular basis (at least once per week) and perform additional surveys (aerial and vessel) to better understand right whale abundance and behavior while using the area.

---

[28] Sean Horgan, Fish panel bans inshore lobstering during whale migration, Gloucester Times, Jan. 28, 2021 https://www.gloucestertimes.com/news/fish-panel-bans-inshore-lobstering-during-whale-migration/article_761e98de-6196-11eb-b9f6-c3c00dd2aecc.html; MA DMF, February 19, 2021, "New Protected Species Regulations Finalized for Fixed Gear Fisheries and Industry Outreach on Required Gear Modifications," https://content.govdelivery.com/accounts/MADMF/bulletins/2c2930d. This highlights why NMFS cannot rely on any risk reduction measures unless those measures are specifically incorporated into the ALWTRP—only then can NMFS assure such measures will in fact be legally required as part of the ALWTRP. NMFS cannot delegate its legal obligation to adopt measures to reduce M/SI to the states.

[29] DEIS Vol. I at 3-71, 72-74.

[30] Telemetry track of "Churchill" from 2001, available at http://www.gulfofmaine.org/times/fall2001/right_whales.html.

D. Weak Rope Will Not Reduce the Risk of Entanglement

1. “Weak Rope” and “Weak Insertions” are Unproven Conservation Measures

Our organizations do not support the weak rope or weak link insertions analyzed in the DEIS. The use of weak rope or weak insertions is unproven and cannot guarantee the projected risk reduction goals in the proposed rule.[31] Any assumptions about the efficacy of weak rope or weak contrivances for reducing serious injuries and mortalities are just that—assumptions—that are largely theoretical and untested in the field.

We have previously expressed concerns regarding the efficacy of using 1,700 lb breaking strength rope. At this time, it is neither commercially available nor proven to reduce serious injury and mortality to right whales. The data presented in Knowlton et al. (2016) were obtained prior to 2011, before right whales significantly shifted their habitat use.[32] In addition, the breaking strength does not appear to reduce risk of serious injury or mortality to right whales under two years of age. Indeed, the single paper on which the concept of weak rope as a mitigation measure was developed is based on the “suggest[ion]” that “**adult** right whales . . . can break free from [] weaker ropes and thereby avoid a life-threatening entanglement.” Younger right whales (calves and juveniles), as well as smaller whales of other species, have a much lower force output than adult right whales,[33] and are less likely to be able to break even lower-pound breaking strength rope.

NMFS’s application of the weak inserts is also problematic as they do not go the entire length of the rope. In the preferred alternative, weak insertions are only proposed down to 50 percent in the rope in nearshore areas and 35 percent in offshore areas. DEIS Vol. I at 1-15.

As NMFS acknowledges in the DEIS, lower-pound breaking strength ropes may reduce the severity of the entanglements, but they will not reduce the encounter rates and associated risk including serious injury or mortality and longer-term sublethal impacts depending on the complexity and specifics of an entanglement event. *Id.* For example, even so-called weak rope could wrap around a whale’s mouth and damage its baleen, thereby impeding its ability to feed, leading to weight loss and starvation. Even if that weight loss is not fatal in and of itself, in females it can contribute to delayed reproduction.[34] During the February 25, 2021 ALWTRT public hearing, a member of the Center for Coastal Studies disentanglement team and co-author of the single study on reduced breaking strength rope, expressed his concerns about lines breaking and making it more difficult for disentanglement teams to free entangled whales.[35]

---

[31] DEIS Vol. I at 3-68, Table 3.4.

[32] Knowlton, A. R., J. Robbins, S. Landry, H. A. McKenna, S. D. Kraus, and T. B. Werner. 2016. Effects of fishing rope strength on the severity of large whale entanglements. Conserv Biol 30:318-328.

[33] Amy Knowlton, Tim Werner and Scott Kraus, *Whale Release Ropes*, Presentation at the Consortium for Wildlife Bycatch Reduction, https://www.mmc.gov/wp-content/uploads/Knowlton2_Marine-Mammal-Commission-Knowlton2-VERSION-2.pdf at 7 (emphasis added).

[34] *See, e.g.*, Moore et al. 2021. “Assessing North Atlantic right whale health: threats, and development of tools critical for conservation of the species.” Dis Aquat Org Vol. 143: 205–226, 2021. https://doi.org/10.3354/dao03578.

[35] NMFS, Atlantic Large Whale Take Reduction Plan Proposed Modifications, Feb. 2021 Presentation, available at https://www.greateratlantic.fisheries.noaa.gov/public/nema/SFD/ALWTRTDEIS-Proposed%20RuleComment%20Opportunity.mp4.

On that note, NMFS inappropriately relies on disentanglement as a tool toward reducing M/SI of right whales and notes that, between 2010 and 2018, seven right whales would have been added to the M/SI list had they not been disentangled. DEIS Vol. I at 2-30; *see also id.* at 3-76. Without intervention, those whales alone would have exceeded PBR for the species. Implementing measures which may result in the loss of these whales by making it more difficult to disentangle them provides no benefit to the species or to the fishing industry who will be once again asked to modify gear at their expense because measures they were mandated to enact by the Agency did not work.

We have similar concerns with the proposed movement of the weak link/line requirement at the buoy. This appears to be an experiment that is being codified before it is tested. In responding to comments, we ask the agency to provide the scientific information that this proposed measure is based upon.

The agency's reliance on weak rope, contrivances or toppers to reduce risk, especially in offshore areas, is particularly unreasonable where (1) lobstermen use a large number of pots per trawl, and have expressed concerns about safety and lost gear; (2) the area is of particularly high risk for right whales due to the heavier line and increased number of traps used there; and (3) there is evidence that whales that become entangled near the bottom (where there will not be nearby weak insertion) have more complex entanglements and cannot break free as easily.[36]

2. Weak Rope Inhibits Species' Recovery

After 50 years of management, conservation and management measures to date have wholly failed to recover the species. A recently published paper summarizing the spiraling health of right whales, the increasing threats they face, and the tools that will be critical for their conservation.[37] The paper concludes that the use of weak rope as a management measure is inconsistent with the recovery of the species and that "to enable species recovery, reduction in mortalities have to be accompanied by substantial reduction of sub-lethal trauma as well," stating:

> The role of sub-lethal entanglement drag in reducing NARW health and fecundity should be a major consideration in comparing the efficacy of potential mitigation measures. Thus, while 1700 lb (~773 kg) breaking strength rope may reduce mortality and severe injury, it will continue to be a source of morbidity. Ultimately, removal of rope from the water column will better enable species recovery.[38]

---

[36] Howle, et al. 2019. Simulation of the entanglement of a North Atlantic right whale (*Eubalaena glacialis*) with fixed fishing gear. MARINE MAMMAL SCIENCE, 35(3): 760–778 (July 2019).

[37] Moore et al. 2021. "Assessing North Atlantic right whale health: threats, and development of tools critical for conservation of the species." Dis Aquat Org Vol. 143: 205–226, 2021. https://doi.org/10.3354/dao03578.

[38] *Id.*

3. NMFS's Risk Reduction Analysis Uses a Flawed Baseline

NMFS estimates that 26% percent of the vertical lines in the water will be converted to weak rope in the Preferred Alternative, and 73% will be converted to full weak rope in Alternative 3 accounting for approximately significant reductions in risk. DEIS Vol. I at 1-15; DEIS Vol. I at 3-68, Table 3.4. For this analysis, the agency unreasonably assumes that inserts placed at least every 40 feet. are equivalent to full weak rope. *Id.* at 1-14. The analysis which compares various proposed insert intervals to a line with weak inserts every 40 feet ("lower bound"), and also recognizes the depth of the lowest insert (upper bound),[39] is flawed. Weak inserts every 40 feet cannot be used as the baseline for determining the percentage of risk reduction that a "full weak rope," would provide because that risk reduction is unknown. Any calculation of the relative risk reduction of the lesser weak insertion methods proposed, should calculate risk reduction relative to no ropes in the water (i.e., zero risk), not a line with inserts every 40 feet.

E. Improved Gear Markings Are Necessary but Will Not Reduce Risk

In our view, none of the gear marking measures analyzed or proposed in the DEIS are sufficient. We strongly urge NMFS, again, to require gear markings that are specific to the fishery and region in which it is fished, and that can be seen from a plane or boat. Appropriate gear marking requirements should also include requirements for groundlines. In addition, as gear marking is implemented solely for the conservation benefit of right whales, it should be a requirement of the Plan rather than managed by state regulations.

Insufficient gear marking requirements for fixed-gear fisheries in the U.S. have demonstrably hindered targeted management measures to reduce risk to endangered right whales. Our organizations have commented several times over the last five years on this issue, yet NMFS has failed to implement new gear marking requirements. In most cases, NMFS cannot determine the origin (to fishery or country) of the gear documented on and/or removed from right whales to the detriment of whales and the fisheries implicated. DEIS Vol. I at 1-5; 2-40. A better understanding of gear origin, particularly since 2010, is necessary to define areas of high risk to the species and is long overdue. In addition, NMFS should work with gear specialists in both the U.S. and Canada to re-analyze gear documented on, or removed from, entangled large whales in the past.

We strongly urge NMFS to require gear marking that is specific both to a fishery and to the region in which it is fished, and that supports observation of marks from platforms such as boats and planes. It is apparent that the current requirement for gear marking is too broad, enabling at least some industry members to deny potential risk from their fishery, even when the gear removed from whales is consistent with that fished in that region.[40] For instance, NMFS's right whale incident data includes several cases of retrieved gear which was marked with a red tracer

---

[39] "The lower bound compares the proposed insert intervals relative to insert intervals every 40 ft and provides the percentage of rope within buoy lines that would be considered weak by that metric. The upper bound recognizes that the depth of the lowest insert is important; a whale hitting the line above the lowest weak insert could break away, preventing attachment to the bottom gear and an acute drowning event, and possibly before a serious entanglement injury can be incurred. That upper bound is the estimated percent of line above the lowest weak insert." *Id.*

[40] Letter from Maine Lobstermen's Association to NMFS, Apr. 30, 2019, https://mainelobstermen.org/wp-content/uploads/2019/08/MLA-TRT-near-consensus-withdrawal_2019.08.30-FINAL.pdf?x44315.

and was attributed to the "Northern inshore/nearshore trap" fishery but in only once case was it identified as lobster gear.[41] More specified gear marking requirements under the Plan would substantially reduce the equivocation of which fisheries do, in fact, pose demonstrable risk to the species.

There are also compelling cases in NMFS's own data set for which gear remains categorized as unknown but for which gear determination cannot rule out U.S. fisheries. For example, right whale 4146 was documented as entangled on April 23, 2017, entangled and images indicate that the entanglement appears recent and therefore likely to have occurred in U.S. waters. Similarly, right whale 4091 is listed on a NMFS incident report on May 12, 2018 as having "Line trailing from right mouthline, with at least one pectoral wrap, and trailing 50 ft. Buoy pinned close to flipper." As stated previously, this whale was sighted gear free in the Cape Cod Bay only six days earlier. It is most likely the whales became entangled in U.S. waters and the most likely source of line in U.S. waters is from U.S. fixed fishing gear. However, in neither case does NMFS provide any attribution of gear. We therefore suggest NMFS include a category in their assessment clarifying when U.S. fishing gear cannot be ruled out.

We continue to recommend significantly improved gear marking requirements on every 40 feet of line in all U.S. fisheries known to interact with right whales to better define the region and fishery beyond the broad regional mandates which currently exist. NMFS itself provided support for the increased frequency of gear marking in its gear marking resources, stating: "[a]lternatively, if rope were marked every 40 feet we could expect [to] get the information provided by the mark 90% of the time, because at least 40 feet of rope is likely to be recovered."[42] In light of the frequency with which right whales encounter the bottom while foraging,[43] we recommend unique markings to identify sinking groundline as part of the vertical line system versus those lines used to connect traps to better inform when and where whales encounter gear.

In addition to improved gear marking in the Northeastern American trap/pot fisheries, NMFS should immediately require enhanced gear marking requirements for all permit holders in all Category I and II fisheries likely to entangle marine mammals including, but not limited to: the Northeast sink gillnet, Northeast drift gillnet, Northeast anchored float gillnet, Southeast Atlantic gillnet, Mid-Atlantic gillnet, Southeastern Atlantic U.S. shark gillnet, Atlantic mixed species trap/pot, Atlantic blue crab trap/pot, and the Mid-Atlantic American lobster trap/pot fisheries.

---

[41] NMFS, 2000-2018 Right Whale Incident Data, Apr. 19, 2019, https://www.greateratlantic.fisheries.noaa.gov/protected/whaletrp/trt/meetings/April%202019/2000-2018_right_whale_incident_data_3_19_19v.xlsx.

[42] NMFS, Past Gear Marking Efforts, updated March 2018, https://www.greateratlantic.fisheries.noaa.gov/protected/whaletrp/trt/meetings/April%202018/past_alwtrt_gear_marking.pdf.

[43] Hamilton PK, Kraus SD (2019) Frequent encounters with the seafloor increase right whales' risk of entanglement in fishing groundlines. Endang Species Res 39:235-246. https://doi.org/10.3354/esr00963.

F. 100% Harvester Reporting, Vessel Tracking Systems, and Enhanced Enforcement Must be Prioritized

As the DEIS acknowledges, Maine still does not have 100% harvester reporting (DEIS Vol. II at 3-102), nor has NMFS finalized a rule requiring it. We urge NMFS to initiate and develop an action that would immediately require: (1) 100% harvester reporting in the entire fishery (2) all federal permit holders to obtain and use a GARFO-approved vessel tracking system; and (2) all federal permit holders to mark all traps electronically in order to provide detailed information on gear type and set location, enhance the enforcement of all regulatory measures in fixed gear fisheries, and help ascertain the ownership of lost or damaged gear.

G. Ropeless Fishing is the Only Way to Adequately Reduce Risk in the Long Term

Our organizations support and appreciate the modifications—in the Preferred Alternative and Alternative 3—that change the existing seasonal restricted areas from areas closed to harvesting lobster and crab to areas closed to persistent buoy lines.[44] 85 Fed. Reg. at 86,887; DEIS Vol. I at 1-7. We also support the measures in both Alternative 2 and 3 that would allow fishing without buoy lines in any newly established restricted areas. *Id.* As a recent paper noted, ropeless fishing is the only way to adequately reduce risk to right whales, while allowing fishing in the long term.[45] However, any authorization to fish in such a closure, such as an exempted fishing permit or letter of authorization, should include conditions to protect right whales such as area restrictions, low vessel speed, observer monitoring, and reporting requirements. *See* DEIS Vol. I at 1-7 ("would" include in Alternative 3 and "likely" in Alternative 2).

III. THE DEIS FAILS TO COMPLY WITH NEPA

NEPA, 42 U.S.C. § 4321 *et seq.*, is the fundamental tool for ensuring that federal agencies properly vet the impacts of major federal actions on wildlife, natural resources, and communities. It requires federal agencies to consider reasonable alternatives and identify the most environmentally preferable one.

A central purpose of NEPA is to assure that federal decision-makers consider the environmental consequences of their actions before a decision to act is made and to provide for "[a]ccurate scientific analysis, expert agency comments, and public scrutiny" of agency decisions. 42 U.S.C. § 4332(C); *Marsh v. Or. Natural Res. Council*, 490 U.S. 360, 371 (1989) (NEPA ensures that "the agency will not act on incomplete information, only to regret its decision after it is too late to correct"). Under NEPA, federal agencies are required to take a "hard look" at environmental consequences in order to integrate environmental impacts into the decision making process. *Kleppe v. Sierra Club*, 427 U.S. 390, 410 n.21 (1976).

Because the proposed rule to amend the Plan is a major federal action significantly affecting the

---

[44] As the relative risk of sinking groundline is still uncertain, it is our view that waters within the Cape Cod Bay where the highest known concentration of right whales seasonally occurs, should remain closed to all fixed gear fishing until additional data about the efficacy of ropeless gear becomes available.

[45] Moore et al. 2021. "Assessing North Atlantic right whale health: threats, and development of tools critical for conservation of the species." Dis Aquat Org Vol. 143: 205–226, 2021. https://doi.org/10.3354/dao03578.

human environment, it is subject to NEPA's "detailed statement" requirement. NMFS's EIS must therefore evaluate: (i) the environmental impact of the proposed action, including the cumulative impacts; (ii) any adverse environmental effects which cannot be avoided should the proposal be implemented; (iii) alternatives to the proposed action; (iv) the relationship between short-term uses of man's environment and the maintenance and enhancement of long-term productivity; and (v) any irreversible and irretrievable commitments of resources which would be involved in the proposed action should it be implemented. 42 U.S.C. § 4332(2)(C).

NMFS cannot avoid its obligation to conduct a comprehensive review of the direct, indirect, and cumulative impacts of the proposed rule by relying on the amendments to NEPA's implementing regulations recently issued by the Council of Environmental Quality ("CEQ"). NMFS began its NEPA process on the proposed rule well before the regulatory amendments went into effect and thus NMFS should apply the old regulations. *Compare* 84 Fed. Reg. 37822 (Aug. 2, 2019) (NMFS's notice of intent to prepare an environmental impact statement on proposed rule to amend the ALWTRP) *with* 85 Fed. Reg. 43304 (July 16, 2020) (final rule amending CEQ regulations, with an effective date of September 14, 2020). Moreover, the new regulations are unlawful and, in any event, cannot trump NMFS's statutory obligations to fully consider the direct, indirect, and cumulative effects of its actions.[46]

A. The DEIS Fails to Properly Define the Purpose and Need for Action

NMFS fails to properly define the purpose and need. In preparing the DEIS, NMFS must define its purpose and need in acting. 40 C.F.R. §§ 1502.13–1502.14 (2019).This is part of the "responsibility for defining at the outset the objectives of an action" to be taken by the agency. *Citizens Against Burlington, Inc. v. Busey*, 938 F.2d 190, 196 (D.C. Cir. 1991). This purpose and need inquiry is crucial for a sufficient environmental analysis because "[t]he stated goal of a project necessarily dictates the range of 'reasonable' alternatives." *Carmel-by- the-Sea v. U.S. Dep't of Transp.,* 123 F.3d 1142, 1155 (9th Cir. 1997). Thus, "an agency cannot define its objectives in unreasonably narrow terms" without violating NEPA. *Id.*

In crafting the purpose and need statement, the agency must incorporate the parameters set by Congress in relevant statutes. *Busey*, 938 F.2d at 196. Here, that means considering the overall goal of the MMPA to protect and recover imperiled marine mammals, 16 U.S.C. § 1361, the goal of section 118 to drive to M/SI of marine mammals in commercial fishing gear to below ZMRG, *id.* § 1387(a)(1), and Congress's directive that "[t]he interest in maintaining healthy populations of marine mammals comes first" under the statute. *Kokechik Fishermen's Ass'n v. Sec'y of Comm.*, 839 F.2d 795, 800, 802 (D.C. Cir. 1988); *see also Animal Welfare Inst. v. Kreps*, 561 F.2d 1002, 1007 (D.C. Cir. 1977) ("the MMPA is . . . motivated by considerations of humaneness toward animals, who are uniquely incapable of defending their own interests").

---

[46] *See* 42 U.S.C. § 4332; *Kleppe*, 427 U.S. at 410 (citing 42 U.S.C. § 4332(2)(C)). There are at least five lawsuits challenging the new regulations. *See* Complaint, *Wild Virginia et al. v. Council on Environmental Quality et al.*, No. 3:20-cv-00045 (W.D. Va. July 29, 2020), ECF No. 1; Complaint, *California et al. v. Council on Environmental Quality et al.*, No. 3:20-cv-06057 (N.D. Cal. Aug. 28, 2020), ECF No. 1; Complaint, *Alaska Community Action on Toxics et al. v. Council on Environmental Quality*, No. 3:20-cv-05199 (N.D. Cal. Jul. 29, 2020), ECF No. 1; Complaint, I*owa Citizens for Community Improvement et al. v. Council on Environmental Quality et al.*, No. 1:20-cv-02715 (D.D.C. Sept. 23, 2020), ECF No. 1; Complaint, E*nvironmental Justice Health Alliance et al. v. Council on Environmental Quality et al.*, No. 1:20-cv-06143 (S.D.N.Y. Aug. 8, 2020), ECF No. 1.

NMFS must also consider the goals of the ESA, which are to protect and recover threatened and endangered species and their habitats, 16 U.S.C. § 1531, and "[t]he plain intent of Congress in enacting this statute . . . to halt and reverse the trend toward species extinction, whatever the cost." *Tenn. Valley Auth. v. Hill*, 437 U.S. 153, 184 (1978); *see also id.* at 185 (agencies must "afford first priority to the declared national polity of saving endangered species").

While NMFS correctly indicates in its purpose and need statement that the agency must take action to further reduce the risk of right whale M/SI in commercial fishing gear to comply with the MMPA, its purpose and need statement is otherwise both too narrow. In particular, the purpose and need statement is too narrow because it is based on the need to reduce M/SI by 60% and ignores the urgent need to reduce the sublethal impacts of entanglement. *See* DEIS Vol. I at 2-41.

As explained above, NMFS's 60% risk reduction target is insufficient. *Supra* Section II.A. Indeed, NMFS's purpose and need is based on outdated information that fails to consider the best available right whale science, including a recent analysis documenting the substantial cryptic mortality right whales suffer, and that entanglements are responsible for the majority of such deaths. *See id*. New information reveals that NMFS should reduce risk by at least 90%, *see id*., meaning the agency must adopt significantly more mitigation measures than what is currently on the table. By narrowly defining the purpose and need statement as measures that achieve a 60% reduction in the risk of right whale M/SI, NMFS arbitrarily makes the preferred alternative the only choice that will meet this goal.

And while the focus of section 118 of the MMPA may be on reducing M/SI from commercial fisheries, NMFS's obligations under the ESA are much broader than that. NMFS must ensure that its actions in authorizing and managing the fisheries neither jeopardize the right whale's continued existence nor adversely modify its critical habitat. *See* 16 U.S.C. § 1356(a)(2). This requires considering not only the deaths and serious injuries caused by entanglement in fishing gear, but all the other impacts such entanglements cause, including impeding the whale's ability to reproduce, or increasing its vulnerability to death or injury from other stressors such as vessel strikes.

It is well established that right whales are negatively impacted by entanglement, not only through a reduction in the numbers of individuals through serious injuries and mortalities, but also through increasing a whale's stress hormone levels, leading to infections; making them more vulnerable to other sources of mortality like vessel strikes; and impeding their ability to feed.[47] For example, studies have concluded that "[p]rotracted entanglement in fishing gear often leads to emaciation through reduced mobility and foraging ability, and energy budget depletion from

---

[47] *See, e.g.*, Julie M. van der Hoop, Douglas P. Nowacek, Michael J. Moore, M. S. Triantafyllou. 2017. Swimming kinematics and efficiency of entangled North Atlantic right whales. Endang. Species Res. Vol. 32: 1–17, 2017, doi: 10.3354/esr00781; Julie van der Hoop, Peter Corkeron and Michael Moore. 2016. Entanglement is a costly life history stage in large whales. Ecology and Evolution, 7: 92–106, doi:10.1002/ece3.2615; Cassoff RM, Moore KM, McLellan WA, Barco SG, Rotstein DS, Moore MJ. 2011. Lethal entanglement in baleen whales. Dis. Aquat. Org. 96: 175−185; Moore, M. and van der Hoop, J. 2012. The Painful Side of Trap and Fixed Net Fisheries: Chronic Entanglement of Large Whales. Journal of Marine Biology. Volume 2012, Article ID 230653, doi.org/10.1155/2012/230653.

the added drag of towing gear for months or years."[48] Additionally, the "chronic effects of entanglement in free-swimming individuals include systemic infection and debilitation from extensive tissue damage . . . More common in protracted cases is severe emaciation due to the inability to cope with a negative energy budget, driven by the combined effects of reduced mobility and foraging ability, and increased energetic demand imposed by towing accessory gear for months to years."[49]

The best available scientific data also indicates that even a single line increases drag on a whale; extra energy demand may affect body condition to the point that individual females' reproductive capacities could be impaired. Indeed, scientific studies have concluded that poor body condition that may result from chronic entanglement in right whales is a serious limitation to reproductive success.[50] Studies have also found that "[r]eproductive females seen alive and carrying gear or with severe wounds from entanglement had a significantly lower chance of calving again. Females that experienced moderate or severe entanglement wounds between calvings had a significantly longer calving interval than females that experienced minor or no entanglement wounds;"[51] that "females that have suffered a severe entanglement are significantly less likely to calve again;"[52] and that "[h]uman impacts are reducing the reproductive success of this population."[53]

Other studies have concluded that entanglements contribute to poor body condition in juvenile right whales, adults, and lactating females, "which could be suppressing their growth, survival, age of sexual maturation and calving rates."[54] Moreover, the poor condition of lactating females, may cause a reduction in calf growth rates, "potentially lead[ing] to a reduction in calf survival or an increase in female calving intervals."[55] As such, "the poor body condition of individuals within the NARW population is of major concern for its future viability."[56] Thus, entanglement is likely one of the major determinants of reproductive failure in right whales, and probably all large whales. NMFS cannot define its purpose and need to focus solely on serious injury and mortality.

---

[48] Julie van der Hoop, et al. 2014. Behavioral impacts of disentanglement of a right whale under sedation and the energetic cost of entanglement. Marine Mammal Science. Vol. 30:1, pp. 282–307.

[49] *Id.*

[50] Miller, C. , D. Reeb, P. Best, A. Knowlton, M.Brown and M.Moore. 2011. Blubber thickness in right whales (Eubalaena glacialis) and (Eubalaena australis) related with reproduction, life history status and prey abundance. Marine Ecology Progress Series. Vol. 438, pp. 267–283.

[51] Knowlton, A., P. Hamilton, M. Marx, H. Pettis, and S. Kraus. 2012. Monitoring North Atlantic right whale (Eubalaena glacialis) entanglement rates: a 30 yr retrospective. Marine Ecology Progress series. Vol. 466, pp 293–302; Knowlton, A., P. Hamilton, and H. Pettis. 2012. Status of Reproductive Females in the North Atlantic Right Whale Population and Impacts of Human Activities on their Reproductive Success. Report Submitted to Woods Hole Oceanographic Institution.

[52] Julie van der Hoop, et al. 2016.

[53] *Id.*

[54] Christiansen, F., Dawson, S.M., Durban, J.W., Fearnbach, H., Miller, C.A., Bejder, L., Uhart, M., Sironi, M., Corkeron, P., Rayment, W., Leunissen, E., Haria, E., Ward, R., Warick, H.A., Kerr, I., Lynn, M.S., Pettis, H.M., & Moore, M.J. 2020. Population comparison of right whale body condition reveals poor state of the North Atlantic right whale. Marine Ecology Progress Series. Vol. 640, pp. 1–16.

[55] *Id.*

[56] *Id.*

B. The DEIS Fails to Properly Examine the Direct and Indirect Impacts to Right Whales

The DEIS fails to take a hard look at the direct and indirect impacts on right whales. The relevant regulations define "direct" effects as those that are "caused by the action and occur at the same time and place;" and "indirect" effects as those that are "caused by the action and are later in time or farther removed in distance, but are still reasonably foreseeable." 40 C.F.R. § 1508.8 (2019).

NMFS fails to properly evaluate the direct impacts of the proposed rule on right whales by failing to base its analysis on accurate scientific information, improperly narrowing the scope of the action under review, and assuming the efficacy of risk reduction measures without any discussion of how these measures will not sufficiently reduce risk. As an initial matter, because the DEIS fails to properly define the proposed rule as part of its authorization and management of operation of the fisheries in state and federal waters under the MMPA, the DEIS improperly characterizes the nature and extent of the direct effects as beneficial, rendering the agency's analysis too narrow. Moreover, the analysis is based on outdated information that does not constitute the best available science on right whales, violating the requirement that "[t]he information must be of high quality" because [a]ccurate scientific analysis, expert agency comments, and public scrutiny are essential to implementing NEPA." 40 C.F.R. § 1500.1(b) (2019).

For example, the proposed rule and DEIS explain that NMFS established the 60% risk reduction target based on a PBR of 0.9. 85 Fed. Reg. at 86,880; DEIS Vol. I at 1-2. However, as NMFS is well aware, the right whale PBR is now officially 0.8 as per the final 2019 Stock Assessment Report and actually 0.7 as per the most recent data on the population estimate.[57] The DEIS further explains that the assumptions underlying this risk reduction target, were based on an estimate that *40%* of mortalities between 2010 and 2018 were unobserved. DEIS Vol. I at 2-39. But a newly-published paper finds that *71%* of mortalities between 2010 to 2017 were unobserved.[58]

In addition, NMFS simply assumes that the proposed rule will adequately mitigate impacts to right whales to achieve the agency's stated risk reduction target, without addressing the likelihood that it will not do so. As the Supreme Court has instructed, "omission of a reasonably complete discussion of possible mitigation measures would undermine the 'action-forcing' function of NEPA. Without such a discussion, neither the agency nor other interested groups and individuals can properly evaluate the severity of the adverse effects." *Robertson*, 490 U.S. at 353. NEPA requires that FERC discuss mitigation measures with "sufficient detail to ensure that environmental consequences have been fairly evaluated." *Id*. at 352. "An essential component of a reasonably complete mitigation discussion is an assessment of whether the proposed mitigation measures can be effective. . . A mitigation discussion without at least *some* evaluation of effectiveness is useless in making that determination." *South Fork Band Council v. U.S. Dep't of the Interior*, 588 F.3d 718, 727 (9th Cir. 2009) (citations omitted).

---

[57] NMFS, Stock Assessment Report: North Atlantic Right Whale, Apr. 2020 at 22; Colleen Coogan, NMFS, Presentation to the Atlantic Large Whale Take Reduction Team, Jan. 2021.

[58] Pace et al. 2021.

Moreover, many of the measures on which NMFS relies in its proposed rule are unproven and therefore not guaranteed to hit the projected risk reduction goal. As explained above, the proposed rule relies extensively on the use of weak rope or weak insertions to reduce risk of right whale M/SI. *See supra* Section II.D. But the efficacy of this rope at reducing M/SI is untested, assumes right whales are entangled in particular ways, and will not address the sublethal impacts impeding the recovery of the species. *Id.* Indeed, numerous scientists recently determined that "while 1700 lb (~773 kg) weak rope breaking strength rope may reduce mortality and sever injury, *it will continue to be a source of morbidity*."[59] As such, "removal of rope from the water column will better enable species recovery."[60]

Indeed, numerous studies have demonstrated that NMFS's long history of implementing a series of complex, inefficient gear modifications via the ALWTRP have been ineffective at reducing M/SI to the levels the agency assumed in those rules and associated documents. For example, a 2007 scientific review panel stated that:

> In general, [NMFS] should set higher standards of protection and place greater reliance on the ability of industry to adapt to those standards, rather than continuing to depend on a complex, shifting, inefficient, and ineffective network of regulatory measures to protect the whales. The guiding principle should be to separate high-risk human activities from right whales, in both space and time, to the maximum extent feasible.[61]

Studies issued since then only reinforce this point. For example, a 2014 study by agency scientists concluded that incremental gear modifications under the ALWTRP from 1999 to 2009 were "generally ineffective in abating whale deaths from entanglements in fishing gear."[62] In October 2018, NMFS's Technical Memorandum observed that, starting in 1997 when the original Plan was put in place, including the 2009 sinking groundline and 2014 vertical line rules, data from 2000 through 2017 showed that "absolute entanglements appear to be on the rise."[63] The same document noted the "unintended consequences" of the 2015 vertical line rule that required trawling up, potentially contributing to the increased severity of entanglements.[64]

NMFS's NEPA evaluation therefore cannot simply assume its proposed rule will achieve its goals and must disclose potential shortcomings, particularly where available evidence indicates the proposed rule will not be sufficiently protective.

NMFS also fails to take a hard look at the indirect impacts of the proposed rule. Because the

---

[59] Moore et al. 2021 (emphasis added).

[60] *Id.*

[61] Reeves, R.R., A.J. Read, L. Lowry, S.K. Katona, and D.J. Boness. 2007. Report of the North Atlantic right whale program review, 13-17 March 2006, Woods Hole, Massachusetts. Marine Mammal Commission, Bethesda, MD.

[62] Pace, R. M. III et al. 2014.

[63] Hayes S.A., Gardner S., Garrison L., Henry A., Leandro L. 2018. North Atlantic right whales - Evaluating their recovery challenges in 2018. NOAA Tech Memo NMFS NE. 247; 24 p. at 8.

[64] *Id.*; *see also* Kenney, R. 2018. What if there were no fishing? North Atlantic right whale population trajectories without entanglement mortality. Endangered Spec. Res. 37:233 ("[d[espite legal requirements to reduce fishery-related mortality, little or no real progress has been made over the last 2 decades").

proposed rule is part of NMFS's authorization of the fisheries under the MMPA, NMFS must consider all the impacts of the fisheries on right whales as part of its analysis. Yet NMFS failed to do so.

Specifically, NMFS failed to take a hard look at the impacts that fishing activity can have on prey availability for right whales. Right whales select foraging areas based on a relatively high threshold of copepod density. *See, e.g.*, DEIS Vol. I at 4-86. Notably, foraging areas with suitable prey density are limited relative to the overall distribution of North Atlantic right whales,[65] meaning that unrestricted and undisturbed access to suitable areas, when they exist, is extremely important for the species to maintain its energy budget. Scientific information on right whale functional ecology also shows that the species employs a "high-drag" foraging strategy that enables them to selectively target high-density prey patches, but is energetically expensive.[66]

Thus, if access to prey is limited in any way, the ability of the whale to offset its energy expenditure during foraging is jeopardized. NMFS itself has elsewhere recognized that these prey disturbances should and could be minimized because it relies on the Massachusetts Restricted Area to "further minimize" such disturbances stating:

> Localized disturbance to dense copepod aggregations by these gear types is further minimized by MMPA gillnet and trap/pot closure areas that exist in temporal and spatial areas where these dense concentrations are expected to trigger foraging behavior (e.g., Massachusetts Bay Restricted Area). 50 CFR 229.23).[67]

While NMFS's DEIS acknowledges that reduced prey availability can negatively affect right whale health, *e.g.*, DEIS Vol. I at 1-4, 4-88, the agency failed to consider the role the proposed action has in exacerbating those impacts.

Relatedly, NMFS also failed to consider the impacts of fishing vessel operations on right whales. This is improper considering that NMFS elsewhere acknowledged that noise pollution from fishing vessels can negatively impact right whales and increase the risk of ship strikes. *See e.g.*, Draft BiOp at 146. Indeed, there have been at least four documented right whale deaths and serious injuries due to vessel strikes in U.S. waters since January 1, 2020, all due to confirmed or suspected recreational fishing vessels less than 65 feet.[68]

C. The DEIS Does Not Examine a Reasonable Range of Alternatives or Adequately Describe Differences Between Alternatives

The DEIS fails to analyze a reasonable range of alternatives, or adequately analyze the differences between alternatives. NEPA requires a "detailed statement" of "alternatives to the

---

[65] *Id.*

[66] Van der Hoop, J., Nousek-McGregor, A.E., Nowacek, D.P., Parks, S.E., Tyack, P., and Madsen, P, "Foraging rates of ram-filtering North Atlantic right whales," *Functional Ecology*, published online May 11, 2019.

[67] Draft BiOp at 87.

[68] Aidan Cox, North Atlantic right whale found dead on Florida beach, CBC News, Feb. 17, 2021, https://www.cbc.ca/news/canada/new-brunswick/right-whale-death-1.5917363.

proposed action." 42 U.S.C. § 4332(2)(c). In considering alternatives, an agency "should present the environmental impacts of the proposal and the alternatives in comparative form, thus sharply defining the issues and providing a clear basis for choice among options by the decisionmaker and the public." 40 C.F.R. § 1502.14 (2019).

The requirement to consider reasonable alternatives "lies at the heart of any NEPA analysis." *California ex rel. Lockyer v. U.S. Dept. of Agric*., 459 F. Supp. 2d 874, 905 (N.D. Cal. 2006). The purpose of this section is "to insist that no major federal project should be undertaken without intense consideration of other more ecologically sound courses of action, including shelving the entire project, or of accomplishing the same result by entirely different means." *Envt'l Defense Fund v. Army Corps of Engr's*, 492 F.2d 1123, 1135 (5th Cir. 1974).

While an agency is not obliged to consider every alternative to every aspect of a proposed action, the agency must "consider such alternatives to the proposed action as may partially or completely meet the proposal's goal." *Nat. Resources Defense Council v. Callaway*, 524 F 2d. 79, 93 (2d Cir. 1975). In considering what constitutes a reasonable alternative, "an agency should always consider the views of Congress, expressed, to the extent that the agency can determine them, in the agency's statutory authorization to act, as well as in other congressional directives." *Citizens Against Burlington v. Busey*, 938 F.2d 190, 196 (D.C. Cir. 1991). The existence of a viable but unexamined alternative renders an EIS inadequate. *Citizens for a Better Henderson* v. *Hodel,* 768 F.2d 1051, 1057 (9th Cir. 1985).

Despite these obligations, NMFS considered only three primary alternatives: (1) Alternative 1 (not issuing the proposed rule); (2) Alternative 2 (issuing the proposed rule); and (3) Alternative 3 (similar to Alternative 2 but with some additional measures). NMFS neglected to consider a range of reasonable alternatives because none of the action alternatives meet NMFS's protective mandates under NEPA and the MMPA (or the ESA) or provide a meaningful range of adequate mitigation measures. *See supra* Section II.

Indeed, there are relatively few differences among the action alternatives. Both alternatives would require a combination of trawling up, seasonal buoy line restricted areas, and weak lines or weak insertions. *See* DEIS Vol. I at 3-52–3-53. NMFS estimates Alternative 2 would reduce M/SI risk by 64.3% while it estimates that Alternative 3 would reduce M/SI risk by 69.6% to 72.6%. *Id.* at 3-68, 3-69. The lack of any meaningful difference between the alternatives considered in detail violates the requirements of NEPA. *See Muckleshoot Indian Tribe v. U.S. Forest Serv*., 177 F.3d 800, 813 (9th Cir. 1999) (federal agency violated NEPA where two action alternatives considered were "virtually identical").

For example, NMFS failed to examine a truly protective alternative: no fishing. Because NMFS's No Action alternative reflects continued fishing under the current ALWTRP, NMFS should have considered an additional alternative that analyzed no commercial fishing, and thus no risk to from entanglements in U.S. fishing gear. This would have provided an important basis for the public and the agency to compare the tradeoffs between continued fishing and continued risk of entanglements, serious injuries, and mortalities in fishing gear, versus an alternative under which there would be zero risk of entanglement in commercial fishing gear in U.S. waters. No fishing protects the critically endangered right whale NMFS is mandated to protect, conserve, and recovery; while continued fishing with unattended vertical line continues to threaten the survival and recovery of this critically endangered species.[69]

At the very least, NMFS must consider an alternative that would reduce serious injury and mortality of right whales in Northeast trap fisheries by 90%. NMFS's failure to do so is especially glaring where the agency itself identified the need to reduce U.S. entanglement-related M/SI by upwards of 80% at a time when PBR for right whales was 0.9, DEIS Vol. I at 3-47, and the PBR for right whales is now 0.7.[70] *See supra* Section II.A. Additionally, NMFS should have evaluated alternatives that considered adopting the closures proposed as part of the Preferred Alternative and Alternative 3 as year-round restricted areas, particularly considering the best available science demonstrates that right whales use the waters in Southern New England in all months of the year. *See supra* Section II.C.2.

NMFS should also consider an alternative that considers a line cap on all gear and include an alternative that address risk from gillnet gear. The agency chose not to focus on gillnets in its current rulemaking because lobster gear makes up a significantly greater portion of the line in right whale habitat. *See, e.g.*, DEIS Vol. I at 2-34, 2-40. However, while gillnets make up a small amount of the line in right whale habitat, they pose a disproportionate risk of entangling a right whale.[71] The presence of one or more nets (up to 300 feet long each) strung together and held up by floats, presents a much bigger target area for whales foraging throughout the water column, as compared to vertical trap/pot buoy lines without net in between. The agency must consider an alternative that evaluates the risk reduction benefits of restricting gillnet fishing.

While not necessarily in the spirit of TRT negotiations, NMFS's failure to examine a no-fishing alternative, or an alternative that would further reduce risk to right whales (to 80% or more), as part of its NEPA analysis is especially arbitrary considering that the status of the species has become particularly dire in the years the much-needed amendments to the ALWTRP have languished. *See Nat. Res. Def. Council v. U.S. Forest Serv.*, 421 F.3d 797, 813–14 (9th Cir. 2005) (NEPA obliges an agency to revisit its alternatives analysis whenever there are "changed circumstances [that] affect the factors relevant to the development and evaluation of alternatives," and "account for such change in the alternatives it considers.").

NMFS's failure to address a reasonable range of alternatives is due, at least in part, to its unfounded rejection of alternatives proposed during scoping or elsewhere. In particular, NMFS rejected several proposals that would have required larger closures than what NMFS has proposed—such as the closure of all of Statistical Area 529, the seasonal closure of LMA3 above

---

[69] That the agency purports to have addressed these impacts in an appendix to its draft biological opinion on operation of the federal fisheries is irrelevant as the agency's obligations under NEPA and the ESA are distinct in several important respects. *See, e.g.*, *Fund for Animals v. Hall,* 448 F. Supp. 2d 127, 136 (D.D.C. 2006) (describing differences). Moreover, "an agency may not circumvent its obligation to provide a clear assessment of environmental impacts simply by placing [vital] analysis in an appendix." *Or. Envt'l Council v. Kunzman*, 817 F.2d 484, 494 (9th Cir. 1987).

[70] *See, e.g.*, Colleen Coogan Presentation to the Atlantic Large Whale Take Reduction Team, Jan. 2021.

[71] "Per the agency's draft North Atlantic Right Whale Conservation Framework for Federal Fisheries in the Greater Atlantic Region, the agency is not even planning on having the ALWTRT evaluate the risk from gillnets and provide recommendations until 2023 and the agency anticipates acting on recommendations from the ALWTRP in 2025." NARWConservationFrameworkGARFO.pdf.

40.3 degrees, or the closure of all waters from January through April—because these measures were "too large" and "unpopular with stakeholders." DEIS Vol. I at 3-79. NEPA does not contain a "popularity" exemption to the requirement to consider a reasonable range of alternatives—indeed, neither do the ESA or MMPA contain a "popularity" exemption to their legal requirements.

NMFS's rejection of these alternatives on this basis is particularly concerning in light of the agency's recognition that the proposed rule will not meet its legal obligation under the MMPA to reduce M/SI to below PBR (not to mention ZMRG), *see supra* Section I; and its acknowledgement over two decades ago, that reducing entanglement risk for right whales would be especially difficult and that "extensive closures of large areas of the ocean to lobster and gillnet fishermen . . . would guarantee reduction of entanglements causing serious injury and mortalities." 62 Fed. Reg. 39,157, 39,159 (July 22, 1997); *cf.*, *Citizens Against Burlington*, 938 F.2d at 196.

In addition to failing to examine a reasonable range of alternatives, NMFS also failed to adequately compare the differences between the alternatives it did consider. For example, NMFS states that the no action alternative would have "high[ly] negative" consequences on right whales because "serious injury and mortality would continue to occur and impact population health," the agency also states that Alternative 2—the preferred alternative— would have a "positive" effect on right whales because it "would reduce right whale co-occurrence by 69%." *See, e.g.*, DEIS Vol. I at 8-276. Similarly, it states that Alternative 3—the non-preferred alternative— would have a "highly positive" effect on right whales by "reduc[ing] right whale co-occurrence by 83–88%. *Id.* These assumptions are unfounded for the reasons described above. *See supra* Section II. But even if true, that would not save the agency's analysis because NMFS failed to acknowledge that even under these alternatives, right whale serious injury and mortality would continue to occur and at unsustainable levels. *See*, *e.g.*, *id.*

D. The DEIS Fails to Properly Examine Cumulative Impacts

To ensure that the full effect of its decision is analyzed, NEPA requires NMFS to examine the potential cumulative impacts. *See* 42 U.S.C. § 4332(2)(C); 40 C.F.R. § 1508.9 (2019); *Te-Moak Tribe of W. Shoshone of Nev.* v. *U.S. Dep't of the Interior*, 608 F.3d 592,602-03 (9th Cir. 2010) (citation omitted). A "cumulative impact" is "the impact on the environment which results from the incremental impact of the action when added to other past, present, and reasonably foreseeable future actions regardless of what agency (Federal or non-Federal) or person undertakes such other actions. Cumulative impacts can result from individually minor but collectively significant actions taking place over a period of time." 40 C.F.R. § 1508.7 (2019). "[I]n considering cumulative impact, an agency must provide some quantified or detailed information; . . . general statements about possible effects and some risk do not constitute a hard look absent a justification regarding why more definitive information could not be provided." *Ocean Advocates v. U.S. Army Corps of Eng'rs*, 361 F.3d 1108,1128 (9th Cir. 2004) (citation omitted); *see also Te-Moak Tribe of W. Shoshone v. U.S. Dep't of the Interior*, 608 F.3d 592, 603-06 (9th Cir. 2010) (rejecting the EA's cumulative impact analysis because it failed to analyze impacts in light of other projects that would impact the same resources).

NMFS failed to comply with these requirements. Its "analysis" of cumulative impacts amounts to nothing more than general statements about activities that impact large whales and other species. As one example, NMFS states that noise can have "low negative to negative" impacts on large whales, DEIS Vol. I at 8-254, 8-259, NMFS makes no attempt to quantify take from noise pollution or otherwise take a hard look at their detrimental impacts. For example, NMFS fails to even acknowledge its rule issued under the MMPA that allows the Navy to harass right whales hundreds of times each year over the next seven years incidental to testing and training activities conducted in the Atlantic Fleet Training and Testing Study Area. *See* 84 Fed. Reg. 70,712, 70,763 (authorizing 471 instances of Level B harassment of right whales from December 2019 through November 2025). Nor does NMFS attempt to quantify or take a hard look at the impacts of noise from vessel traffic.

Noise from the Navy's activities, the maritime industry, and the numerous offshore wind projects in Southern New England waters[72] will certainly "impact" right whales, and likely significantly so. For example, scientific research reveals that chronic stress in North Atlantic right whales is associated with exposure to low frequency noise from ship traffic.[73] Specifically, "the adverse consequences of chronic stress often include long term reductions in fertility and decreases in reproductive behavior; increased rates of miscarriages; increased vulnerability to diseases and parasites; muscle wasting; disruptions in carbohydrate metabolism; circulatory diseases; and permanent cognitive impairment."[74] As such, "over the long term, chronic stress itself can reduce reproduction, negatively affect health, and even kill outright."[75] In addition, right whales will experience temporary threshold shifts, behavioral response (including foraging displacement), and stress throughout the Atlantic from Navy sonar and other transducers,[76] as well as offshore wind projects. All of the existing and increasing ocean noise impacts important communications, including those between mothers and calves.[77]

In fact, NMFS lumps its analysis of the cumulative impacts on right whales together with other whales by only generally describing impacts on "large whales." *See, e.g.*, DEIS Vol. I at 8-250–8-251, 8-259. But this fails to constitute the hard look required by law and obfuscates the

---

[72] BOEM, Atlantic OCS Renewable Energy – Massachusetts to South Carolina, Mar. 2020, https://www.boem.gov/sites/default/files/images/Map%20of%20Atlantic%20OCS%20renewable%20energy%20areas.jpg.

[73] Rolland, R, et al. 2012. Evidence that ship noise increases stress in right whales. Proc. R. Soc. B. 279: 2363–2368.

[74] Rolland, R.M., K.E. Hunt, G.J. Doucette, L.G. Rickard, and S.K. Wasser. 2007. The inner whale: hormones, biotoxins and parasites. In: Kraus S.D. and R.M. Rolland, (eds.). The Urban Whale: North Atlantic Right Whales at the Crossroads. Harvard University Press, Cambridge, MA.

[75] *Id.*; *see also* Mayo, C.S., Page, M., Osterberg, D., and Pershing, A., "On the path to starvation: the effects of anthropogenic noise on right whale foraging success," North Atlantic Right Whale Consortium: Abstracts of the Annual Meeting (2008) (finding that decrements in North Atlantic right whale sensory range due to shipping noise have a larger impact on food intake than patch-density distribution and are likely to compromise fitness).

[76] *See, e.g.*, NMFS, Biological and Conference Opinion on U.S. Navy Atlantic Fleet Training and Testing and the National Marine Fisheries Service's Promulgation of Regulations Pursuant to the Marine Mammal Protection Act for the Navy to "Take" Marine Mammals Incidental to Atlantic Fleet Training and Testing (Nov. 2018) at 508.

[77] *See, e.g.*, NMFS, Biological Opinion on the Bureau of Ocean Energy Management's Issuance of Five Oil and Gas Permits for Geological and Geophysical Seismic Surveys off the Atlantic Coast of the United States, and the National Marine Fisheries Services' Issuance of Associated Incidental Harassment Authorizations (Nov. 2018) at 87 ("North Atlantic right whales shift calling frequencies, particularly those of upcalls, and increase call amplitude over both long and short term periods due to exposure to vessel sound, which may limit their communication space by as much as 67 percent compared to historically lower sound conditions").

distinct, significant cumulative impacts that will likely befall right whales in light of their critically endangered status and sensitivity to the various stressors listed, such as the fact that right whales, and female and their calves in particular, are more at risk of vessel strikes than other species.[78]

NMFS also seems to have artificially narrowed the definition of the action area for purposes of its cumulative impacts analysis. Specifically, NMFS defines the action area as "focused primarily on the Northeast Region Trap/Pot Management Area." DEIS Vol. I at 8-248. But this ignores the behavioral characteristics of right whales and other species who migrate hundreds or thousands of miles in the Atlantic and thus will be exposed to the risk of vessel strikes, noise pollution, and other stressors in areas outside the narrow circle NMFS has drawn for purposes of its cumulative impacts analysis. While the agency considers the impacts of entanglements and vessel strikes "in Canadian waters . . . because of the magnitude of impact this is have on the population," *id.*, NMFS must also analyze the combined impacts of the species' exposure to other stressors outside New England. *See, e.g.*, *Nat. Res. Def. Council v. Hodel*, 865 F.2d 288, 297–300 (D.C. Cir. 1988) (rejecting EIS where it failed to properly consider the impacts of offshore oil and gas activities on species who migrate through multiple planning areas); *Utahns v. U.S. Dep't of Transportation*, 305 F.3d 1152, 1180 (10th Cir. 2002) (holding EIS inadequate where it only evaluated impacts within 1,000 feet of proposed project because it limited analysis to smaller, less mobile species and ignored impacts to migratory species). For example, it is not clear if the agency considered the impacts of vessel strikes in the mid- and south-Atlantic regions, despite this stressor having significant impacts on the population in these waters. Indeed, in the last 14 months alone numerous right whales have been killed or seriously injured by vessel strikes in U.S. waters outside New England.[79] Additionally, it is unclear whether the agency considered other stressors right whales also face, or are reasonably likely to face in the foreseeable future, in waters outside New England and Canadian waters such as vessel noise or plastic pollution.

While NMFS may consider the impacts from the proposed rule to be minor (or beneficial), that does not absolve the agency of its duty under NEPA to consider the combined impacts of the regulations on imperiled right whales or other species, particularly because the regulations are part of NMFS's authorization of the operation of the fisheries under the MMPA. As one appellate court has explained:

> the addition of a small amount of [pollution] to a [waterway] may have only a limited impact on [fish] survival, or perhaps no impact at all. But the addition of a small amount here, a small amount there, and still more at another point could add up to some-thing with a much greater impact, until there comes a point where even a marginal increase will mean that *no* [fish] survive.

---

[78] *See, e.g.*, 78 Fed. Reg. 73726, 73727 (Dec. 9, 2013) ("Right whales appear to be more vulnerable to ship strikes than other large whale species"); NMFS, North Atlantic Right Whale (Eubalaena glacialis) Vessel Speed Rule Assessment (June 2020) at 23.

[79] *See, e.g.*, NMFS, 2017–2021 North Atlantic Right Whale Unusual Mortality Event, https://www.fisheries.noaa.gov/national/marine-life-distress/2017-2021-north-atlantic-right-whale-unusual-mortality-event (updated Feb. 28, 2021).

Klamath-Siskiyou Wildlands Ctr. v. Bureau of Land Mgmt., 387 F.3d 989, 994 (9th Cir. 2004). The same is true for impacts to right whales from entanglements in commercial fishing gear, vessel strikes, noise pollution, and other stressors—the addition of some impacts here, and some impacts there, could add up to cumulatively significant impacts, particularly where NMFS has found that protecting every individual right whale is essential to its recovery; that its extinction is almost certain in the immediate future if existing threats are not dramatically reduced; and the best available science indicates that ongoing entanglements and vessel strikes are not only impeding the species' recovery but actively driving the species toward extinction.[80] NMFS must carefully examine and disclose these impacts to comply with NEPA.

E. The Economic Analysis in the DEIS Is Fundamentally Flawed

NMFS's economic analysis of the proposed rule in the DEIS is flawed in two fundamental ways. First, it fails to properly consider that reduced effort does not equate to reduced catch. Second, it fails to consider the significant economic benefit from preventing whale entanglements.
The DEIS overestimates the economic impact of the proposed rule on industry by incorrectly assuming reduced effort will lead to reduced landings. Research examining the catch of lobsters in Maine and Canada concluded that there is far more effort in the U.S. than is needed to obtain the same level of catch.[81] Accordingly, seasonal closures and trap reductions could provide substantial benefit to endangered whales while having little economic impact on fishermen.[82] The authors of a 2007 study stated, for example, that "if Maine restricted its fishing season to 6 months and reduced the number of traps by a factor of 10, the same amount of lobster could be landed with greatly reduced risk to right whales and other species."[83]

Recent studies have reached similar conclusions. For example, a 2020 study found that Canadian fishers in the Gulf of Maine caught about the same about of lobster using 7.5 times less effort than Maine fishers in U.S. waters.[84] In particularly, the study determined that from 2007 to 2013 in Maine, lobster landings doubled as the number of traps fell 10.5% and landings per trap increased by about 125%; and that Massachusetts achieved record-high landings since the implementation of trap/pot seasonal closures, especially within those areas most affected by the closures.[85] As such, "a negative economic impact should not be assumed with effort reduction."[86]

The DEIS also overestimates the economic impacts by ignoring the economic benefits of

---

[80] *See, e.g.*, Pace et al 2021; NMFS, Immediate Action Needed to Save North Atlantic Right Whales, July 3, 2019, https://www.fisheries.noaa.gov/leadership-message/immediate-action-needed-save-north-atlantic-right-whales; NMFS, Species in the Spotlight, https://www.fisheries.noaa.gov/topic/endangered-species-conservation#species-in-the-spotlight (last visited Feb. 3, 2021).

[81] Myers, R.A., S.A. Boudreau, R.D. Kenney, M.J. Moore, A.A. Rosenberg, S.A. Sherrill-Mix, and B. Worm. 2007. Saving endangered whales at no cost. Curr. Biol. 17(1): R10–R11.

[82] *Id.*

[83] *Id.*

[84] Hannah J. Myers and Michael J. Moore. 2020. Reducing effort in the U.S. American lobster (Homarus americanus) fishery to prevent North Atlantic right whale (Eubalaena glacialis) entanglements may support higher profits and long-term sustainability. Marine Policy. Vol. 118: 103399.

[85] *Id.*

[86] *Id.*

reducing entanglement risk. While putting a dollar figure on an individual whale is not necessarily the best way to measure its inherent value, NMFS cannot focus solely on the cost to industry while ignoring the significant benefits provided by large whales—including to the fisheries themselves—particularly where tools exist to estimate the economic benefits of whales. For example, the International Monetary Fund recently issued a "conservative estimate[]" that placed the average value of an individual large whale at more than $2 million due to the ecosystem services individual whales provide in carbon sequestration and fertilizing activity that adds significantly to phytoplankton growth in the areas whales frequent.[87] In addition, reducing the frequency and severity of whale entanglements, will also reduce the expense associated with disentanglement efforts. But NMFS failed to consider these benefits in evaluating the economic impact of the proposed rule. This is improper.

Courts have held that it is arbitrary for an agency to focus solely on the costs to industry from enacting regulations while ignoring the economic benefits of the new standards. *See, e.g.*, *Ctr. for Biological Diversity v. Nat'l Highway Traffic Safety Admin.*, 538 F.3d 1172, 1203 (9th Cir. 2008) (holding that it was arbitrary for an agency to consider the economic benefits of decreased carbon emissions from tailpipes when establishing corporate average fuel economy standards for light trucks when it considered economic costs to industry from enacting stricter standards); *see also High Country Conservation Advocates v. U.S. Forest Serv.*, 52 F. Supp. 3d 1174, 1190-93 (D. Colo. 2014) (holding that it was arbitrary for the agency to consider the economic benefits of a coal mine expansion without also assessing the climate consequences of the end use of coal using the Social Cost of Carbon protocol).

In other words, NMFS "cannot put a thumb on the scale by undervaluing the benefits and overvaluing the costs of more stringent standards." *Ctr. for Biological Diversity*, 538 F.3d at 1198; *see also Mont. Envtl. Info. Ctr. v. U.S. Office of Surface Mining,* Case No. 15-106-M-DWM, 2017 WL 3480262, at *15 (D. Mont. Aug. 14, 2017). Yet that is just what NMFS's DEIS does. While it contains a lengthy analysis of the economic impact to industry, it has no analysis or discussion of the economic benefit of the regulations—whether quantitative or qualitative. While there may be a range of values, the value of saving whales "is certainly not zero" as NMFS irrational treats such value in its DEIS. *See Ctr. for Biological Diversity*, 538 F.3d at 1200.

V. CONCLUSION

NMFS's proposed rule and its associated DEIS are fundamentally flawed and fail to comply with the agency's legal obligations under the MMPA, ESA, and NEPA in numerous ways. NMFS must revise its risk reduction target, proposed rule and associated documents, reissue them for public notice and comment, and implement emergency measures to significantly reduce entanglement risk in the interim. Failure to do so would be a gross dereliction of the agency's duties and condemn the right whale to suffer yet more of the entanglements in commercial fishing that are not only impeding the species recovery, but actively driving it closer to the brink of extinction.

---

[87] *Id.*; *see also* Carl Wilson, Manipulative Trapping Experiments In The Monhegan Island Lobster Conservation Area, Jan. 2010; Stephanie A. Boudreau & Boris Worm. 2010. Top-down control of lobster in the Gulf of Maine: insights from local ecological knowledge and research surveys. Mar. Ecol. Prog. Ser. Vol. 403: 181–191.

Sincerely,

<u>/s/ *Kristen Monsell*</u>
Kristen Monsell
Oceans Legal Director & Senior Attorney
Center for Biological Diversity
kmonsell@biologicaldiversity.org

<u>/s/ *Erica Fuller*</u>
Erica Fuller
Senior Attorney
Conservation Law Foundation
efuller@clf.org

<u>/s/ *Jane Davenport*</u>
Jane Davenport
Senior Attorney
Defenders of Wildlife
jdavenport@defenders.org

<u>/s/ *Sharon Young*</u>
Sharon Young
Senior Strategist, Marine Issues
The Humane Society of the United States
syoung@humanesociety.org

<u>*/s/ Keisha Sedlacek*</u>
Keisha Sedlacek
Director of Regulatory Affairs
Humane Society Legislative Fund
ksedlacek@hslf.org

Attachment B

Center for Biological Diversity • Conservation Law Foundation •
• Defenders of Wildlife •

June 29, 2021

Gina Raimondo, Secretary of Commerce
U.S. Department of Commerce
1401 Constitution Avenue, NW, Rm 5516
Washington, DC 20230
TheSec@doc.gov

Janet Coit, Assistant Administrator for Fisheries
NOAA Fisheries
1315 East-West Highway
Silver Spring, MD 20910
Janet.Coit@noaa.gov

Re: New Scientific Information Necessitates Immediate Re-examination of Assumptions on the Efficacy of So-called Weak Rope to Protect North Atlantic Right Whales

Dear Secretary Raimondo and Ms. Coit,

On behalf of the Center for Biological Diversity, Conservation Law Foundation, and Defenders of Wildlife, we write to notify you that the National Marine Fisheries Service "(NMFS") must reinitiate consultation on its recently-issued biological opinion[1] ("2021 BiOp") and reconsider certain aspects of the forthcoming rule to amend the Atlantic Large Whale Take Reduction Plan ("Plan") in order to address newly-available scientific evidence that casts significant doubt on key assumptions of those documents: namely, the efficacy of so-called "weak rope" or "weak insertions" to mitigate the impacts of entanglements on the critically endangered North Atlantic right whale.

NMFS's decisions under the Marine Mammal Protection Act (MMPA) and Endangered Species Act (ESA) and its environmental analysis under the National Environmental Policy Act (NEPA) must be based on the best available scientific information (also termed evidence or data) to meet statutory requirements and to pass judicial muster under the Administrative Procedure Act. *See, e.g.*, *Conner v. Burford*, 848 F.2d 1441, 1454 (9th Cir. 1988) (ESA); *Brower v. Evans*, 257 F.3d 1058, 1070–71 (9th Cir. 2001) (MMPA). Under the ESA, a final biological opinion must not only be based on the best available scientific data, 16 U.S.C. § 1536(a)(2), but when "new

---

[1] *See* NMFS, *Endangered Species Act Section 7 Consultation on the: (a) Authorization of the American Lobster, Atlantic Bluefish, Atlantic Deep-Sea Red Crab, Mackerel/Squid/Butterfish, Monkfish, Northeast Multispecies, Northeast Skate Complex, Spiny Dogfish, Summer Flounder/Scup/Black Sea Bass, and Jonah Crab Fisheries and (b) Implementation of the New England Fishery Management Council's Omnibus Essential Fish Habitat Amendment 2 [Consultation No. GARFO-2017-00031]*, May 27, 2021.

information reveals effects of the action that may affect listed species . . . in a manner or to an extent not previously considered," 50 C.F.R. § 402.16(a)(2), NMFS must reinitiate consultation.

A recently-published paper by NMFS scientist Joshua Stewart and co-authors, titled "Decreasing body lengths in North Atlantic right whales,"[2] constitutes significant new information directly relevant not only to NMFS's no-jeopardy conclusion in the 2021 BiOp but also to specific aspects of the proposed rule to amend the Plan and the environmental analysis of the proposed rule and alternatives set forth in the Draft Environmental Impact Statement (DEIS). This paper compares length measurements of 129 individual whales born between 1981 and 2019 for which age and length data were collected in two periods, from 2000–2002 and from 2016–2019.[3] It demonstrates that right whales "born in recent years have experienced stunted growth, and over the same period that we have detected this effect they have experienced increasing rates of entanglement."[4]

Sublethal effects of entanglements may decrease reproductive success and increase risk of lethal entanglement

Noting that, in baleen whales, "larger maternal size and body condition are associated with faster calf growth rates and larger calves," the paper observes that "Decreasing body size may therefore be associated with smaller calves and lower calf survivorship, or potentially delayed first calving and lower reproductive success in females. [Right whales] exhibit generally poor body condition compared to other populations of right whales, which could contribute to synergistic negative effects where females in poor condition produce smaller calves that ultimately reach smaller maximum sizes, further contributing to reduced calf growth and declining calf condition."[5] Although the paper posits that "birth year effects on asymptotic length represents the cumulative effects of dynamic and hard-to-observe impacts on individual [right whales] that may include unrecorded entanglements, shifting prey seascapes, vessel strikes, and foraging interference from vessel traffic,"[6] its results "suggest that sub-lethal entanglements constrain overall body size in [right whales], which may in turn make them less resilient to future entanglements by reducing their absolute energetic reserves and increasing the probability of a lethal entanglement."[7]

The Stewart et al. paper is thus directly relevant to and casts doubt on NMFS's no-jeopardy conclusion in the 2021 BiOp, which already inadequately and unlawfully failed to consider the impacts of sublethal entanglements on the species' likelihood of survival and recovery under the proposed amendments to the Plan.[8] Unlike the model-based papers the 2021 BiOp implicitly

---

[2] Stewart et al., Decreasing body lengths in North Atlantic right whales, *Current Biology* (2021), available at https://doi.org/10.1016/j.cub.2021.04.067

[3] *Id.* at 1.

[4] *Id.* at 2.

[5] *Id.* at 3.

[6] *Id.* at 2.

[7] *Id.* at 3.

[8] *See, e.g.*, 2021 BiOp at 220–21; *see also id.* at 221 ("However, at this time, there is no further evidence to make the conclusion that sublethal effects from fishing gear entanglement alone causes [sic] a decline in large whale health."); *id.* at 338–39 ("sublethal effects analysis" of jeopardy analysis, acknowledging that the proposed Plan amendments will not decrease sublethal effects or improve calving rates); *id.* at 341–342 (no-jeopardy determination, also acknowledging

disparages as "postulations,"[9] the Stewart paper presents concrete photogrammetric evidence of the stunting associated with sublethal entanglements both of a right whale directly and of a right whale's mother during lactation.[10] NMFS must reinitiate consultation on the 2021 BiOp and, before finalizing the Plan amendments or the Final Environmental Impact Statement (FEIS)/Record of Decision (ROD), take this information into account.

Also highly relevant to the sublethal entanglements issue are two additional papers that NMFS failed to cite or analyze in the 2021 BiOp, the proposed rule, or the DEIS. The first, by Sarah Fortune and co-authors, titled "Body growth of North Atlantic right whales (*Eubalaena glacialis*) revisited" and published in October 2020[11]demonstrates that healthy right whales are considerably heavier than previously estimated and that therefore previously estimated energy requirements have been underestimated for some age-classes. Specifically, "sexually mature right whales require more energy per unit body mass than previously thought because their estimated body mass exceeds the upper limits of previous estimates."[12]

The second, by Katherine Graham and co-authors, titled "Stress and reproductive events detected in North Atlantic right whale blubber using a simplified hormone extraction protocol" and published in January 2021,[13] confirms that the highest detected levels of stress hormones from biopsy or necropsy samples of right whales with known life history states came from whales with active entanglements or that died from acute entanglements. In light of the accepted scientific literature demonstrating the high energetic and stress costs of sublethal entanglements to individual females,[14] NMFS must consider both Fortune et al. (2020) and Graham et al. (2021) in a reinitiated consultation and prior to finalizing the Plan amendments and FEIS/ROD.

NMFS must reexamine its assumptions that weak ropes/contrivances will significantly reduce right whale mortalities/serious injuries in smaller/weaker animals

In addition to its relevance on the sublethal effects of entanglements, the Stewart et al. (2021) paper also has serious implications for the efficacy of NMFS's proposed risk reduction measures based on the unproven assumption that weak rope, weak insertions, and/or weak toppers will

---

that the proposed Plan amendments will not reduce sublethal effects or improve calving rates). In every section of the 2021 BiOp in which NMFS purports to address the sublethal effects of entanglement, it essentially punts its obligation to engage in a meaningful analysis of these effects with the excuse that they cannot be quantified.

[9] *Id.* at 221.

[10] *Id.* at 2.

[11] Fortune et al., Body growth of North Atlantic right whales (*Eubalaena glacialis*) revisited, *Marine Mammal Science* (2020), available at https://doi.org/10.1111/mms.12753

[12] *Id.* at 10; *see also id.* at 12 ("Consequently, the new predictions of body mass result in elevated metabolic rates, lending further support to certain ages of right whales being more vulnerable to nutritional stress than others. This is particularly important for reproductively mature females, who may be able to withstand short periods of reduced feeding if they can replenish their blubber reserves during the postlactation period.").

[13] Graham et al., Stress and reproductive events detected in North Atlantic right whale blubber using a simplified hormone extraction protocol, *Conservation Physiology* (2021), available at https://doi.org/10.1093/conphys/coaa133.

[14] *See, e.g.,* 2021 BiOp at 220–21 (citing papers).

substantially reduce right whale mortalities and serious injuries (M/SI) in fixed-gear fisheries using static vertical buoy lines.[15] This unproven assumption is based on a single paper, Knowlton et al. (2016),[16] that concluded that 1700 pound-force (lbf) breaking strength rope could reduce M/SI for right whales. Even more fundamentally, the Stewart et al. (2021) paper calls into question the entire Decision Support Tool, where the gear risk component consists of "a gear threat model to determine the relative threat of gear based on gear strength."[17]

All of the ropes studied in Knowlton et al. (2016) were taken from gear collected from large whale entanglements between 1994 and 2010.[18] In other words, the entanglements from which the studied ropes were collected occurred not only before the documented shift in right whale distribution, increase in right whale mortality, and decline in right whale abundance all starting in 2010, but also before the documented decreases in body length and stunted growth of calves demonstrated by Stewart et al. (2021).

Stewart et al. (2021) conclude that "With the maximum effect of birth year applied, a whale born in 2019 is expected to reach a maximum length approximately 1 m shorter than a whale born in 1981."[19] The consequences of this meter reduction in length with respect to mass are illustrated by Table 2 in Fortune et al. (2020). There, the authors model a 13.6 m right whale's weight at 35,277 kg (age 25) versus a 12.6 m right whale's weight at 28,187 kg (age 9), a full 25% decrease.[20]

Shorter right whales, with commensurately less mass, cannot be assumed to be able to exert the same forces as longer right whales, casting into doubt NMFS's "suggestion" that "right whales may be able to break free of rope that is weaker than 1700 lbf . . . consistent with estimates of the force that large whales are capable of applying, based on an axial locomotor muscle morphology study." *See* 2021 BiOp at 25; DEIS at 3-64, 5-134, 5-161, 5-172 (citing Arthur et al. (2015)[21]).

Taken together, these papers demonstrate that NMFS cannot rely on the assumptions undergirding the gear threat component of the Decision Support Tool or on the assumptions in the 2021 BiOp, proposed rule, and DEIS, that weak ropes/weak contrivances will significantly reduce M/SI in right whales.

Conclusion

In our comments on the draft 2021 BiOp and the draft proposed rule/DEIS, we detailed the many significant legal and scientific shortcomings of those documents. NMFS has already explicitly violated a federal district court's opinions and orders by issuing the 2021 BiOp without a lawful

---

[15] *See, e.g.*, DEIS at 5-157–5-162 (§ 5.2.13., "Weak Rope").

[16] Knowlton et al., Effects of fishing rope strength on the severity of large whale entanglements, *Conservation Biology* (2016), available at https://doi.org/10.1111/cobi.12590

[17] *See, e.g.*, DEIS at 3-65; *id.* at 3-74 (describing adjustments to model assumptions on weak rope based on weak insertions).

[18] *Id.* at 320.

[19] Stewart et al. (2021) at 2.

[20] Fortune et al. (2020) at 9, Table 2.

[21] Arthur et al., Estimating maximal force output of cetaceans using axial locomotor muscle morphology, *Marine Mammal Science* (2015), available at https://doi.org/10.1111/mms.12230.

incidental take statement for the lethal take of right whales that the document bluntly concedes will continue to occur even if the Plan amendments are fully successful. The proposed rule does not even pretend to meet the MMPA's explicit requirements of bringing M/SI below the potential biological removal level. The Stewart et al. (2021) paper, together with other sources of the best available scientific data that the agency has failed to consider and incorporate into its decision-making, only reinforce that the agency is currently on a collision course with disaster for both the right whale and the fishing industry. With an extremely limited window in which to act, NMFS should finally open its eyes to the fact that its proposed rule is a failure both scientifically and legally.

We reiterate that the only reasonable course of action is for NMFS to withdraw the proposed rule and reinitiate consultation to drastically rework the Plan to bring it into conformity with the requirements of the ESA and MMPA. In the interim, NMFS must finally act on our December 2, 2020 petition for emergency rulemaking under MMPA section 118(g), 16 U.S.C. § 1387(g).

Please do not hesitate to contact us with any questions or to discuss the issues we raise.

Sincerely,

/s/ Jane P. Davenport
Jane P. Davenport
Senior Attorney
Defenders of Wildlife
jdavenport@defenders.org
202-772-3274

/s/ Erica Fuller
Erica Fuller
Senior Attorney
Conservation Law Foundation
efuller@clf.org
617-850-1727

/s/ Kristen Monsell
Kristen Monsell
Oceans Legal Director, Senior Attorney
Center for Biological Diversity
kmonsell@biologicaldiversity.org
510-844-7137

cc: Samuel D. Rauch, III, Deputy Assistant Administrator for Regulatory Programs
samuel.rauch@noaa.gov
Michael Pentony, GARFO Regional Administrator
michael.pentony@noaa.gov
Colleen Coogan, GARFO Marine Mammal & Sea Turtle Branch Chief
colleen.coogan@noaa.gov

Attachments

Report

Current Biology

Decreasing body lengths in North Atlantic right whales

Highlights

- Whales with severe entanglements in fishing gear are stunted
- Whales whose mothers were entangled while nursing are stunted
- Body lengths have been decreasing since 1981
- Cumulative impacts in addition to entanglements may contribute to stunted growth

Authors

Joshua D. Stewart, John W. Durban,
Amy R. Knowlton, ...,
Wayne L. Perryman, Carolyn A. Miller,
Michael J. Moore

Correspondence

joshua.stewart@noaa.gov

In brief

Stewart et al. examine trends in body lengths in endangered North Atlantic right whales using aerial photogrammetry. They show that whales that have experienced severe entanglements in fishing gear are shorter than whales with no documented entanglements, and that body lengths of right whales have been decreasing over the past four decades.

Stewart et al., 2021, Current Biology *31*, 1–6
July 26, 2021
https://doi.org/10.1016/j.cub.2021.04.067

CellPress

Please cite this article in press as: Stewart et al., Decreasing body lengths in North Atlantic right whales, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.04.067

Current Biology

CellPress

Report

Decreasing body lengths in North Atlantic right whales

Joshua D. Stewart,[1,7,8,*] John W. Durban,[2,3] Amy R. Knowlton,[4] Morgan S. Lynn,[2] Holly Fearnbach,[5] Jacob Barbaro,[2] Wayne L. Perryman,[2] Carolyn A. Miller,[6] and Michael J. Moore[6]
[1]National Research Council Postdoctoral Fellow for Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, La Jolla Shores Drive, La Jolla, CA, 92037, USA
[2]Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, La Jolla Shores Drive, La Jolla, CA, 92037, USA
[3]Southall Environmental Associates, Inc., Soquel Dr., Aptos, CA, 95003, USA
[4]Anderson Cabot Center for Ocean Life, New England Aquarium, Boston, MA, 02110, USA
[5]Marine Mammal Research Program, SR3, SeaLife Response, Rehabilitation and Research, S 216th St., Des Moines, WA, 98198, USA
[6]Department of Biology, Woods Hole Oceanographic Institution, Woods Hole Rd., Woods Hole, MA, 02543, USA
[7]Twitter: @NOAAFish_WCRO
[8]Lead contact
*Correspondence: joshua.stewart@noaa.gov
https://doi.org/10.1016/j.cub.2021.04.067

SUMMARY

Whales are now largely protected from direct harvest, leading to partial recoveries in many previously depleted species.[1] However, most populations remain far below their historical abundances and incidental human impacts, especially vessel strikes and entanglement in fishing gear, are increasingly recognized as key threats.[2] In addition, climate-driven changes to prey dynamics are impacting the seasonal foraging grounds of many baleen whales.[2] In many cases these impacts result directly in mortality. But it is less clear how widespread and increasing sub-lethal impacts are affecting life history, individual fitness, and population viability. We evaluated changes in body lengths of North Atlantic right whales (NARW) using aerial photogrammetry measurements collected from crewed aircraft and remotely operated drones over a 20-year period (Figure 1). NARW have been monitored consistently since the 1980s and have been declining in abundance since 2011 due primarily to deaths associated with entanglements in active fishing gear and vessel strikes.[3] High rates of sub-lethal injuries and individual-level information on age, size and observed entanglements make this an ideal population to evaluate the effects that these widespread stressors may have on individual fitness. We find that entanglements in fishing gear are associated with shorter whales, and that body lengths have been decreasing since 1981. Arrested growth may lead to reduced reproductive success[4,5] and increased probability of lethal gear entanglements.[6] These results show that sub-lethal stressors threaten the recoveries of vulnerable whale populations even in the absence of direct harvest.

RESULTS AND DISCUSSION

We combined age and length data collected from crewed aircraft in 2000–2002 and from remotely operated drones in 2016-2019 in a growth model mirroring a previous analysis of the 2000–2002 data.[7] We modified the 2-phase Gompertz growth equation to include model-estimated effects on asymptotic length for: (a) birth year, (b) duration of entanglements with attached fishing gear, (c) whether a whale's mother experienced a severe entanglement injury while nursing that whale, and (d) the number of lactation events a female whale experienced, which is known to be one of the most significant energetic expenditures for right whales.[8] We considered the cumulative effects of covariates from birth until age 10 (or until the time of measurement if it occurred prior to age 10), as the expected length at age 10 is more than 95% of the estimated asymptotic length and constraints to growth after that point would be unlikely to measurably affect whale lengths.

Across all years we collected 202 length measurements of 129 individual whales: 133 measurements from crewed aircraft and 69 from remotely operated drones. 76 whales were measured once, 36 twice (in separate years), 14 three times, and 3 four times. The ages of measured whales ranged from <1 to 37 years old, including whales born from 1981 to 2019. Eleven whales in our dataset were observed with attached gear; 8 of those whales were measured once, 2 were measured twice, and 1 was measured four times. Gear entanglement durations (midpoints) ranged from 65 to 334 days. Seven measured whales had known severe maternal entanglement injuries; 1 of those whales was measured twice. No whales in our dataset had both a maternal entanglement injury and an entanglement with attached gear. Nine measured whales had one lactation event, and 1 whale had two lactation events prior to age 10.

Birth year had the greatest effect on the estimated asymptotic length of NARW (99.8% of posterior distribution <0). The estimated

Please cite this article in press as: Stewart et al., Decreasing body lengths in North Atlantic right whales, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.04.067

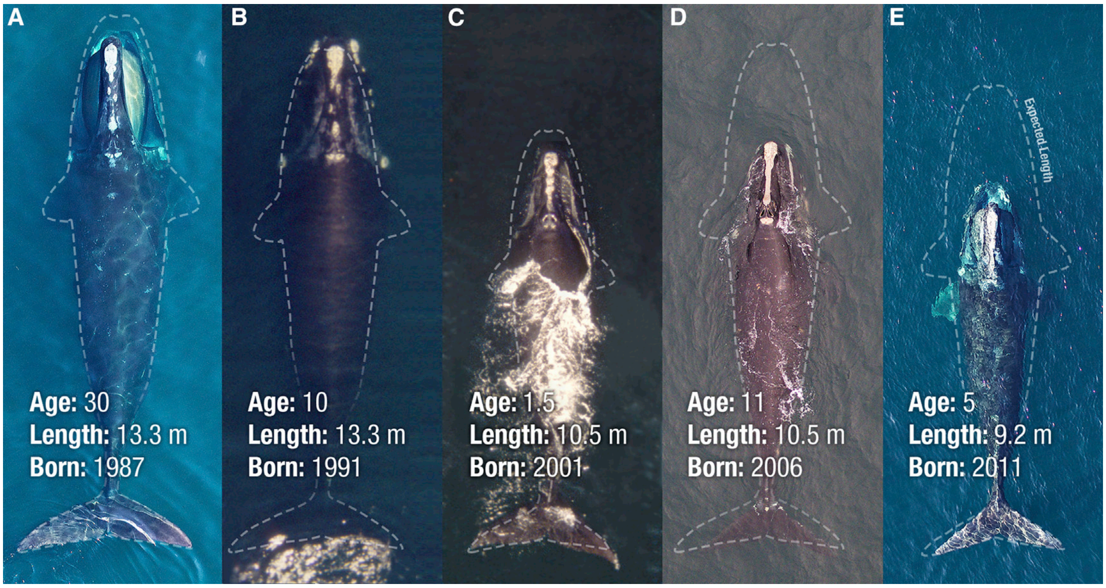


Figure 1. Stunted North Atlantic right whales

A scaled photo illustration comparing the body lengths of (A) Whale 1703, imaged in 2017 at age 30 using a remotely operated drone, (B) Whale 2145, imaged in 2001 at age 10 from a crewed aircraft, (C) Whale 3180, imaged in 2002 at age 1.5 from a crewed aircraft, (D) Whale 3617, imaged in 2017 at age 11 using a drone, and (E) Whale 4130, imaged in 2016 at age 5 using a drone. The dashed outline in each panel represents the median model-estimated body length for a whale of the same age born in 1981 with no history of entanglements or maternal entanglements. Note the entanglement scarring around the caudal peduncle in (D). Figure design by Madeline Wukusick.

effect of birth year was an asymptotic length 0.025 m (95% credible intervals 0.01–0.04) shorter than the baseline asymptotic length per year born after 1981. With the maximum effect of birth year applied, a whale born in 2019 is expected to reach a maximum length approximately 1 m shorter than a whale born in 1981 (Figure 2). This corresponds to a 7.3% decline in maximum body length. Known entanglements of a whale with attached gear (97.4% of posterior distribution <0) and entanglements of its mother during nursing (99.7% of posterior distribution <0) also had negative effects on expected maximum length, of approximately −0.64 m (4.7% length reduction) and −0.69 m (5.0% length reduction), respectively. The effect of entanglement with attached gear was applied as a continuous effect, so a whale with an entanglement duration that is half the maximum duration is expected to experience half of that negative effect on asymptotic length, or an expected asymptotic length 0.32 m shorter than baseline. There was no significant effect of the number of lactation events (61.2% of posterior distribution >0) on expected maximum length of right whales (Figure 3). The estimates of error around the model-estimated mean length-at-age were different across altimeter types. GPS altimeter measurements had the highest error (median 0.63, 95% CI 0.26–1.01 m), followed by laser altimeter measurements (0.52, 0.19–0.77 m) and radar altimeter measurements (0.27, 0.01–0.48 m).

Our results demonstrate that NARW born in recent years have experienced stunted growth, and over the same period that we detected this effect they have experienced increasing rates of entanglement.[3] As a result, NARW appear to have less energy to devote to early growth. A portion of the estimated length reduction was directly attributable to entanglements, but the effect size of entanglements was smaller than the effect size of birth year. We posit that the birth year effects on asymptotic length represent the cumulative effects of dynamic and hard-to-observe impacts on individual NARW that may include unrecorded entanglements, shifting prey seascapes, vessel strikes, and foraging interference from vessel traffic (Figure 4). For example, entanglements of NARW are imperfectly observed, and many whales have evidence of entanglement injuries without direct observations of attached gear; in these scar-only cases it is impossible to determine the duration of those entanglements.[9] Even direct observations of attached gear events have only approximate entanglement durations (we considered the midpoint between minimum and maximum possible duration of each entanglement) and there is almost certainly a large amount of noise introduced into our analyses as a result of these imperfect observations. Consequently, while our analyses detected a negative effect of entanglements on whale length, we cannot rule out a larger true effect size than our estimate; for example, if entanglements that were not recorded in our dataset contributed to restricted growth that was instead reflected in birth year effects.

The abundance of *Calanus finmarchicus*, a primary copepod prey item for NARW, has fluctuated in the Gulf of Maine over the past 40 years (Figure 4), apparently driving reproductive output in the NARW population.[11] *C. finmarchicus* is a subarctic species, and its distribution is expected to shift poleward as the North Atlantic warms,[12] leading to projected abundance declines in the Gulf of Maine.[13] There has not been a steady decline in *C. finmarchicus* abundance coincident with the decreasing NARW body lengths reported here. However, in the past decade, sighting rates of NARW on their typical foraging grounds have declined, and the timing and geographic distribution of peak

Please cite this article in press as: Stewart et al., Decreasing body lengths in North Atlantic right whales, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.04.067

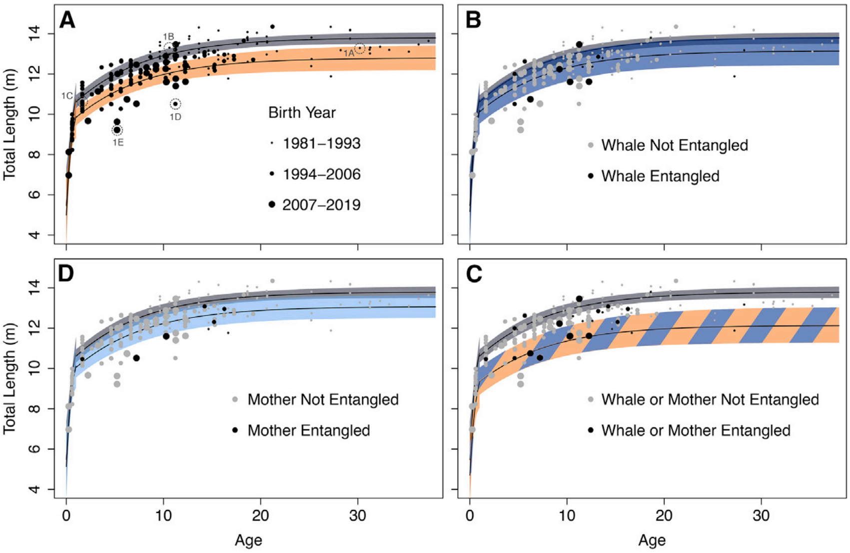


Figure 2. Growth curves for North Atlantic right whales

The gray curve in each panel represents the expected length at age for a typical NARW born in 1981 that experiences no entanglements and does not have an entangled mother while nursing. Solid lines represent median estimates and colored curves represent 95% Bayesian credible intervals for the mean length at age of whales with covariate effects applied.

(A) The expected length at age for a typical whale born in 2019 that experiences no entanglements and does not have an entangled mother while nursing (orange curve). Black points are observed lengths of known-age whales, with point size indicating the birth year of the whale (in three ranges for clarity; all panels). The dashed circles and corresponding labels indicate the whales pictured in Figure 1 panels A–E.

(B) The expected length at age for a typical whale born in 1981 that experiences a severe attached-gear entanglement (maximum effect size of a 334-day entanglement duration applied; dark blue curve). Light gray points are whales with no observed attached-gear entanglements; black points are whales with observed attached-gear entanglements. Note that duration of entanglement is not indicated.

(C) The expected length at age for a typical whale born in 1981 whose mother is entangled while that whale is nursing (light blue curve). Black points are whales whose mothers were detected with a severe entanglement injury while the measured whale was a nursing calf.

(D) The expected length at age for a typical whale born in 2019 that experiences a severe entanglement (maximum effect size; orange and blue striped curve). In other words, the cumulative effects of birth year and entanglements. Black points are whales with observed attached-gear entanglements or whales whose mother was known to have a severe entanglement injury while the measured whale was nursing, as these effect sizes were comparable. See model diagnostics in Figures S1–S3.

C. finmarchicus densities have been shifting.[14] These changes may indicate a deteriorating foraging environment in the Gulf of Maine. Given that NARW are dependent on hyper-dense patches of copepods to maximize foraging efficiency,[15] coarse regional indices of *C. finmarchicus* abundance (e.g., Figure 4) may not adequately represent foraging conditions that could affect growth rates. Other anthropogenic factors such as increasing vessel noise could also be interfering with foraging behavior and restricting NARW growth[16] (Figure 4).

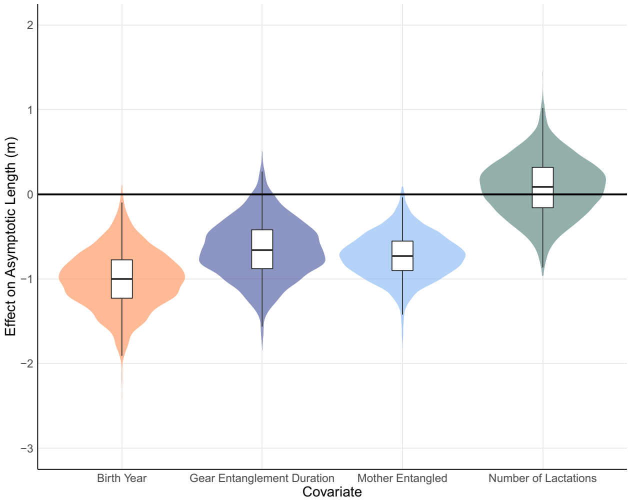


Figure 3. Covariate effects on asymptotic length of North Atlantic right whales

Violin plots represent the Bayesian posterior distributions of the estimated effect (in meters) of each covariate on the asymptotic length parameter in the 2-phase Gompertz growth equation. The interior boxplots represent the median effect size (horizontal black line), the 50% posterior density intervals (white box) and the 95% credible intervals (vertical black line). The effects of birth year, gear entanglement duration, maternal entanglement, and number of lactations are scaled to the maximum effect size as the minimum covariate values for each of these is zero. We considered an effect significant if >95% of posterior draws were below (or above) zero.

In baleen whales, larger maternal size and body condition are associated with faster calf growth rates and larger calves.[4,5] Decreasing body size may therefore be associated with smaller calves and lower calf survivorship, or potentially delayed first calving and lower reproductive success in females. NARW exhibit generally poor body condition compared to other populations of right whales,[17,18] which could contribute to synergistic negative effects where females in poor condition produce smaller calves that ultimately reach smaller maximum sizes, further contributing to reduced calf growth and declining calf condition. In addition, our results suggest that sub-lethal entanglements constrain overall body size in NARW, which may in turn make them less resilient to future entanglements by reducing their absolute energetic reserves and increasing the probability of a lethal entanglement.[6]

Mortality from vessel strikes and entanglements in fishing gear are thought to be a major driver of the current NARW population decline,[3] but the observed changes in body lengths also indicate a troubling trend that may have further negative effects on population viability in this critically endangered species, with chronic sub-lethal health effects slowing growth and potentially reducing reproductive success. Changes in body size can also be a leading indicator of population collapse,[19–21] further highlighting the ongoing and compounding threats to the NARW population. Implementing solutions to reduce entanglements and other anthropogenic impacts could give North Atlantic right whales increased

Please cite this article in press as: Stewart et al., Decreasing body lengths in North Atlantic right whales, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.04.067

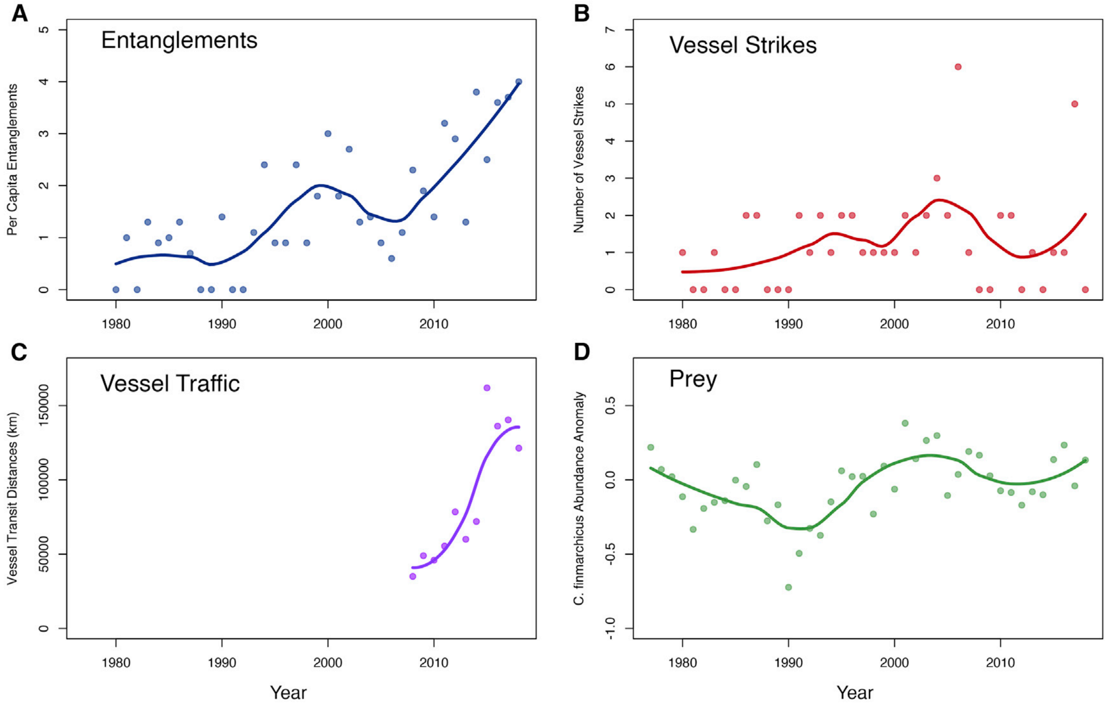


Figure 4. Possible cumulative impacts affecting right whale growth

Time series of potential stressors that could affect right whale energy budgets and foraging success.

(A) Number of new serious entanglements (attached gear or severe injuries) observed each year, standardized by the number of individual whales observed during field surveys; source ref.[9]

(B) Number of vessel strikes resulting in blunt trauma or deep lacerations observed each year. Note that vessel strikes are raw counts and not per capita rates; source ref.[10]

(C) Cumulative vessel transit distances (in kilometers) within three special management areas that are NARW foraging hotspots: Cape Cod Bay, Race Point, and Great South Channel; source NMFS Right Whale Vessel Speed Rule Assessment, June 2020.

(D) *Calanus finmarchicus* abundance anomalies for the Gulf of Maine; source NOAA Ecosystem Dynamics and Assessment Branch ecodata. The lines in each panel are a loess smooth to the annual data.

resilience to adapt to changing prey dynamics and other climate-related impacts while maintaining population viability.

Changes to life history traits, such as growth rates and age or size at maturity, are well documented in heavily exploited species (in particular fishes).[22] Body size changes in mammals (both positive and negative) are also expected under changing climate conditions.[23,24] Our results suggest that humans are impacting the demographic characteristics of endangered and protected marine mammals through indirect and incidental pressures on vulnerable populations. Entanglements in fishing gear are a growing problem for migratory baleen whale species and a wide variety of marine mammals.[25] Extensive survey effort for the NARW population allowed the sub-lethal effects of entanglements to be directly (if imperfectly) estimated, but it is likely that other marine mammal species that experience chronic entanglements are being similarly affected.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
    - ○ Lead Contact
    - ○ Materials Availability
    - ○ Data and Code Availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2021.04.067.

ACKNOWLEDGMENTS

Hollis Europe and Brandon Tao contributed to drone photogrammetry data collection in 2018 and 2019, respectively. Technical support from Don LeRoi, Aerial Imaging Solutions, significantly contributed to the successes of both the crewed and drone photographic sampling efforts. All photo-identification data were processed by the New England Aquarium. Life history, entanglement and vessel strike events for identified individuals were provided with approval from the North Atlantic Right Whale Consortium. We thank Peter Corkeron and Sean Hayes for supporting data collection efforts in Cape Cod Bay. We are grateful to the NOAA Fisheries Office of Science and Technology for supporting the development and application of photogrammetry drones and to the

Please cite this article in press as: Stewart et al., Decreasing body lengths in North Atlantic right whales, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.04.067

NOAA Office of Marine and Aviation Operations for supporting photogrammetry operations. We appreciate the efforts of the Atlantic Large Whale Disentanglement Network in documenting entanglement sightings. We thank Sean Hayes, Allison Henry, and Caroline Good for their assistance in locating additional data sources of entanglements, vessel strikes and vessel traffic. We are grateful for feedback on earlier version of this manuscript by Jim Carretta, Tomoharu Eguchi, Dave Weller, and two anonymous reviewers. Photogrammetry data from 2016-2019 were collected with support from NOAA grant NA14OAR4320158. Funding to the New England Aquarium for curation of the photo-identification catalog is provided by NOAA Contract 1305M2-18-P-NFFM-0108. This analysis was performed while J.D.S. held an NRC Research Associateship award at the NOAA Southwest Fisheries Science Center.

AUTHOR CONTRIBUTIONS

J.D.S., J.W.D., and M.J.M. conceived the analysis; J.W.D., M.J.M., and H.F. conceived the study; J.W.D., M.J.M., A.R.K., H.F., and W.L.P. obtained funding for data collection; J.W.D., M.S.L., M.J.M., H.F., J.B., A.R.K., C.A.M., and W.L.P. collected and processed data; J.D.S. analyzed data and drafted the manuscript; all authors edited and revised the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: February 16, 2021
Revised: April 12, 2021
Accepted: April 26, 2021
Published: June 3, 2021

REFERENCES

1. Magera, A.M., Mills Flemming, J.E., Kaschner, K., Christensen, L.B., and Lotze, H.K. (2013). Recovery trends in marine mammal populations. PLoS ONE *8*, e77908.
2. Thomas, P.O., Reeves, R.R., and Brownell, R.L. (2016). Status of the world's baleen whales. Mar. Mamm. Sci. *32*, 682–734.
3. National Marine Fisheries Service (2019). North Atlantic Right Whale (*Eubalaena glacialis*) (Western Atlantic Stock. NOAA Mar. Mammal Stock Assess).
4. Christiansen, F., Vivier, F., Charlton, C., Ward, R., Amerson, A., Burnell, S., and Bejder, L. (2018). Maternal body size and condition determine calf growth rates in Southern right whales. Mar. Ecol. Prog. Ser. *592*, 267–282.
5. Christiansen, F., Dujon, A.M., Sprogis, K.R., Arnould, J.P.Y., and Bejder, L. (2016). Noninvasive unmanned aerial vehicle provides estimates of the energetic cost of reproduction in humpback whales. Ecosphere *7*, 1–18.
6. van der Hoop, J.M., Corkeron, P., Henry, A.G., Knowlton, A.R., and Moore, M.J. (2017). Predicting lethal entanglements as a consequence of drag from fishing gear. Mar. Pollut. Bull. *115*, 91–104.
7. Fortune, S.M.E., Trites, A.W., Perryman, W.L., Moore, M.J., Pettis, H.M., and Lynn, M.S. (2012). Growth and rapid early development of North Atlantic right whales (*Eubalaena glacialis*). J. Mammal. *93*, 1342–1354.
8. Fortune, S.M.E., Trites, A.W., Mayo, C.A., Rosen, D.A.S., and Hamilton, P.K. (2013). Energetic requirements of North Atlantic right whales and the implications for species recovery. Mar. Ecol. Prog. Ser. *478*, 253–272.
9. Knowlton, A.R., Hamilton, P.K., Marx, M.K., Pettis, H.M., and Kraus, S.D. (2012). Monitoring North Atlantic right whale E*ubalaena glacialis* entanglement rates: A 30 yr retrospective. Mar. Ecol. Prog. Ser. *466*, 293–302.
10. Moore, M.J., Rowles, T.K., Fauquier, D.A., Baker, J.D., Biedron, I., Durban, J.W., Hamilton, P.K., Henry, A.G., Knowlton, A.R., McLellan, W.A., et al. (2021). REVIEW: Assessing North Atlantic right whale health: threats, and development of tools critical for conservation of the species. Dis. Aquat. Organ. *143*, 205–226.
11. Meyer-Gutbrod, E.L., Greene, C.H., Sullivan, P.J., and Pershing, A.J. (2015). Climate-associated changes in prey availability drive reproductive dynamics of the North Atlantic right whale population. Mar. Ecol. Prog. Ser. *535*, 243–258.
12. Reygondeau, G., and Beaugrand, G. (2011). Future climate-driven shifts in distribution of *Calanus finmarchicus*. Glob. Change Biol. *17*, 756–766.
13. Grieve, B.D., Hare, J.A., and Saba, V.S. (2017). Projecting the effects of climate change on *Calanus finmarchicus* distribution within the U.S. Northeast Continental Shelf. Sci. Rep. *7*, 6264.
14. Record, N.R., Runge, J.A., Pendleton, D.E., Balch, W.M., Davies, K.T.A., Pershing, A.J., et al. (2019). Rapid climate-driven circulation changes threaten conservation of endangered North Atlantic right whales. Oceanography (Wash. D.C.) *32*, 162–169.
15. Kenney, R.D., Mayo, C.A., and Winn, H.E. (2001). Migration and foraging strategies at varying spatial scales in western North Atlantic right whales: a review of hypotheses. J. Cetacean Res. Manag. *2*, 251–260.
16. Blair, H.B., Merchant, N.D., Friedlaender, A.S., Wiley, D.N., and Parks, S.E. (2016). Evidence for ship noise impacts on humpback whale foraging behaviour. Biol. Lett. *12*.
17. Christiansen, F., Dawson, S., Durban, J., Fearnbach, H., Miller, C., Bejder, L., Uhart, M., Sironi, M., Corkeron, P., Rayment, W., et al. (2020). Population comparison of right whale body condition reveals poor state of the North Atlantic right whale. Mar. Ecol. Prog. Ser. *640*, 1–16.
18. Miller, C.A., Reeb, D., Best, P.B., Knowlton, A.R., Brown, M.W., and Moore, M.J. (2011). Blubber thickness in right whales *Eubalaena glacialis* and *Eubalaena australis* related with reproduction, life history status and prey abundance. Mar. Ecol. Prog. Ser. *438*, 267–283.
19. Clements, C.F., and Ozgul, A. (2016). Including trait-based early warning signals helps predict population collapse. Nat. Commun. *7*, 10984.
20. Calkins, D.G., Becker, E.F., and Pitcher, K.W. (1998). Reduced body size of female steller sea lions from a declining population in the Gulf of Alaska. Mar. Mamm. Sci. *14*, 232–244.
21. Guthrie, R.D. (2003). Rapid body size decline in Alaskan Pleistocene horses before extinction. Nature *426*, 169–171.
22. Hutchings, J.A., and Baum, J.K. (2005). Measuring marine fish biodiversity: Temporal changes in abundance, life history and demography. Philos. Trans. R. Soc. B Biol. Sci. *360*, 315–338.
23. Isaac, J.L. (2009). Effects of climate change on life history: Implications for extinction risk in mammals. Endanger. Species Res. *7*, 115–123.
24. Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L., and Heinsohn, R. (2011). Declining body size: a third universal response to warming? Trends Ecol. Evol. *26*, 285–291.
25. Read, A.J. (2008). The looming crisis: Interactions between marine mammals and fisheries. J. Mammal. *89*, 541–548.
26. Durban, J.W., Fearnbach, H., Perryman, W.L., and Leroi, D.J. (2015). Photogrammetry of killer whales using a small hexacopter launched at sea. J. Unmanned Veh. Syst. *3*, 131–135.
27. Dawson, S.M., Bowman, M.H., Leunissen, E., and Sirguey, P. (2017). Inexpensive aerial photogrammetry for studies of whales and large marine animals. Front. Mar. Sci. *4*, 1–7.
28. Perryman, W.L., and Lynn, M.S. (1993). Identification of geographic forms of common dolphin (*Delphinus delphis*) from aerial photogrammetry. Mar. Mamm. Sci. *9*, 119–137.
29. Miller, C.A., Best, P.B., Perryman, W.L., Baumgartner, M.F., and Moore, M.J. (2012). Body shape changes associated with reproductive status, nutritive condition and growth in right whales Eubalaena glacialis and E. australis. Mar. Ecol. Prog. Ser. *459*, 135–156.
30. Perryman, W.L., and Lynn, M.S. (2002). Evaluation of nutritive condition and reproductive status of migrating gray whales (*Eschrichtius robustus*) based on analysis of photogrammetric data. J. Cetacean Res. Manag. *4*, 155–164.
31. Kraus, S.D., Moore, K.E., Price, C.A., Crone, M.J., Watkins, W.A., Winn, H.E., et al. (1986). The use of photographs to identify individual North Atlantic right whales (*Eubalaena glacialis*). Rep. Int. Whaling Comm. *10*, 145–151.

Please cite this article in press as: Stewart et al., Decreasing body lengths in North Atlantic right whales, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.04.067

32. North Atlantic Right Whale Consortium (2020). North Atlantic Right Whale Consortium Identification Database 09/18/2020 (Anderson Cabot Cent. Ocean Life New Engl. Aquarium).
33. Knowlton, A.R., Robbins, J., Landry, S., McKenna, H., Kraus, S.D., and Werner, T.B. (2016). Effects of fishing gear strength on the severity of large whale entanglements. Conservation Biology *30*, 318–328.
34. van der Hoop, J., Corkeron, P., and Moore, M. (2016). Entanglement is a costly life-history stage in large whales. Ecol. Evol. *7*, 92–106.
35. Kato, H. (1988). Ossification Pattern of the Vertebral Epiphyses in the Southern Minke Whale (Sci. Reports Whales Res. Inst.), pp. 11–19.
36. Moran, M.M., Bajpai, S., George, J.C., Suydam, R., Usip, S., and Thewissen, J.G.M. (2014). Intervertebral and Epiphyseal Fusion in the Postnatal Ontogeny of Cetaceans and Terrestrial Mammals. J. Mamm. Evol. *22*, 93–109.
37. Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Proc. 3rd Int. Work. Distrib. Stat. Comput *124*.
38. R Core Team (2016). R: A language and environment for statistical computing (R Foundation for Statistical Computing).
39. Gelman, A., and Rubin, D.B. (1992). Inference from Iterative Simulation Using Multiple Sequences. Stat. Sci. *7*, 457–472.

Please cite this article in press as: Stewart et al., Decreasing body lengths in North Atlantic right whales, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.04.067

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
R	The R Project for Statistical Computing	V4.0.0
Just Another Gibbs Sampler (JAGS)	Plummer 2013	V4.2.0
Other		
126mm Reconnaissance Camera	Chicago Aerial	KA-76A
Remotely Operated Hexacopter	Aerial Imaging Solutions	APH-22
Digital Camera System	Olympus	E-PM2; 25mm Zuiko Lens

RESOURCE AVAILABILITY

Lead Contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Joshua Stewart (joshua.stewart@noaa.gov)

Materials Availability

This study did not generate new unique reagents

Data and Code Availability

All data and R code to replicate these analyses are available at http://github.com/stewart6/NARW-Growth.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Aerial photogrammetry measurements were collected from free-ranging North Atlantic Right Whales under NOAA National Marine Fisheries Service permits 21371, 17355 and 17355-01.

METHOD DETAILS

From 2000-2002, we used a fixed-winged, crewed airplane to collect aerial images of North Atlantic right whales (NARW) in the Bay of Fundy, Canada.[7] A 126mm format military reconnaissance camera captured images on film from approximately 250 m altitude. From 2016-2019 we flew a remotely controlled hexacopter drone at altitudes of approximately 50 m to collect images of NARW in Cape Cod Bay, U.S.A,[17] taking digital images using a 25mm lens mounted on an Olympus camera with micro 4/3 sensor.[26] Both methods achieved flat images that were undistorted across the entire frame. We collected altitude measurements using radar altimeters in 2000-2002,[7] drone GPS in 2016[17] and a laser altimeter[27] mounted on the vertical gimbal of the drone camera in 2017-2019. We established length estimates from image measurements by using altimetry data to convert image sensor distances to distances on the real scale.[7,26] We only selected images for use in length measurements when a whale was fully visible and appeared to be in flat orientation parallel to the water surface. In general, variability in repeated-measurements of total lengths of cetaceans is low, with average coefficients of variation typically ranging from approximately 1%–3%.[27–29] While altimeter inaccuracies can lead to both positive and negative length measurement errors, any movement or curvature of an animal will result in the animal appearing shorter from above than it actually is. To minimize this negative bias, and following previous studies using aerial photogrammetry to estimate cetacean lengths, we selected the longest measurement of each whale in cases of multiple measurements of an individual within a single sampling season[7,28,30]

We individually identified whales from aerial images based on their callosity patterns,[31] with known ages and birth years for individual whales provided by the Right Whale Consortium.[32] Directly observed entanglements with attached gear, as well as indirect evidence of entanglements (e.g., scarring) have been recorded for NARW since 1980.[9,32] Scarring patterns can provide approximate information about the severity of an entanglement injury (minor, moderate or severe),[33] but it is impossible to establish the duration of an entanglement based on scarring alone. Entanglements with attached gear provide quantitative—although still

Please cite this article in press as: Stewart et al., Decreasing body lengths in North Atlantic right whales, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.04.067

imperfect—information about entanglement duration. We estimated the minimum and maximum duration of entanglements with attached gear based on a whale's sighting records.[33] The minimum duration was calculated as the number of days between the date that a whale was first observed with gear attached and the date that a whale was last observed with gear attached. If a whale was first seen with attached gear on the same day that the gear was removed by a disentanglement team or shed by its next sighting, the minimum duration was recorded as one day. The maximum duration was calculated as the number of days between the most recent date that a whale was observed without attached gear prior to the first observation with attached gear, and the first observation without attached gear after the last observation with attached gear. For example, consider a whale that was seen on February 1st with no attached gear, March 10th with attached gear, May 1st with attached gear, and July 10th with no attached gear. The minimum entanglement duration would be March 10th – May 1st (52 days), and the maximum entanglement duration would be February 1st – July 10th (160 days). To account for the uncertainty in true entanglement duration, we used the midpoint between the minimum and maximum durations as our best estimate of entanglement duration. Growth rates in NARW slow considerably after age 10[7], so we used mid-point entanglement durations for any measured whale in our aerial photogrammetry dataset seen with attached gear during the first 10 years of life to represent a cumulative entanglement burden during early growth. If a length measurement was taken prior to age 10, we used the entanglement duration midpoint prior to that measurement. Entanglement duration was included as a continuous effect on asymptotic length (see model description below).

Maternal size and condition have been demonstrated to substantially impact calf growth rates in several populations of baleen whales, including southern hemisphere right whales.[4,5] This suggests that entanglements of a female with a dependent, nursing calf could affect calf growth if maternal energy stores are lost to excess drag from an entanglement.[34] In our dataset of aerial photogrammetry measurements, we had no records of measured whales whose mothers had an observed entanglement with attached gear while the measured whale was a nursing calf. However, there were three records of measured whales whose mothers were seen with attached gear that first appeared while the measured whale was < 1 year old and likely still nursing and eight records of measured whales whose mother was detected with attached gear or severe injuries that may have occurred when the calf was < 1 year old.[32] For measured whales whose mother had evidence of a severe entanglement injury or attached gear known to or likely to have occurred while the measured whale was nursing, we included a fixed effect of maternal entanglement on asymptotic length.

Lactation is an extremely costly life history event for right whales.[8] The energetic burden of supporting dependent calves could in theory reduce the amount of energy a female whale can devote to its own growth. We therefore considered the number of lactation events that a whale experienced[32] prior to age 10 as a continuous effect on the expected asymptotic length of that whale. If a whale was measured prior to age 10, we considered the number of lactation events experienced prior to measurement, similar to our handling of entanglement durations. For entanglement duration and number of lactation events, we scaled the covariate values associated with each measured whale to 1 by dividing the observed covariate by the maximum covariate value.

QUANTIFICATION AND STATISTICAL ANALYSIS

We based our growth model on the two-phase Gompertz growth function that was fit previously to age and length data for North Atlantic right whales collected between 2000 and 2002:[7]

$$S_t = Ae^{-ce^{-kt}}$$

where S is the expected length at age t, A is asymptotic length, c is the constant of integration, and k is the growth rate. This equation is fit separately in two phases to whales < 1 year old (Phase 1) and > 1 year old (Phase 2). We modified this equation to apply covariate effects to asymptotic length, such that:

$$S_{t,i} = A_i e^{-ce^{-kt}}$$

$$A_i = \widehat{A} + O_i$$

$$O_i = \sum_{j=1}^{n} Cov.Eff_{j,i}$$

$$Cov.Eff_{j,i} \sim N[Cov_{j,i} * \beta_j, \sigma_j]$$

where S is the expected length at age t for individual i, A is expected asymptotic length for individual i, $\widehat{A}$ is the asymptotic length shared across all whales before covariate effects are applied, and O is the asymptotic length offset for individual i. Cov is the covariate j (e.g., birth year, entanglement duration, etc.) experienced by whale i, and β is the model-estimated effect of covariate j. We introduce process error by allowing the estimated covariate effect $Cov.Eff$ to vary around the expected covariate effect with an independently estimated standard deviation σ for each covariate j. O is then calculated by summing the covariate effects $Cov.Eff$ for each

Please cite this article in press as: Stewart et al., Decreasing body lengths in North Atlantic right whales, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.04.067

individual *i.* We chose to apply covariate effects to asymptotic length because growth rate and asymptotic length are typically highly correlated in growth models, making it inappropriate to apply the same covariate to both parameters simultaneously. Whales are expected to have determinate growth due to the fusing of growth plates,[35,36] and we therefore applied covariate effects to asymptotic length rather than growth rate. This was based on the assumption that reduced early growth would lead to a truncated maximum attainable length for an individual, rather than slower growth that could eventually result in a similar maximum length to unaffected whales. In other words, we assume that the length a whale reaches by age 10-15 is likely to be close to the maximum size that whale can achieve. We applied the same model-estimated offset on asymptotic length to both growth phases. Our limited sample size of whales age < 1 (less than 10% of measured whales) contained no whales with attached gear or known maternal entanglements, and all but four measured calves were born in 2001, making the estimation of independent covariate effects for each growth phase impossible.

Previous analyses of NARW growth incorporated lengths from both aerial photogrammetry and necropsies from stranded whales. We excluded necropsied individuals from our analysis because we were investigating potentially small changes in body length as a result of covariate effects. Changes in body length are known to occur in stranded whales that have been towed to shore (stretching), and correction factors for these stretching effects are approximate.[7] As a result, our sample size of whales < 1 year old was smaller than in previous studies, so we applied an informative prior to $\widehat{A}$, *k,* and *c* for both Phase 1 & 2 based on the estimated parameters from the same Gompertz 2-phase growth equation fit using length data from both photogrammetry and necropsies:[7]

$$\widehat{A}_{\mathrm{Phase1}} \sim N[11.93,\ 2.83]$$

$$\widehat{A}_{\mathrm{Phase2}} \sim\ N[13.82, 0.28]$$

$$k_{Phase1} \sim N[2.325,\ 1.25]$$

$$k_{Phase2} \sim N[0.13,\ 0.03]$$

$$C_{Phase1} \sim N[1.017,\ 0.195]$$

$$\mathrm{C}_{\mathrm{Phase2}} \sim\ N[0.33,\ 0.02]$$

where each prior is normally distributed around a mean with standard deviation. This allowed parameter estimates to depart from the provided informative priors if there was sufficient information in the data to estimate a different value, but helped align baseline estimates of growth parameters with previous studies if there were insufficient data to produce a new estimate (see Figure S1 & Table S1).

To account for different aerial photogrammetry platforms that used different methods to calculate aircraft altitude (radar altimeter, GPS altimeter, and laser altimeter), we applied three separate model-estimated error terms to individual observations of length data, such that:

$$s_{t,i} \sim N[S_{t,i}, \sigma_{pt,i}]$$

where *s* is the measured length of individual *i* at age *t*, which is normally distributed around the expected length *S* of individual *i* based on its age *t* and applied covariate effects, with a unique standard deviation σ for each photogrammetry platform *p*, which is applied based on the platform used to measure individual *i* at time *t*.

We constructed and fit these models using the JAGS Bayesian modeling software[37] run via R.[38] We ran three chains, each of 100,000 iterations with a burn-in period of 50,000 iterations and a thinning interval of 50, for a total of 3,000 draws from the posterior distribution. Model convergence was determined based on visual inspection of chains and $\widehat{R}$ values < 1.05, which indicates that an infinite number of iterations would lead to potential reduction of posterior intervals by less than 5%.[39] We considered covariate effects to be significant if 95% of posterior draws for the estimated effect were < 0 for negative effects or > 0 for positive effects. To determine whether the model was specified appropriately, we performed posterior predictive checks on all 202 length measurements in our dataset. We applied the model-estimated covariate effects to the recorded covariates for each whale, and sampled from those mean values using the model-estimated observation error terms specific to the platforms used to image each whale. We then compared observed values to the 95% posterior prediction intervals (Figures S2 and S3).

Current Biology, Volume *31*

Supplemental Information

Decreasing body lengths in North Atlantic right whales

Joshua D. Stewart, John W. Durban, Amy R. Knowlton, Morgan S. Lynn, Holly Fearnbach, Jacob Barbaro, Wayne L. Perryman, Carolyn A. Miller, and Michael J. Moore

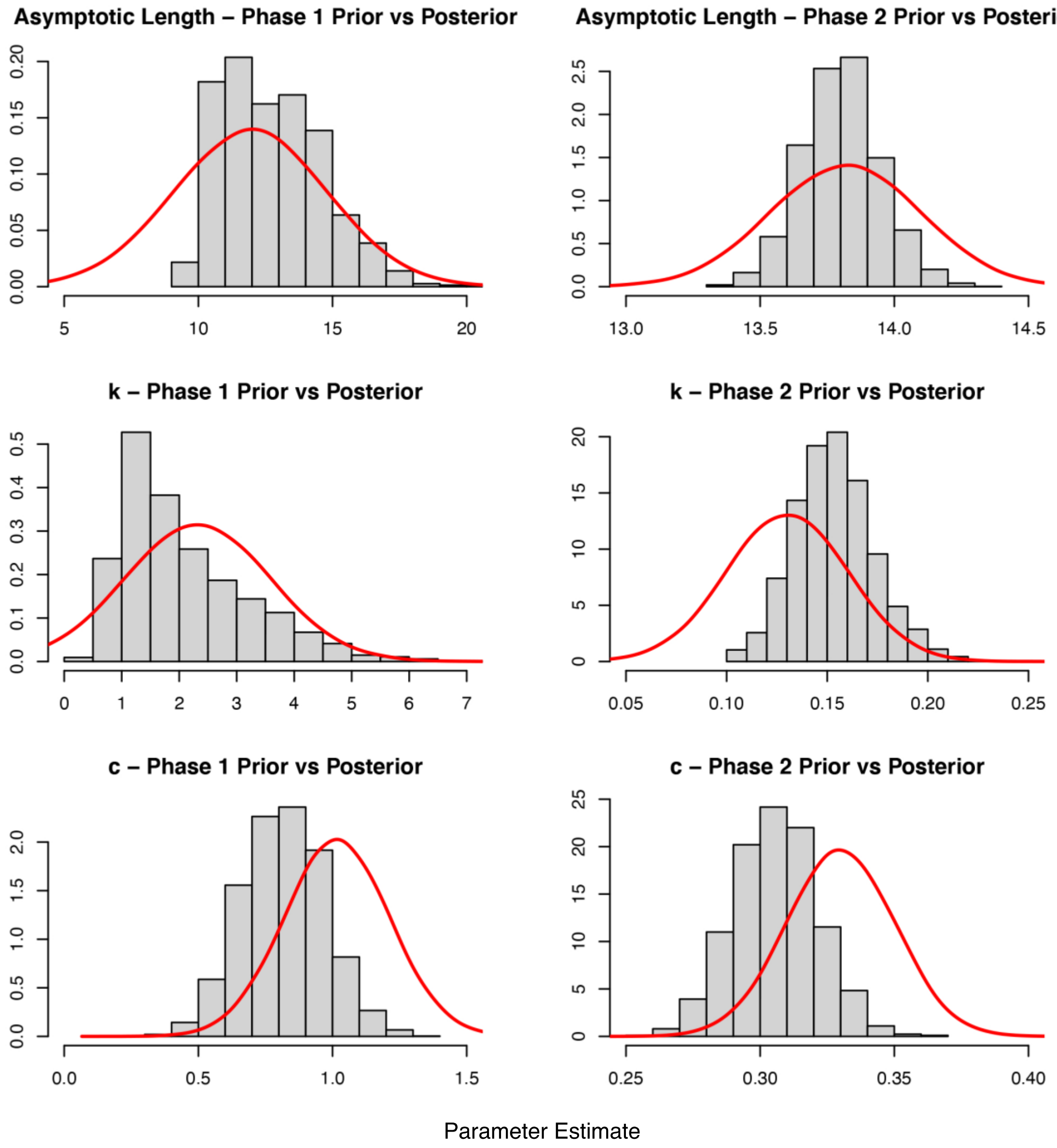


Figure S1. Priors versus posteriors for growth parameters in the Gompertz 2-Phase growth model, **Related to STAR Methods & Figure 2.** Red curves indicate the Bayesian priors used in the model, which are based on previous estimates of these parameters using aerial photogrammetry data from 2000-2002 and necropsy data. Gray histograms indicate the model posterior estimates for each parameter.

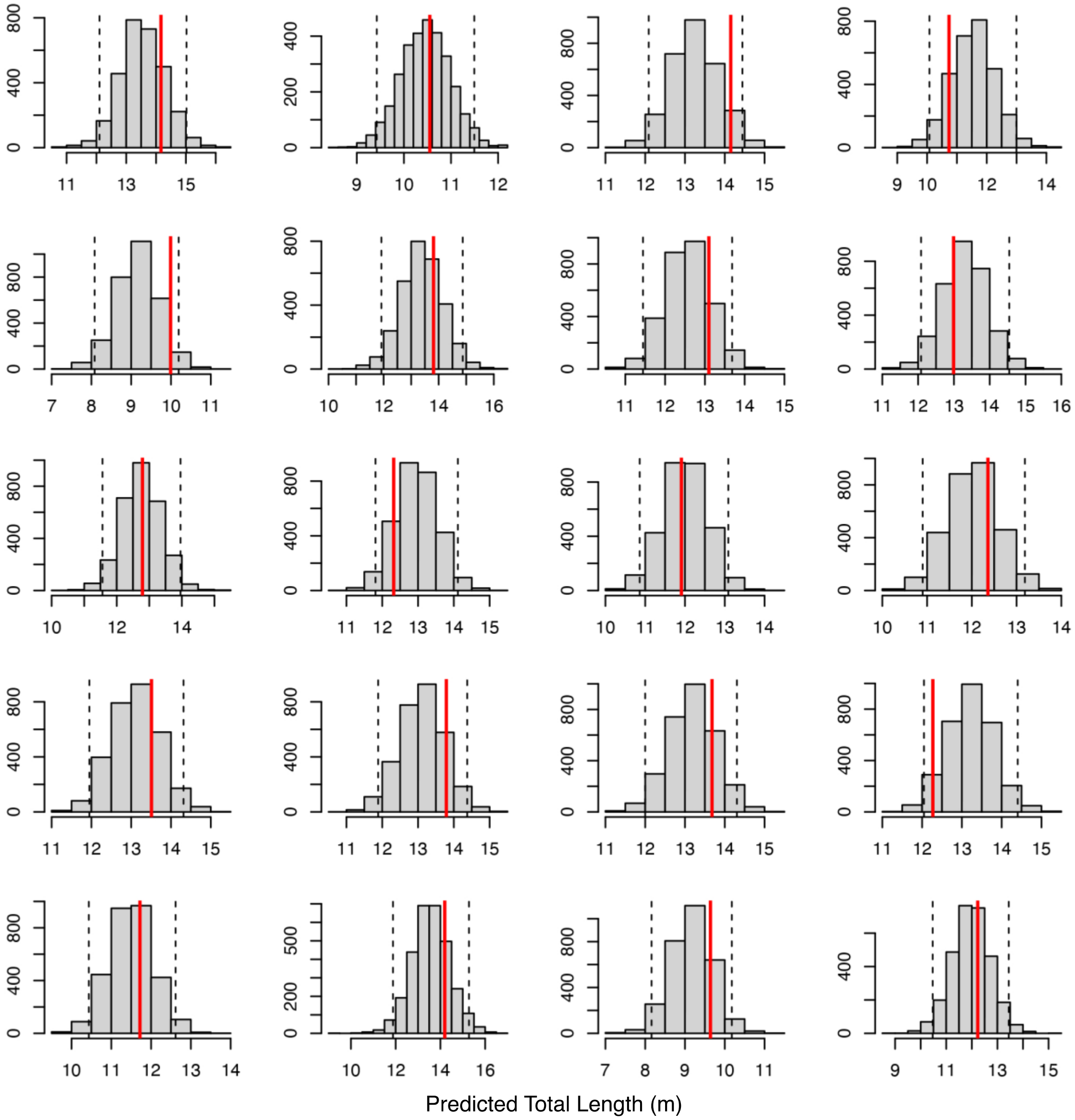


Figure S2. Posterior predictive checks of 20 randomly selected length-at-age observations, Related to STAR Methods & Figure 2. The gray histograms indicate the model-estimated range of predicted lengths for a whale based on its age and observed covariate values (birth year, entanglement history, maternal entanglements, number of lactations). The vertical red line indicates the observed length of that whale, and the vertical dashed lines indicate the 95% prediction intervals. 195 out of 202 observed lengths (96.5%) fell within the 95% posterior prediction intervals based on whales' ages and recorded covariate values.

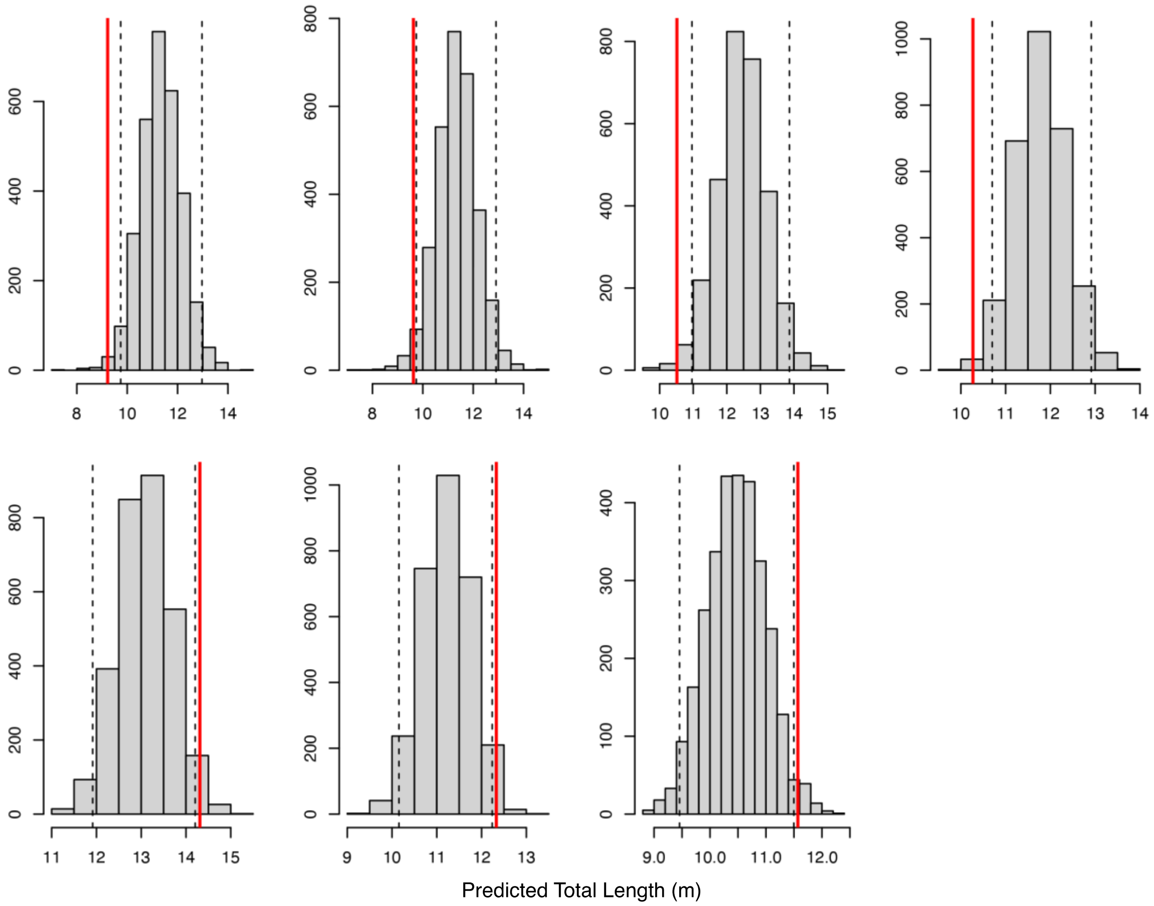


Figure S3. Posterior predictive distributions of seven whales whose observed lengths were outside of the 95% prediction intervals (but within the full posterior prediction distributions), Related to STAR Methods & Figure 2. Whales in the top row were born between 1996 and 2011 (whale IDs 2601, 3617, 4130 & 4140), and whales in the bottom row were born between 1987 and 2001 (whale IDs 1706, 2709 & 3110). The gray histograms indicate the model-estimated range of predicted lengths for a whale based on its age and observed covariate values (birth year, entanglement history, maternal entanglements, number of lactations). The vertical red line indicates the observed length of that whale, and the vertical dashed lines indicate the 95% prediction intervals. None of these seven whales had recorded attached-gear entanglements, maternal entanglements, or lactation events prior to age 10.

Parameter	**Phase 1 Estimate (95% CI)**	**Phase 2 Estimate (95% CI)**
$\hat{A}$	12.55 (10.04 – 16.78)	13.80 (13.52 – 14.10)
k	1.77 (0.71 – 4.80)	0.15 (0.12 – 0.20)
c	0.82 (0.53 – 1.13)	0.31 (0.28 – 0.34)

Table S1. Posterior estimates of growth curve parameters for the Gompertz 2-Phase growth model, Related to STAR Methods & Figure 2. Values are median estimates with 95% Bayesian credible intervals in parentheses. Note that $\boldsymbol{\hat{A}}$ is the baseline asymptotic length, before covariate effects are applied.

Body growth of North Atlantic right whales (Eubalaena glacialis) revisited

Article *in* Marine Mammal Science · October 2020

DOI: 10.1111/mms.12753

4 authors, including:

Sarah M E Fortune
Fisheries and Oceans Canada
17 PUBLICATIONS **94** CITATIONS
SEE PROFILE

Wayne Perryman
National Oceanic and Atmospheric Administration
59 PUBLICATIONS **1,772** CITATIONS
SEE PROFILE

Andrew W. Trites
University of British Columbia - Vancouver
309 PUBLICATIONS **9,719** CITATIONS
SEE PROFILE

Received: 24 June 2020 | Accepted: 5 September 2020
DOI: 10.1111/mms.12753

ARTICLE

Marine Mammal Science

Body growth of North Atlantic right whales (*Eubalaena glacialis*) revisited

Sarah M. E. Fortune[1,2] | **Michael J. Moore**[3] | **Wayne L. Perryman**[4] | **Andrew W. Trites**[1]

[1]Marine Mammal Research Unit, Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, British Columbia, Canada

[2]Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, Manitoba, Canada

[3]Biology Department, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts

[4]Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, California

Correspondence
Sarah Fortune, Freshwater Institute, Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, Manitoba R3T 2N6, Canada.
Email: sarahmefortune@gmail.com

Abstract

Knowing size-at-age is important for determining food requirements and making inferences about the nutritional status of individuals and their populations. Accurate growth curves are also needed to quantify drug dosages to treat wounded or entangled animals. However, body sizes are often based on small numbers of measured animals that must be improved as new data become available. We updated an existing body growth model for North Atlantic right whales (NARWs) using new data from dead animals and from older individuals. Our models indicate that NARWs attain mean lengths and weights of 4.3 m and 1.0 mt at birth, and 13.1 m and 31.7 mt when sexually mature. Calves more than double their length and attain nearly three-quarters of their asymptotic adult size during their first year of life. Overall, our length estimates agreed well with previous estimates, but our mass-at-age values were considerably higher. These differences revealed that necropsy data used alone in allometric models underestimate mass due possibly to several of the stranded animals in the database having been chronically entangled and in poor body condition. Augmenting the database with healthier individuals, such as harvested North Pacific right whales, yielded mass predictions that reflect both healthy and unhealthy individuals.

KEYWORDS
body size, *Eubalaena glacialis*, growth models, length, mass, morphometry, photogrammetry

1 | INTRODUCTION

Body size is related to sexual maturity, longevity, reproductive strategies, metabolic needs, and abundance, and is arguably the most important trait of individual animals (Kenagy & Trombulak, 1986; Laws, 1956; Speakman, 2005; White, Ernest, Kerkhoff, & Enquist, 2007). Because body mass is largely linked to age at sexual maturity, fast growing species reach maturity sooner than slower growing species. Such is the case for cetacean species that are expected to attain sexual maturity after reaching ~85% of their maximum length (Laws, 1956). Rates of body growth thus influence reproductive output and population dynamics, while body mass affects metabolic rates, energy expenditure, and food requirements (Brodie, 1975). Overall, body size is important when it comes to several aspects of the biology, ecology, and management of species.

Growth curves for North Atlantic right whales (*Eubalaena glacialis*) have been derived from small numbers of opportunistic measurements of dead animals collected by different institutions and individuals over many years (Moore, Knowlton, Kraus, McLellan, & Bonde, 2004; Sharp et al., 2019). This database has evolved and grown with time as errors were corrected and new information became available. Given the importance of having accurate growth curves to determine food requirements and make inferences about the reproductive and nutritional status of populations, or to set drug dosages of sedatives and antibiotics to treat injured whales (Barratclough et al., 2014; Moore et al., 2010), it is important to periodically review the existing morphometric database and update the published growth curves as necessary.

The most recent growth curve for North Atlantic right whales was published in 2012 (Fortune et al., 2012) using measures of length and mass from necropsied animals (Moore et al., 2004), and photogrammetric measurements from live animals (Perryman & Lynn, 2002). Since then, new body size data were added to the database (including animals >22 years old, the upper limit for the previous growth curve), and some of the morphometric measurements included in the North Atlantic Right Whale Consortium Necropsy Database were removed when discovered to have had been estimated rather than measured (North Atlantic Right Whale Consortium, 2018). As a result of these shortcomings, the existing body growth curves for North Atlantic right whales need to be corrected and updated.

Our goal was to use recently acquired data to improve the existing growth models for right whales and generate more robust estimates of body size at age to allow better predications of food requirements to be made, as well as drug dosages to be determined. We also sought to better understand the rapid growth of nursing calves and decelerated growth of juveniles and adults.

2 | MATERIALS AND METHODS

2.1 | Length

We modeled the relationship between length and age for North Atlantic right whales using data obtained during necropsies (lengths were measured directly from dead animals) and from photogrammetry (lengths were obtained from photographs of live animals at-sea). Photogrammetric measurements (*n* = 133) were taken from 94 unique individuals in the Bay of Fundy between 2000 and 2002 as described by Fortune et al. (2012). Aerial images of individual right whales were collected from a Twin Otter aircraft equipped with a KA-76A United States military reconnaissance camera that was mounted over an 18-in. camera port located in the hull of the aircraft. The majority of the photogrammetric data were obtained using a fixed focal length 126-mm lens with Kodak Aerial Ektachrome film. The aircraft altitude and ground speed of the aircraft were used to determine the camera cycle rate, whereby adjacent frames overlapped by 60%–80%. The goal of the rapid cycle rate was to permit each whale to be photographed on 3–4 frames during a single photo pass. For each image taken, location (global positioning system) and altitude (radar altimeter) data were simultaneously recorded. Prior to each field season, the radar altimeter bias was determined by collecting a series of images of a floating target of known size and conducting a regression analysis. The altimeter bias was subsequently used to correct the altitude for each image used for photogrammetric measurements (Perryman & Lynn, 2002).

Body lengths were measured during necropsies of 29 known-age individuals between 1970 and 2017 and represented the straight-line distance from the snout to the fluke notch. The straight-line distance was determined by laying a measuring tape parallel to the animal on the ground and measuring the distance from the tip of the rostrum to the fluke notch. Measurement errors can be attributed to the many individuals who took these body length measurements, as well as the difficulty associated with placing the tape measure at the precise location that is perpendicular to the snout tip and fluke notch. Body lengths of necropsied individuals that were mechanically hauled onto the beach prior to measurement were corrected for potential stretching (~9% body length; George, Zeh, Suydam, & Clarkm, 2004).

Age classes of all measured animals were determined for individual whales by matching photographs of their unique callosity patterns (Kraus et al., 1986) using the North Atlantic Right Whale Consortium Identification Database (North Atlantic Right Whale Consortium, 2018). We also estimated the ages of individuals (in decimal years) based on when they stranded or were photogrammetrically measured, and their estimated median date of birth of January 5 (Fortune et al., 2012). Detailed descriptions of how ages were estimated, and how necropsies and aerial photogrammetry were conducted are contained in Fortune et al., (2012).

2.2 | Growth curves

We fit four standard growth functions to the length-at-age data, including the Putter (Equation 1; von Bertalanffy, 1938; Ricker, 1979), von Bertalanffy (Equation 2; von Bertalanffy, 1938; Ricker, 1979), Gompertz (Equation 3; Gompertz, 1825; Zach, Liner, Rigby, & Mayoh, 1984), and logistic equation (Equation 4; Ricker, 1979):

$$S_t = A\left(1 - e^{-k(t-t_0)}\right) \tag{1}$$

$$S_t = A\left(1 - e^{-k(t-t_0)}\right)^3 \tag{2}$$

$$S_t = Ae^{-ce^{-kt}} \tag{3}$$

$$S_t = \frac{A}{1 + e^{-k(t-t_0)}} \tag{4}$$

where S is length at age t for males and females, A is asymptotic size, t_0 is time at which size is theoretically zero, c is the constant of integration (Zach et al., 1984) and k is indicative of growth rate (Ricker, 1979).

We fit length-at-age models as per Fortune et al. (2012) in a 2-phased approach with nonlinear least squares regression. We fit standard growth functions to length-at-age data for individuals aged 0–1.65 years (*Phase 1*) and older animals aged 1.65–30.5 years (*Phase 2*). We used the statistical program R (nls package; R Development Core Team, 2016) for analysis. *Phase 1* represented rapid calf growth and *Phase 2* represented decelerated growth of juveniles and adults. The inflection point between models was determined based on the age where the difference between predicted lengths of *Phase 1* and *2* models was equal to zero. Model selection was made by observing the Akaike information criterion (AIC) and selecting the model with the lowest AIC and greatest weight. Since some photogrammetrically measured animals were seen in more than 1 year and were measured as many as three times, we created (i.e., bootstrapped) 10,000 data sets from the 162 measurements by randomly selecting duplicate length measurements to be removed. Resampling was done to avoid issues related to nonindependence of observations whereby one length-at-age measurement per individual per model simulation was selected randomly. Growth curves were fit to the bootstrapped samples and mean model parameters were extrapolated from the bootstrap replicates to define the "best model." Confidence intervals (95%) were subsequently calculated by ordering bootstrap replicates into the 2.5% and 97.5% quartiles.

We used a linear mixed-effects model and a repeated-measures analysis of variance (ANOVA) to test for sexual dimorphism through comparison of mean length-at-age measurements for adult (9–30 years) male and female right whales. This analysis accounted for violations of independence by including animal ID as a random factor as there were duplicate length measurements for photogrammetrically measured individuals.

2.3 | Mass

Mass-at-age was derived from the allometric relationship of length and mass determined from 13 dead whales (North Atlantic Right Whale Consortium, 2018; Moore et al., 2004; Sharp et al., 2019) as described by Fortune et al. (2012). We linearized Schultz's (1938) allometric model:

$$W = aL^b \tag{5}$$

to predict mass based from body length:

$$\log_{10}W = b\log_{10}L + \log_{10}a \tag{6}$$

where W is mass in kilograms, L is length in centimeters, a is a constant factor, and b is an exponential constant. We tested the significance of coefficients using a two-tailed Student's t-test (Zar, 1996). Model uncertainty was incorporated by bootstrapping the allometric model 10,000 times to generate a distribution of predicted masses for given lengths. We also compared the relationship derived for North Atlantic right whales to that derived for 16 North Pacific right whales (*Eubalaena japonica*) (Omura, Oshumi, Nemoto, Nasu, & Kasuya, 1969).

3 | RESULTS AND DISCUSSION

3.1 | Length

The 2-phased Gompertz model best described the growth of North Atlantic right whales (Figure 1, Table 1), although the von Bertalanffy and Putter models presented similar AIC scores and weights suggesting that right whale growth may be adequately described using several growth functions (Anderson, 2008). We nevertheless selected the model with the lowest AIC and greatest weight. Furthermore, we biologically justified using the Gompertz model over the von Bertalanffy model because the Gompertz equation accounted for somatic and reproductive development, while the von Bertalanffy model only accounted for somatic growth (Neuenhoff, Cowan, Whitehead, & Marshall, 2011).

To find a point of inflection where the multiphase growth curves met, we fit two Gompertz growth models to data for younger (0–1.65 years) and older (1.65–30.5 years) animals. Morphometric data were only available for one individual between 0.65 and 1.65 years (1.27 years). We found that the inflection point occurred at 0.79 years and that the average age of individuals used to fit the *Phase 1* was 0.78 ± 0.62 *SD* and 9.70 ± 6.68 *SD* years for *Phase 2* (Figure 1).

The Gompertz growth functions were fit in a two-phased approach whereby *Phase 1* included animals between 0 and 1.65 years and *Phase 2* included whales between 1.27 and 30.5 years and bootstrapping was used to account for model uncertainty. We found that the point of inflection (i.e., where the two-phased growth curves met) occurred at 0.79 years. Since we did not have morphometric data for animals >0.65 and ≤ 1.26 years (*Phase 1*)

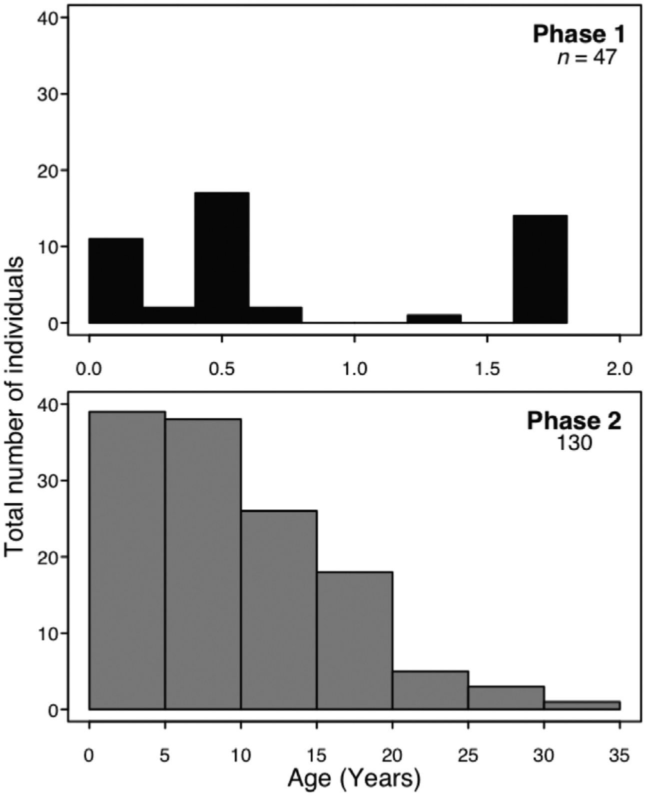


FIGURE 1 Distribution of ages for the morphometric measurements used to generate multiphase length-at-age growth curves for North Atlantic right whales calves (*Phase 1* model fit to data spanning birth to 1.65 years) and juveniles and adults (*Phase 2* fit to data >1.28 years). To ensure both models intersected, some of the same measurements for young juveniles were used to fit both phases of the model. After finding the inflection point at 0.79 years, the models were truncated whereby *Phase 1* included animals between 0 and 0.79 years and *Phase 2* included whales between 0.80 and 30.5 years.

and > 0.79 and < 1.27 years (*Phase 2*) length-at-age predictions for these age ranges using the Gompertz equation should be interpreted with caution. Mean (± *SD*) Gompertz model parameters (from 10,000 bootstrap replicates) were: 1,067.19 ± 19.67 for *A*, 0.93 ± 0.08 for *c*, and – 3.11 ± 0.28 for *k* for *Phase 1*; and 1,362.75 ± 22.88 for *A*, 0.37 ± 0.03 for *c*, and – 0.18 ± 0.03 for *k* for *Phase 2*. The average age of individuals used to fit the *Phase 1* was 0.78 ± 0.62 *SD* and 9.70 ± 6.70 *SD* years for *Phase 2* (Figure 1).

The rapid growth of calves occurred between ages 0 and 0.79 years (*Phase 1*; Figure 2; 288.35 days), and the decelerated growth of older animals occurred from 0.80 to 30 years old (*Phase 2*; Figure 2). Calves were estimated to gain an average of 559 cm (± 43 *SD*) from birth to near weaning (0.79 years), representing 1.94 cm per day (± 0.15) if a constant growth rate is assumed.

Right whales attained 90% of their maximum body length (1,362 cm) at 8 years of age—which is about when females become sexually mature (assuming age at first parturition is 9 years and pregnancy lasts ~12 months; Hamilton, Knowlton, Marx, & Kraus, 1998). Sexual dimorphism appears to occur near sexual maturity based on the measured sizes of males and females between 8.0 and 8.9 years (females measured 1,309 cm ± 0.177 *SD*, *n* = 2, on average and males measured 1,197 cm ± 0.183 *SD*, *n* = 4).

Predicted asymptotic length (~95% of maximum length) occurred at 12 years, which follows findings from previous studies (Fortune et al., 2012). Thus, calves were estimated to more than double their length and to attain almost three-quarters of the asymptotic adult length at 1 year old (when weaning is assumed to occur).

Including sex as a fixed factor yielded a better linear mixed-effects model than a null model that did not distinguish between the body length of adult males and females (Log Likelihood ratio test LRT = 9.7, *p* = .002). Slopes (repeated-measures ANOVA, *F*(1,41) = 10.5, *p* = .002) and intercepts (repeated-measures ANOVA, *F* (1,41) = 22,356.3, *p* < .0001) of the model for adult males and females (≥9 years old) differed significantly from one

TABLE 1 Parameter estimates (A, k, c, t_0) (± *SE*) for the 2-phased growth models (Putter, von Bertalanffy, Gompertz, and logistic; Equations 1–4) for North Atlantic right whales (see "Materials and Methods" for model parameters description), where A is asymptotic size, k is indicative of growth rate, c is the constant of integration, and t_0 is time at which size is zero. Length measurements are in centimeters and age is in decimal years. AIC values are shown along with the difference in AIC values between fitted models, the likelihood of each model, and the weight of each model (i.e., the weight of evidence in favor of each model). The model with the greatest AIC weight was considered to be the "best" model.

Model	A	k	c	t_0	AIC values	AIC differences	Likelihoods	AIC weights
Phase 1 (0–0.79 years)								
Putter	1,079.037 ± 23.676	0.613 ± 0.025	—	2.336 ± 0.281	540.658	1.748	0.417	0.187
von Bertalanffy	1,071.000 ± 21.260	0.267 ± 0.015	—	2.824 ± 0.301	539.324	0.414	0.813	0.364
Gompertz	1,067.353 ± 20.479	0.923 ± 0.058	−3.075 ± 0.315	—	538.910	0.000	1.000	0.448
Logistic	1,039.574 ± 22.351	—	—	3.328 ± 0.424	551.5023	12.593	0.002	0.001
Phase 2 (0.80–30 years)								
Putter	1,365.000 ± 21.120	0.311 ± 0.017	—	0.149 ± 0.025	1,471.243	0.307	0.858	0.305
von Bertalanffy	1,362.000 ± 20.000	0.114 ± 0.007	—	0.160 ± 0.026	1,471.031	0.095	0.954	0.339
Gompertz	1,360.675 ± 19.501	0.361 ± 0.023	−0.166 ± 0.026	—	1,470.936	0.000	1.000	0.356
Logistic	1,285.664 ± 10.285	—	—	0.639 ± 0.046	1,540.582	69.646	0.000	0.000

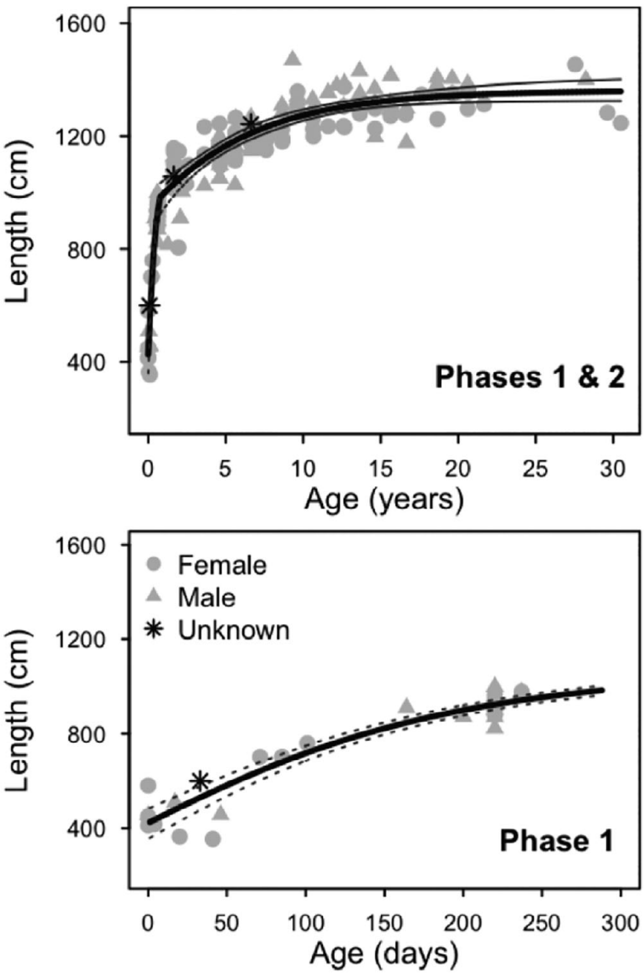


FIGURE 2 Mean 2-phase (*Phase 1* and *2*) and 1-phase Gompertz growth curves for North Atlantic right whales. The 95% confidence intervals (dashed lines) were derived from 10,000 bootstrap replicates. Length-at-age can be calculated using the equations provided in the upper graph with age expressed in years. *Phase 1* includes growth from birth to 0.79 years old, and *Phase 2* describes growth for right whales >0.79 years old. The multiphase Gompertz growth equations based on mean model parameters as determined by bootstrapping were *Phase 1* length = 1,067.35 * exp[−0.923 * exp (−3.08 * Age]) and *Phase 2* length = 1,360.68 * exp[−0.36 * exp (−0.16 * Age)].

another. This was consistent with sexual dimorphism, with adult females (1,345.7 cm ± 61.2 *SD*) being 4% larger on average than adult males (1,291.9 cm ± 56.1 *SD*) (Figure 3).

3.2 | Mass

In terms of body mass, our models show that North Atlantic right whales gain considerable mass during their first year of life, with calves growing an average of ~42 kg/day and weighing over 13 mt after 0.79 years (based on the mean birth mass of 1,022 ± 252 kg and mean inflection mass of 13,206 ± 747 kg; Table 2). Calves near the onset of independence (9.6 months) were 13 times heavier than their birth mass and had attained 47% of the mass of a sexually mature animal. However, this rate of increase in body mass dropped significantly between weaning (~1 year) and sexual maturity (9 years), i.e., ~4.9 kg/day. Mean body mass was an estimated 13.7 mt at weaning, and 28.2 mt when mature.

The mass-to-length relationship did not differ significantly between North Atlantic and North Pacific right whales (two-tailed *t*-test, $t(27) = 2.05$, $p > .05$), although the harvested North Pacific right whales were likely older and bigger animals compared to the North Atlantic right whales in the analyses (Figure 4, Table 3). We found that mass-at-age estimates differed considerably depending on which allometric model was used. For example, mass-at-

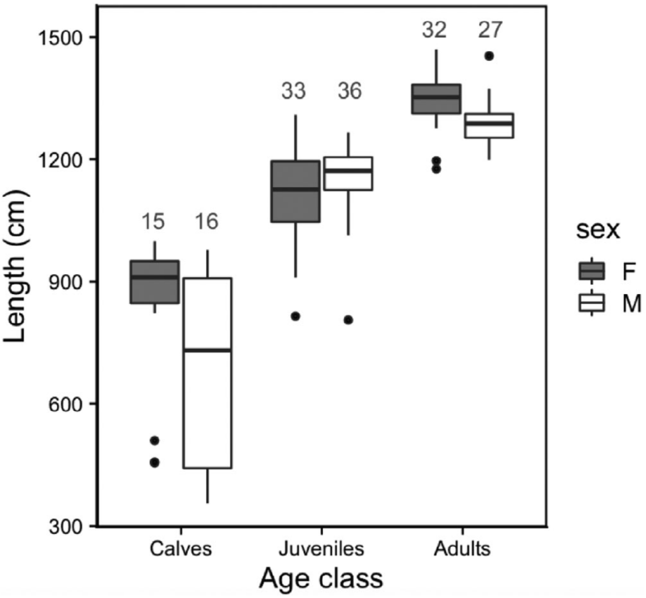


FIGURE 3 Body length (cm) for necropsied and photogrammetrically measured male and female North Atlantic right whales by age class (calves ≤1 year; juveniles >1 and < 9 years; adults ≥9 years). The horizontal black bar represents the medians, the interquartile range is represented by the box, the whiskers indicate nonextreme maximum and minimum values, and outliers are represented by black dots.

age estimates were lower when using an allometric model constructed for North Atlantic right whale necropsy data alone compared to the model that included North Pacific right whale whaling data (Figure 5). Additionally, we found that by increasing the sample size to include North Pacific right whales and adding larger and likely older animals to the data set, we reduced model uncertainty (i.e., smaller 95% confidence limits). Consequently, it appears that including North Pacific right whales results in body mass predictions that are more precise and better represent healthy individuals.

Comparing our new estimates with previous studies (Fortune et al., 2012) shows similar body lengths-at-age whereby updated lengths are 4.6% ± 9.47 *SD* lower than previous estimates on average. However, mass-at-age estimates differ considerably such that updated weights are 12.8% ± 6.03% *SD* heavier on average compared to our earlier predictions. This notable difference in predicted mean body mass is due to excluding masses that were estimated rather than weighed from the North Atlantic right whale necropsy database, the addition of new animals weighed since 2012 and the inclusion of North Pacific right whales that were presumably healthy at their time of death.

In the previous study (Fortune et al., 2012), a significant difference between allometric models for North Pacific and North Atlantic right whales led us to only use North Atlantic right whale weights to predict the age-specific weights of North Atlantic right whales. However, our new allometric model for North Atlantic right whales derived from additional morphometric data (and the removal of estimated weights from the database) did not differ significantly from the North Pacific allometric model. Further support for combining morphometric data from the two species of right whales comes from a recent photogrammetric study that found genetically related *Eubalaena* species share a similar morphology (Christiansen et al., 2020). We consequently combined both data sets into a single model that encompassed a much broader range of ages and sizes of right whales. This new model, built with a more inclusive data set of right whale body sizes and ages, yields estimates that better reflect body weights of healthy right whales.

A second notable difference between our previous and revised growth models for North Atlantic right whales is the placement of the inflection point between *Phase 1* and *Phase 2* growth. Our revised model indicates that it occurs earlier (0.79 years) than we previously estimated (1.05 years), i.e., at 9.6 months rather than at 13 months of age. These differences in length-at-age estimates reflect inclusion of the new data from older animals in our analysis.

TABLE 2 Predicted mean mass and length measurements (± *SD*) for North Atlantic right whales. Daily growth rates in length (cm/day) and mass (kg/day) were calculated using mean model predictions for length-at-age and mass-at-age. Mean allometric model coefficients for *Phase 1* growth were $a = -5.091821 \pm 0.2578327$ and $b = 3.077823 \pm 0.08325852$. Mean parameter estimates for *Phase 2* growth were $a = -5.096379 \pm 0.2592405$ and $b = 3.079408 \pm 0.08360103$.

Age (years)	Mass (kg)	Mass growth (kg/day)	Length (cm)	Length growth (cm/day)
0	1,022 ± 252	0.00	426 ± 33	0.00
0.25	4,553 ± 444	38.70	695 ± 17	2.95
0.5	9,220 ± 594	51.15	875 ± 11	1.97
0.75	12,771 ± 724	38.92	973 ± 10	1.07
0.79	13,206 ± 747	29.79	989 ± 27	1.10
1	13,737 ± 1,270	6.93	996 ± 26	0.25
2	16,026 ± 1,122	6.27	1,048 ± 18	0.14
3	18,236 ± 1,063	6.05	1,093 ± 14	0.12
4	20,319 ± 1,087	5.71	1,132 ± 12	0.11
5	22,244 ± 1,156	5.27	1,167 ± 11	0.10
6	23,994 ± 1,234	4.79	1,194 ± 11	0.08
7	25,564 ± 1,302	4.30	1,218 ± 11	0.07
8	26,959 ± 1,354	3.82	1,239 ± 11	0.05
9	28,187 ± 1,392	3.36	1,256 ± 10	0.05
10	29,262 ± 1,421	2.95	1,272 ± 10	0.04
11	30,197 ± 1,445	2.56	1,285 ± 9	0.04
12	31,007 ± 1,470	2.22	1,296 ± 9	0.03
13	31,707 ± 1,497	1.92	1,306 ± 9	0.03
14	32,310 ± 1,530	1.65	1,315 ± 9	0.02
15	32,829 ± 1,568	1.42	1,322 ± 9	0.02
16	33,274 ± 1,611	1.22	1,328 ± 10	0.02
17	33,656 ± 1,657	1.05	1,333 ± 10	0.01
18	33,983 ± 1,706	0.90	1,338 ± 11	0.01
19	34,263 ± 1,757	0.77	1,342 ± 12	0.01
20	34,504 ± 1,807	0.66	1,345 ± 13	0.01
21	34,709 ± 1,857	0.56	1,348 ± 14	0.01
22	34,885 ± 1,905	0.48	1,351 ± 15	0.01
23	35,036 ± 1,951	0.41	1,353 ± 15	0.01
24	35,166 ± 1,994	0.36	1,355 ± 16	0.01
25	35,277 ± 2,035	0.30	1,357 ± 17	0.01
26	35,372 ± 2,073	0.26	1,358 ± 17	0.00
27	35,453 ± 2,109	0.22	1,359 ± 18	0.00
28	35,523 ± 2,141	0.19	1,360 ± 19	0.00
29	35,584 ± 2,171	0.17	1,361 ± 19	0.00
30	35,635 ± 2,198	0.14	1,362 ± 20	0.00

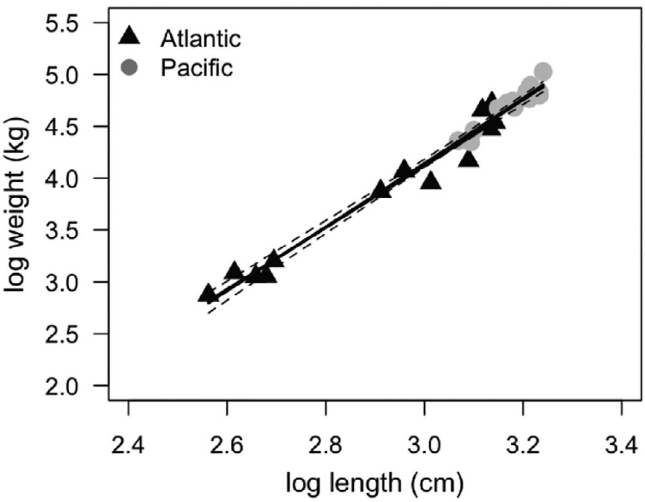


FIGURE 4 Mass-length relationships for North Atlantic (▲) and North Pacific (●) right whales (*Eubalaena glacialis* and *E. japonica*). A linear regression was fit to the log-transformed data for both species: $r^2 = 0.98$, $p < .001$. Fitted parameters for North Atlantic and North Pacific right whales ($a = 0.000008634158$, $b = 3.06$) were used to model mass-at-age.

3.3 | Biological implications of new growth curves

Our updated growth models indicate that right whales are considerably larger in mass than previously recognized, which means that previously estimated energy requirements have been underestimated for some age-classes on a mass-specific basis. More specifically, sexually mature right whales require more energy per unit body mass than previously thought because their estimated body mass exceeds the upper limits of previous estimates (Fortune et al., 2012). However, the predicted mass of calves and juveniles compare favorably to previous estimates and are within the reported uncertainty. For example, the predicted weights of sexually immature whales (0–8 years) were 8.67% (± 6.91 *SD*) heavier on average than previous estimates. Conversely, sexually mature animals (9–22 years) were 16.3% (± 0.73 *SD*) heavier on average.

Our body mass estimates are also higher than what others have predicted using three-dimensional volumetrics (Christiansen et al., 2019, 2020). For example, Christiansen et al. (2019, 2020) predicted that North Atlantic right whales weighed 940 kg at birth (8% lower than our mean model predictions, but within the 95% CIs). They also predicted that right whales weigh 7,830 kg when weaned, which is 15% lower than our model predictions and outside the 95% CIs (based on a body length of 8.8 m). They further predicted that right whales weigh 20,680 kg at sexual maturity (27% lower than our model predictions and outside the 95% CIs based on the assumption that right whales attain sexual maturity at 9 years of age). Reconciling these differences in predicted mass is challenging because live animals cannot be weighed to validate model predictions and dead animals often include few mature animals and many animals in poor health.

Informative comparisons can be made between model predictions and morphometric measurements obtained from necropsies. For example, our model predictions were just 3% heavier than the weight of a recently born calf (Case number 80; Table 3) that weighed 1,586 kg and measured 495 cm in body length. Another necropsied calf measuring 910 cm weighed 11,772 kg, which was 15% heavier than our mean model predictions (9,984.7 kg), but within the 95% confidence limits. Lastly, an animal approaching sexual maturity measuring 12.29 m and weighing 14,785 kg was considerably underweight compared to our model predictions (24,535 kg). However, this animal was entangled and considerably emaciated at the time of measurement.

Although it is unknown how much weight chronically entangled whales may lose, substantial decreases in blubber thickness have been documented (van der Hoop, Corkeron, & Moore, 2017). Lactating North Atlantic right whale mothers, for example, are believed to lose 25% of their total body weight during the lactation period (Christiansen et al., 2018). As such, the differences between predicted and observed weight values (40% difference in mass) may

TABLE 3 North Atlantic right whale necropsy and Pacific right whale whaling data used in allometric mass models. One animal (No. 27) was weighed without baleen, and others (No. 34, 44, and 49) were weighed in parts and had 6.8% added to their measured mass estimates to account for fluid loss. A fourth animal (No. 45) was likely underweight relative to its body length, and as was entangled in fishing gear, appeared thin to emaciated and was weighed without baleen. Similarly, animals 32 and 120 were also entangled at the time of death and were in poor nutritive condition. Animal No. 80 was also emaciated at the time of necropsy, likely due to the inability to obtain sufficient energy as a nursing calf. Note that the previous analysis (Moore et al., 2007) included body masses for Case No. 28, 29, and 40, which were estimated rather than measured. Furthermore, body masses of Case No. 34, 21, and 32 were corrected after verifying necropsy reports, and Case No. 106, 120, and 139 are new animals that were added to our analysis.

Species	Sex	Length (cm)	Weight (kg)	Case No.	Field ID/EgNo
Atlantic	M	412	1,225	21	MH89-424-Eg
Atlantic	F	1,360	29,700	27	EgNo 1223
Atlantic	M	1,030	9,035	32	EgNo 2366*
Atlantic	F	478	1,136	34	Eg_Jan_02_96 calf
Atlantic	F	455	1,130	42	RKB-1451
Atlantic	F	1,370	52,804	44	EgNo 1014
Atlantic	F	1,229	14,785	45	EgNo2030*
Atlantic	F	910	11,772	49	NY-2680-2001
Atlantic	M	365	749	73	EgNEFL0704
Atlantic	M	495	1,586	80	KLC 022 Eg**
Atlantic	F	1,390	34,600	106	EgNo 2320
Atlantic	F	1,310	45,359	120	MME-16-249Eg*
Atlantic	F	815	7,481	139	IFAW17-182Eg
Pacific	M	1,470	52,870	NA	NA
Pacific	M	1,510	55,250	NA	NA
Pacific	M	1,520	48,250	NA	NA
Pacific	M	1,610	67,770	NA	NA
Pacific	M	1,640	78,500	NA	NA
Pacific	M	1,700	65,760	NA	NA
Pacific	M	1,710	67,240	NA	NA
Pacific	M	1,240	22,250	NA	NA
Pacific	M	1,710	63,490	NA	NA
Pacific	F	1,170	22,870	NA	NA
Pacific	F	1,630	58,590	NA	NA
Pacific	F	1,660	63,130	NA	NA
Pacific	F	1,710	63,490	NA	NA
Pacific	F	1,740	106,500	NA	NA
Pacific	F	1,260	28,920	NA	NA
Pacific	M	1,410	47,560	NA	NA

Note: For reference purposes, animal FieldID/EgNo marked with one asterisk (*) denote animals that were entangled and underweight and animals with two asterisks (**) were not entangled but were underweight at the time of death presumably due to issues with energy acquisition while nursing.

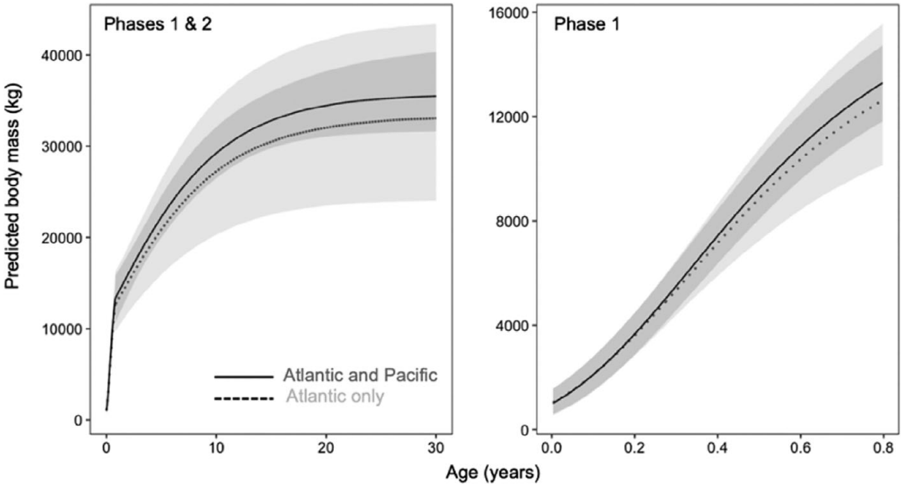


FIGURE 5 Predicted body mass (kg) at age (years) for North Atlantic right whales using the bootstrapped multiphase Gompertz length-at-age predictions (*n* = 10,000 replicates) and an allometric mass-at-length model that was constructed using (1) North Atlantic right whale necropsy (Atlantic only) data and (2) North Pacific right whale whaling data and North Atlantic right whale data (Atlantic and Pacific). We bootstrapped the model to generate 10,000 predictions of mass-at-age and sorted the predicted values into 95% quartiles by ordering the bootstrap replicates of mass-at-age into 2.5% and 97.5% quartiles. The light gray shaded region represents the 95% confidence limits for the Atlantic only model and the smaller, dark gray region reflects the confidence limits for the Atlantic and Pacific model.

be attributed to compromised body condition caused by lactation, reduced feeding efficiency, and increased energetic costs associated with being entangled (van der Hoop et al., 2017), and may provide insight into the extreme physiological consequences of chronic entanglement.

The comparatively low predicted body weights previously estimated for mature North Atlantic right whales were likely due to biases in the source data used to establish the earlier allometric relationship between body length and mass. Several of these data came from underweight North Atlantic right whales that were emaciated and in poor overall health due to entanglement in fishing gear (Sharp et al., 2019). Supplementing this database with lengths and weights of North Pacific right whales recorded during commercial whaling provided a more comprehensive set of measurements of healthy-sized individuals.

Bigger body sizes require more energy for growth and maintenance of mass. In our case, our revised growth model has little consequence for the energy needs of young animals (e.g., predicted mean mass gains were 33.9 kg/day for previous models and are 34.8 kg/day for the updated equations between 0 and 1 year). However, the considerably greater body mass of adult right whales suggests they have higher metabolic demands. It appears, for example, that sexually mature right whales (9 years) require 12.9% (or 82.53 MJ) greater food intake per day to meet their basal metabolic costs. Assuming the costs associated with swimming (or active metabolism) are twice maintenance costs, the energy needed to meet active and basal metabolism for a 9-year-old animal will be 25.8% higher in total than previously predicted. In contrast, the basal metabolisms of older individuals between 20 and 22 years are 12% higher than previously estimated (i.e., 760.13 MJ/day for a 22-year-old animal based on the new model using an average mass of 34,885 kg compared with 662.03 MJ/day using the previous model assuming a mean mass of 26,639 kg). Consequently, the new predictions of body mass result in elevated metabolic rates, lending further support to certain ages of right whales being more vulnerable to nutritional stress than others. This is particularly important for reproductively mature females, who may be able to withstand short periods of reduced feeding if they can replenish their blubber reserves during the postlactation period (Christiansen et al., 2018; Miller et al., 2011).

Improved estimates of body mass models contribute to the care and conservation of North Atlantic right whales. Ship strikes (Kite-Powell, Knowlton & Brown, 2007; Vanderlaan & Taggart, 2007) and fishing gear entanglements (Caswell, Fujiwara, & Brault, 1999; Clapham, Young, & Brownell, 1999; Hamilton & Kraus, 2019; Johnson et al., 2005) are the leading causes of mortality for this endangered species. Consequently, accurate estimates of right whale mass are needed to help mitigate anthropogenic mortality. As an example, an adult right whale 9 years old, weighing 23.4 tons, and not emaciated due to chronic entanglement (Barratclough et al., 2014) would require 2.34 kg (i.e., 0.1 mg/kg; van der Hoop et al., 2014) of anesthetic (butorphanol and midazolam) to facilitate disentanglement by reducing swimming speed and evasiveness (Noren, 2011). Conversely, we predict that a whale of the same age, that is 16.9% heavier (28,187 kg) than previously predicted, would require 2.82 kg of sedation. These revised mass estimates will enable more accurate drug dosages to be determined and administered to animals prior to disentanglement.

A limitation of our earlier growth equations was that veterinarians needed to extrapolate beyond the upper age-limits of the model (i.e., 22 years). However, the additional data used to derive the updated growth curves means that dosages can now be determined with greater confidence for older animals (between 22 and 30 years). Overall, our updated mass-at-age predictions will assist in determining the correct dosages of medication for right whales that need to be sedated or treated for infections caused by entanglement and ship strike wounds.

3.4 | Conclusions

Adding new body size data, correcting errors in some of the previous records, and using an improved allometric model to predict mass that includes North Pacific right whale measurements from whaling records has yielded better models of body growth for North Atlantic right whales. The new models show that right whales are on average larger than originally predicted and that the inflection point in their 2-phased growth occurs earlier in development than previously thought (i.e., at ~10 months compared with 13 months; Fortune et al., 2012). This suggests that calves experience a deceleration in growth prior to weaning (assuming whales wean after 12 months). The revised growth models show that right whale calves experience rapid growth between 0 and 9.6 months, and decelerated growth between 9.7 months and 9 years.

Our revised growth models have implications for the conservation and management of North Atlantic right whales. Most notably, they indicate that energetic requirements associated with basal and active metabolism are likely higher than previously believed—particularly for adult animals (9 years) and juveniles that are approaching sexual maturity. These are important findings because juveniles and lactating North Atlantic right whales have the highest predicted daily energy needs, and may experience periods of food shortage based on comparisons with prey ingestion (Fortune, Trites, Mayo, Rosen, & Hamilton, 2013). Consequently, the energy deficit incurred by these demographic groups may be greater than originally thought. They also indicate that higher dosages of sedatives and antibiotics than originally predicted should be used to treat wounded animals that are not emaciated due to chronic entanglement.

ACKNOWLEDGMENTS

North Atlantic right whale identification data used to age animals in decimal years were maintained by the New England Aquarium and provided by the North Atlantic Right Whale Consortium. We appreciate the contributions of the many organizations to this database. We are also grateful to the many people who have assisted with right whale necropsies and right whale aerial photogrammetry research over the years—and particularly thank S. Sharp, W. A. McLellan, R. A. Bonde, M. Lynn, and D. Potter. Aerial photogrammetry data were collected under Northeast Fisheries Science Center Permits 775-1600 and 917-1600 and postmortem procedures were done under National Oceanic and Atmospheric Administration (NOAA) Permit 932-1905-01-MA-009526. We appreciate the helpful edits provided by three anonymous reviewers and our editor, which improved this manuscript.

AUTHOR CONTRIBUTIONS

Sarah Fortune: Conceptualization; formal analysis; investigation; methodology; project administration; visualization; writing-original draft; writing-review and editing. **Michael Moore:** Data curation; funding acquisition; methodology; project administration; writing-review and editing. **Wayne Perryman:** Conceptualization; data curation; funding acquisition; methodology; writing-review and editing. **Andrew Trites:** Investigation; resources; supervision; writing-review and editing.

ORCID

Sarah M. E. Fortune https://orcid.org/0000-0001-6505-9378
Wayne L. Perryman https://orcid.org/0000-0003-2312-8552

REFERENCES

Anderson, D. R. (2008). *Model based inference in the life sciences: A primer on evidence*. New York, NY: Springer.

Barratclough, A., Jepson, P. D., Hamilton, P. K., Miller, C. A., Wilson, K., & Moore, M. J. (2014). How much does a swimming, underweight, entangled right whale (*Eubalaena glacialis*) weigh? Calculating the weight at sea, to facilitate accurate dosing of sedatives to enable disentanglement. *Marine Mammal Science*, *30*, 1589–1599.

Brodie, P. F. (1975). Cetacean energetics, an overview of intraspecific size variation. *Ecology*, *56*, 152–161.

Caswell, H., Fujiwara, M., & Brault, S. (1999). Declining survival probability threatens the North Atlantic right whale. *Proceedings of the National Academy of the Sciences of the United States of America*, *96*, 3308–3313.

Christiansen, F., Dawson, S., Durban, J., Fearnbach, H., Miller, C., Bejder, L., & Moore, M. (2020). Population comparison of right whale body condition reveals poor state of the North Atlantic right whale. *Marine Ecology Progress Series*, *640*, 1–16.

Christiansen, F., Sironi, M., Moore, M. J., Di Martino, M., Ricciardi, M., Warick, H. A., & Uhart, M. M. (2019). Estimating body mass of free-living whales using aerial photogrammetry and 3D volumetrics. *Methods in Ecology and Evolution*, *10*, 2034–2044.

Christiansen, F., Vivier, F., Charlton, C., Ward, R., Amerson, A., Burnell, S., & Bejder, L. (2018). Maternal body size and condition determine calf growth rates in southern right whales. *Marine Ecology Progress Series*, *592*, 267–282.

Clapham J, P., Young B., S., & Brownell, R. L., Jr. (1999). Baleen whales: Conservation issues and the status of the most endangered populations. *Mammal Review*, *29*, 35–60.

Fortune, S. M., Trites, A. W., Mayo, C. A., Rosen, D. A. S., & Hamilton, P. K. (2013). Energetic requirements of North Atlantic right whales and the implications for species recovery. *Marine Ecology Progress Series*, *478*, 253–272.

Fortune, S. M., Trites, A. W., Perryman, W. L., Moore, M. J., Pettis, H. M., & Lynn, M. S. (2012). Growth and rapid early development of North Atlantic right whales (*Eubalaena glacialis*). *Journal of Mammalogy*, *93*, 1342–1354.

George, J. C., Zeh, J., Suydam, R., & Clark, C. (2004). Abundance and population trend (1978–2001) of western Arctic bowhead whales surveyed near Barrow, Alaska. *Marine Mammal Science*, *20*, 755–773.

Gompertz, B. (1825). On the nature of the function expressive of the law of human mortality, and on the new mode of determining the value of life contingencies. *Philosophical Transactions of the Royal Society of London*, *115*, 513–583.

Hamilton, P. K., & Kraus, S. D. (2019). Frequent encounters with the seafloor increase right whales' risk of entanglement in fishing groundlines. *Endangered Species Research*, *39*, 235–246.

Hamilton, P. K., Knowlton, A. R., Marx, M. K., & Kraus, S. D. (1998). Age structure and longevity in North Atlantic right whales *Eubalaena glacialis* and their relation to reproduction. *Marine Ecology Progress Series*, *171*, 285–292.

Johnson, A., Salvador, G., Kenney, J., Robbins, J., Landry, S., & Clapham, P. (2005). Fishing gear involved in entanglements of right and humpback whales. *Marine Mammal Science*, *21*, 635–645.

Kenagy, G. J., & Trombulak, S. C. (1986). Size and function of mammalian testes in relation to body size. *Journal of Mammalogy*, *67*, 1–22.

Kite-Powell, H. L., Knowlton, A. R., & Brown, M. W. (2007). Modeling the effect of vessel speed on right whale ship strike risk. *Project Report for NOAA/NMFS Project NA04NMF472*.

Kraus, S. D., Moore, K. E., Price, C. A., Crone, M. J., Watkins, W. A., Winn, H. E., & Prescott, J. H. (1986). The use of photographs to identify individual North Atlantic right whales *Eubalaena glacialis*. *Report of the International Whaling Commission, Special Issue 10*, 145–151.

Laws, R. M. (1956). Growth and sexual maturity in aquatic mammals. *Nature*, *178*, 193–194.

Miller, C. A., Reeb, D., Best, P. B., Knowlton, A. R., Brown, M. W., & Moore, M. J. (2011). Blubber thickness in right whales *Eubalaena glacialis* and *Eubalaena australis* related with reproduction, life history status and prey abundance. *Marine Ecology Progress Series*, *438*, 267–283.

Moore, M. J., Knowlton, A. R., Kraus, S. D., McLellan, W. A., & Bonde, R. K. (2004). Morphometry, gross morphology and available histopathology in North Atlantic right whale (*Eubalaena glacialis*) mortalities (1970–2002). *Journal of Cetacean Research and Management*, *6*, 199–214.

Moore, M., Walsh, M., Bailey, J., Brunson, D., Gulland, F., Landry, S., & Rowles, T. (2010). Sedation at sea of entangled North Atlantic right whales (*Eubalaena glacialis*) to enhance disentanglement. *PLoS ONE*, *5*(3), e9597.

Neuenhoff, R. D., Cowan, D. F., Whitehead, H., & Marshall, C. D. (2011). Prenatal data impacts common bottlenose dolphin (*Tursiops truncatus*) growth parameters estimated by length-at-age curves. *Marine Mammal Science*, *27*, 195–216.

Noren, D. P. (2011). Estimated field metabolic rates and prey requirements of resident killer whales. *Marine Mammal Science*, *27*, 60–77.

North Atlantic Right Whale Consortium. (2018). *North Atlantic Right Whale Consortium identification database*. Boston, MA: New England Aquarium. https://www.narwc.org/.

Omura, H., Oshumi, S., Nemoto, T., Nasu, K., & Kasuya, T. (1969). Black right whales in the North Pacific. *Scientific Reports of the Whales Research Institute, Tokyo*, *21*, 1–78.

Perryman, W. L., & Lynn, M. S. (2002). Evaluating the nutritive condition and reproductive status of migrating gray whales (*Eschrichtius robustus*) based on analysis of photogrammetric data. *Journal of Cetacean Research and Management*, *4*, 155–164.

R Development Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Ricker, W. E. (1979). Growth rates and models. In W. S. Hoar, D. J. Randall, & J. R. Bret (Eds.), *Fish physiology: Bioenergetics and growth* (Vol. 8, pp. 677–743). Orlando, FL: Academic Press.

Schultz, L. P. (1938). Can the weight of whales and large fish be calculated? *Journal of Mammalogy*, *19*, 480–487.

Sharp, S. M., McLellan, W. A., Rotstein, D. S., Costidis, A. M., Barco, S. G., Durham, K., & Moore, M. J. (2019). Gross and histopathologic diagnoses from north atlantic right whale eubalaena glacialis mortalities between 2003 and 2018. *Diseases of Aquatic Organisms*, *135*, 1–31. https://doi.org/10.3354/dao03376

Speakman, J. R. (2005). Body size, energy metabolism and lifespan. *Journal of Experimental Biology*, *208*, 1717–1730.

van der Hoop, J., Corkeron, P., & Moore, M. (2017). Entanglement is a costly life-history stage in large whales. *Ecology and Evolution*, *7*, 92–106.

van der Hoop, J., Moore, M., Fahlman, A., Bocconcelli, A., George, C., Jackson, K., & Zoodsma, B. (2014). Behavioral impacts of disentanglement of a right whale under sedation and the energetic cost of entanglement. *Marine Mammal Science*, *30*, 282–307.

Vanderlaan, A. S. M., & Taggart, C. T. (2007). Vessel collisions with whales: The probability of lethal injury based on vessel speed. *Marine Mammal Science*, *23*, 144–156.

von Bertalanffy, L. (1938). A quantitative theory of organic growth (inquiries on growth laws. II). *Human Biology*, *10*, 181–213.

White, E. P., Ernest, S. K. M., Kerkhoff, A. J., & Enquist, B. J. (2007). Relationships between body size and abundance in ecology. *Trends in Ecology & Evolution*, *22*, 323–330.

Zach, R., Liner, Y., Rigby, G. L., & Mayoh, K. R. (1984). Growth curve analysis of birds: The Richards model and procedural problems. *Canadian Journal of Zoology*, *62*, 2429–2435.

Zar, J. H. (1996). *Biostatistical analysis* (3rd ed.). Upper Saddle River, NJ: Prentice-Hall.

How to cite this article: Fortune SME, Moore MJ, Perryman WL, Trites AW. Body growth of North Atlantic right whales (*Eubalaena glacialis*) revisited. *Mar Mam Sci*. 2020;1–15. https://doi.org/10.1111/mms.12753

Conservation Physiology

Volume 9 • 2021 10.1093/conphys/coaa133

SOCIETY FOR EXPERIMENTAL BIOLOGY

Research article

Stress and reproductive events detected in North Atlantic right whale blubber using a simplified hormone extraction protocol

Katherine M. Graham*, **Elizabeth A. Burgess and Rosalind M. Rolland**

Anderson Cabot Center for Ocean Life at the New England Aquarium, Central Wharf, Boston, MA 02110, USA

***Corresponding author:** Anderson Cabot Center for Ocean Life at the New England Aquarium, Central Wharf, Boston, MA 02110, USA.
Email: kgraham@neaq.org

As studies quantifying steroid hormones in marine mammal blubber progress, methodological refinements may improve the utility and consistency of blubber hormone measurements. This study advances blubber extraction methodologies by testing a simplified extraction protocol that reduces time and complexity compared to a protocol widely used in cetacean blubber studies. Using blubber samples archived from remote biopsy ($n = 21$ live whales) and necropsy collection ($n = 7$ dead whales) of North Atlantic right whales (NARW; *Eubalaena glacialis*) of known life history states, we performed analytical and biological validations to assess the feasibility of measuring reproductive (testosterone, progesterone) and glucocorticoid (cortisol) hormones in blubber via enzyme immunoassay following the simplified extraction. Analytical validations (parallelism, accuracy, extraction efficiency, repeatability) showed the simplified extraction produced similar results to the extended protocol, offering a more efficient and consistent technique. In live, apparently healthy whales, blubber testosterone concentrations (mean ± SE) were significantly higher in males (2.02 ± 0.36 ng/g) compared to females (0.81 ± 0.15 ng/g). Blubber progesterone was highest in a confirmed pregnant female (60.3 ng/g), which was 12-fold greater than the mean concentration of non-pregnant females (4.56 ± 0.88 ng/g). Blubber cortisol concentrations in whales that died from anthropogenic causes averaged 5.31 ± 2.28 ng/g, whereas most live, healthy whales had cortisol values below 1 ng/g. Among living whales, a whale actively entangled in fishing gear had the highest blubber cortisol measurement (3.51 ng/g), exhibiting levels similar to whales that died from acute entanglement (2.88 ± 0.42 ng/g). Overall, the highest blubber cortisol concentration (18.0 ng/g) was measured in a dead whale with a severe chronic entanglement, approximately 30-fold greater than mean blubber cortisol of apparently healthy whales (0.58 ± 0.11 ng/g). The methodological approach presented here provides a reference for researchers interested in an alternative, streamlined technique for hormone extraction of cetacean blubber and contributes to the diverse tool set for stress and reproductive assessments of endangered NARWs.

Key words: Anthropogenic impact, blubber hormones, entanglement, North Atlantic right whale, steroid hormone extraction, validation

Editor: Steven Cooke

Received 15 May 2020; Revised 16 October 2020; Editorial Decision 11 December 2020; Accepted 14 December 2020

Cite as: Graham KM, Burgess EA, Rolland RM (2021) Stress and reproductive events detected in North Atlantic right whale blubber using a simplified hormone extraction protocol. *Conserv Physiol* 9(1): coaa133; doi:10.1093/conphys/coaa133.

Introduction

Blubber has become a widely used sample matrix for reproductive and stress assessments of both odontocete (for examples see: Kellar *et al*., 2006, Kellar *et al*., 2009, Trego *et al*., 2013, Kellar *et al*., 2015, Trana *et al*., 2016, Champagne *et al*., 2018), and mysticete whales (e.g. Mansour *et al*., 2002, Kellar *et al*., 2013, Vu *et al*., 2015, Mello *et al*., 2017, Pallin *et al*., 2018, Carone *et al*., 2019, Atkinson *et al*., 2020). For instance, pregnant females can be readily identified using blubber progesterone concentrations in several whale species (Mansour *et al*., 2002, Kellar *et al*., 2013, Pallin *et al*., 2018, Inoue *et al*., 2019, Atkinson *et al*., 2020), and blubber cortisol measurements have shown promise for assessing human impacts (Kellar *et al*., 2015) and environmental stressors (Trana *et al*., 2016) on cetaceans. Blubber collected from free-swimming whales using remote biopsy methods or from dead whales during necropsy procedures can be used to explore physiological questions about specific individuals and populations (Hunt *et al*., 2013, Rolland and Moore, 2018). Furthermore, the acquisition of blubber from numerous cetaceans has routinely occurred for other studies focusing on genetic or contaminant analysis (Noren and Mocklin, 2012, Booth *et al*., 2020), with archived collections from previous efforts potentially available for hormone analysis (e.g. Trego *et al*., 2013, Boggs *et al*., 2019, Cates *et al*., 2019).

Most blubber hormone studies have utilized immunoassays for quantification. In preparation for immunoassay, hormones are extracted from blubber tissue using an organic solvent. Nearly all published blubber hormone studies using immunoassays follow an extraction method outlined by Kellar *et al*. (2006, 2015), which was originally modified from Mansour *et al*. (2002). Although successful for tested species, this methodology is relatively complex, consisting of repeated solvent and supernatant transfers and requiring a variety of relatively hazardous chemicals (including diethyl ether, an extremely flammable chemical). Hormone extraction is the most labour-intensive component of sample analysis, and hence possibly the most error-prone part of the process because the margin of error increases with each additional step, which in turn could have consequences for data interpretation (Palme, 2005, Palme *et al*., 2013). In the field of wildlife endocrinology, methodologies for extracting steroid hormones from many alternative sample matrices have been expanded and optimized over time (Wasser *et al*., 2000, Palme, 2005, Hunt *et al*., 2014, Burgess *et al*., 2016, Hunt *et al*., 2017, Richard *et al*., 2017, Rolland *et al*., 2019). Exploring simplification of complex extraction protocols, in tandem with validation testing of the procedure and resultant data, can help advance physiologic studies of wildlife populations (Palme *et al*., 2013, Palme, 2019). Thus, it would be advantageous to develop a more streamlined hormone extraction protocol for cetacean blubber.

Endocrine studies using blubber tissue require careful biological validation and interpretation because blubber hormone measurements could be affected by sample collection (e.g. sampling depth, sample mass, specimen condition) and/or intrinsic factors (such as body condition or metabolism) (Kellar *et al*., 2009, Kellar *et al*., 2006, Kellar *et al*., 2015, Trana *et al*., 2015, Mello *et al*., 2017, Pettis *et al*., 2017). Many of the factors involved in the collection of blubber from cetaceans are inherently variable and not under the full control of researchers due to the logistics of remotely darting a free-swimming animal (e.g. the mass of blubber collected is influenced by the angle at which the dart strikes the whale) (Noren and Mocklin, 2012), or accessibility of carcasses (most whale caracasses beach in a state of advanced decomposition) (Mello *et al*., 2017). Given these circumstances, evaluation of hormone measurements can be strengthened by studying well-known individuals and populations. As demonstrated in a number of studies, the critically endangered North Atlantic right whale (NARW; *Eubalaena glacialis*) is a model species that has provided physiological validation of hormone analyses in alternative matrices (e.g. faeces, baleen, respiratory vapor) (Rolland *et al*., 2005, Hunt *et al*., 2016, Burgess *et al*., 2018). This large whale species has been consistently monitored since 1980, and the North Atlantic Right Whale Identification and Sightings Database (www.rwcatalog.neaq.org) holds comprehensive sighting and life history data for individually identifiable whales (Hamilton *et al*., 2007). Additionally, long-term assessment of faecal hormones in right whales have yielded extensive data on the endocrine patterns expected for various reproductive states in this species (Rolland *et al*., 2005, Hunt *et al*., 2006, Burgess *et al*., 2017, Rolland *et al*., 2017). Because NARWs face increased anthropogenic and environmental pressures (fishing gear entanglements, vessel interactions, human-generated underwater noise, climate change and shifting prey distributions) and non-sustainable reproductive rates (Meyer-Gutbrod and Greene, 2017, Corkeron *et al*., 2018, Sharp *et al*., 2019), the availability of efficient and diverse tool sets to monitor stress and reproduction is critical to guiding management and recovery efforts (Harcourt *et al*., 2019).

The objectives of this study were to analytically validate a simplified protocol for extracting steroid hormones from blubber tissue and then, utilizing this simplified extraction method, characterize reproductive and stress-related hormones in blubber of live and dead NARWs of known life history states. To this end, we (i) conducted immunoassay validations to determine the feasibility of measuring three steroid hormone types (testosterone, progesterone and cortisol) in blubber of NARWs; (ii) evaluated a simplified blubber hormone extraction method alongside a more complex extraction protocol that is widely used in cetacean blubber studies; (iii) compared hormone concentrations in matched blubber and faecal samples to preliminarily examine concordance of blubber hormone measurements relative to a well-studied sample matrix for NARWs; (iv) examined blubber hormone profiles in apparently healthy, free-swimming NARWs of known sex and reproductive states; and (v) investigated blubber cortisol concentrations in whales that died from anthropogenic causes of entanglement in fishing gear and vessel strikes versus living whales.

Materials and methods

Sample collection

A total of 28 blubber samples archived from remote biopsy or necropsy of individual NARWs were used in this study. All samples were collected under federal permits to the New England Aquarium (NEAq) and Canadian Whale Institute (National Marine Fisheries Service permits: 655-1652, 655-1652-01, 14 233 and 19 674; Canada's Department of Fisheries and Oceans permits under the Species at Risk Act) and the International Fund for Animal Welfare (National Marine Fisheries Service permits: 18786 and 18 786-02) and approved by NEAq's Institutional Animal Care and Use Committee. Blubber biopsy samples ($n = 21$) were collected from free-swimming NARWs in the Bay of Fundy, Canada, from July through September in 2006–2017. Biopsy sampling was conducted using an Excalibur crossbow with 150-pound draw weight fitted with a custom made, floating dart containing a stainless steel collection tip of 7 mm diameter by 3 cm length (Brown *et al.*, 1991). The dart was aimed at the dorsal lateral region of the whale to remove a small plug of epidermis and underlying blubber (ranging in depth from 0.2 to 1.7 cm; mean 0.8 ± 0.43 cm). The biopsy sample was retrieved, and the epidermal layer was removed for genetic analysis (Frasier *et al.*, 2006). The remaining dermis and hypodermis (referred to as blubber) was archived for hormone analysis.

Blubber tissue sections (~10 x 10 x 10 cm) were dissected from dead whales ($n = 7$) during necropsies conducted in the months of April, May and August–October in 2016–2018 following standard necropsy procedures for NARWs (McLellan *et al.*, 2004; Sharp *et al.*, 2019). The state of carcass decomposition was graded based on Geraci and Lounsbury (2005; see Table 1). If present, faeces were collected from the rectum during necropsy. Matched blubber and faecal samples were available from three whales, enabling comparison of hormone concentrations across matrices. All samples were kept frozen at −20°C or − 80°C until hormone analysis.

Individual whales were photographed and identified based on unique patterns of cornified epithelium (i.e. callosities) and permanent scars using the North Atlantic Right Whale Identification Database (Kraus *et al.*, 1986, Hamilton *et al.*, 2007, Right Whale Consortium, 2019), as well as genetic profiling of epithelial DNA (Frasier *et al.*, 2006, Frasier *et al.*, 2013, Right Whale Consortium, 2019). Whales were categorized based on age and reproductive history (Table 1; Hamilton *et al.*, 1998): calves (<1 year old, associated with their mother, likely nursing), juveniles (never calved and 1–8 y.o.), adults (year before first calving or ≥ 9 y.o.). Pregnancy was confirmed by identification of the female with a newborn calf in the year following sampling. Females sighted with a dependent calf at time of sampling were considered lactating. Adult females that were not pregnant or lactating were referred to as 'resting' (Rolland *et al.*, 2005). Biopsied whales were free-swimming and considered apparently healthy at sampling, except for one juvenile female (Eg4510) that was entangled in snow crab fishing gear at the time of sample collection. This whale was observed with a buoy and line exiting the left side of the mouth, and line exiting the right side of the mouth which was being pulled downward below the surface by the heavy weight of the gear. The whale had extensive rope abrasions across wide regions of the body and active bleeding at the peduncle region. Based on these observations, the entanglement injury was classified as moderate (defined as extensive skin abrasions or cuts that extended into the blubber; Knowlton *et al.*, 2015). These factors suggest that this whale had recently (within the last month) become entangled (Right Whale Consortium, 2019).

For necropsy cases, each dead whale was given a case number (Table 1). Two of the dead NARWs could not be assigned an individual identification due to decomposition of carcass; however, for both whales, sex was determined by visual observation or genetic analysis and age class (calf, juvenile or adult) was based on body length (Moore *et al.*, 2004). Cause of death was attributed to acute entanglement (hours to days) in four cases, chronic entanglement (weeks to months) in one case and blunt force and/or propeller trauma from vessel strike in two cases (Table 1). Further details on pathology and cause of death of these whales are described in Sharp *et al.* (2019).

Hormone extraction

Blubber samples were trimmed of any remaining epidermal tissue using a clean scalpel blade. For all samples, 0.1 ± 0.05 g of blubber tissue was extracted. Sample masses of 0.1 g to 0.2 g have been widely used in blubber hormone studies; here, we chose to test protocols using the lower mass due to restricted amounts of tissue from biopsy collection. For biopsy samples less than 0.1 g, the entire blubber plug was extracted and only samples greater than 0.07 g were included in the study. For necropsy specimens, blubber was subsampled at a similar mass (0.1 g) and depth below the epidermis as biopsy samples to increase comparability between both sources of tissue collection.

Two different protocols for extracting hormones from blubber were tested: (1) an 'extended' protocol following methods described by Kellar *et al.* (2006, 2015), which was a modification of Mansour *et al.* (2002); and (2) a 'simplified' protocol adapted from a steroid tissue extraction protocol by immunoassay manufacturer, Arbor Assays (Ann Arbor, MI); see https://www.arborassays.com/assets/Tissue-Extraction-190402.pdf), with slight modifications to accommodate our laboratory equipment and reduce reagent volumes for a smaller sample mass.

Extended protocol: Full details are described in Kellar *et al.* (2015). In brief, this was a multi-step organic extraction

Table 1: Life history details of individual whales that were sampled for blubber in this study (total $n = 28$) using either remote biopsy (live whales) or necropsy procedures (dead whales).

Biopsy samples ($n = 21$)		
Age class and sex	*Number of individuals*	*Notes*
Adult females	5	pregnant, $n = 1$; lactating, $n = 3$; resting, $n = 1$
Juvenile females	4	active entanglement (moderate severity), $n = 1$
Adult males	7	
Juvenile males	5	
Necropsy samples ($n = 7$)		
Age class and sex	*Case number*[#]	*Cause of death*
Adult female	MME16–249 (3)	Chronic entanglement
Adult female	IFAW18–281 (4)	Acute entanglement
Juvenile female	IFAW17–182 (3)	Blunt force trauma, vessel strike
Juvenile male	IFAW17–320 (4)	Acute entanglement
Juvenile male	IFAW17–375 (4)	Acute entanglement
Juvenile male	IFAW18–244 (3)	Acute entanglement
Calf male	IFAW16–082 (3)	Propeller trauma, vessel strike

[#] The decomposition code (graded from 2–5) assigned to the carcass at time of necropsy, as described by Geraci and Lounsbury (2005). Code 3: decomposed, but with organs intact. Code 4: severe decomposition, organs not recognizable, but carcass intact. Cause of death is the underlying condition that started the chain of events leading to death; from Sharp *et al*. (2019).

consisting of homogenizing blubber ($\sim$0.1 g) in 1.0 ml of 100% ethanol (ACS reagent grade $\geq$ 99.5%; #459844, Sigma Aldrich) using an Omni Bead Ruptor 4 (catalogue #25–010, Omni International), followed by another wash step of 0.5 ml of ethanol. Resulting supernatants were collected, combined and evaporated and the residue resuspended in 2.0 ml of ethanol:acetone mix (4:1). The supernatant was transferred and evaporated before further extraction with 2.0 ml of diethyl ether. The supernatant was again collected and evaporated, then resuspended in 1.5 ml of acetonitrile (#271004, Sigma Aldrich) followed by the addition of 1.5 ml of hexane (#34859, Sigma Aldrich). The acetonitrile portion was separated, and an additional 1.5 ml of hexane added. The acetonitrile portion was again transferred, evaporated, and the final residue stored frozen at −20°C. Prior to immunoassay, sample extracts were resuspended in 0.5 ml of assay buffer (#X065, Arbor Assays) and vortexed thoroughly.

Simplified protocol: Blubber tissue ($\sim$0.1 g) was placed into homogenization tubes with grinding media (2.8 mm ceramic beads (catalogue #19–628) and one 6.5 mm ceramic bead (#19–682; Omni International)) and 1.0 ml of 100% ethanol. The sample was homogenized for six 45 s intervals using an Omni Bead Ruptor 4, similar to the extended protocol. The homogenate-ethanol mixture was transferred to a glass test tube (T1). The original homogenization tube with remaining grinding media was rinsed with 1.0 ml ethanol, vortexed and the supernatant was transferred to T1. Fluid in T1 was evaporated under airflow. Next, 2.0 ml of acetonitrile was added to the homogenate residue in T1, and the tube was vortexed (10 min) and then centrifuged (3500 rpm for 10 min at 4°C). The supernatant was transferred to a new tube (T2) followed by the addition of 4.0 ml of hexane, and the contents vortexed (5 min) then centrifuged to separate the acetonitrile and hexane layers. The acetonitrile layer was aspirated, transferred into a final tube (T3) and evaporated under airflow. Final dried extract residues were capped, sealed with parafilm and stored frozen (−20°C). Prior to immunoassay, sample extracts were resuspended in a mixture of 0.1 ml ethanol and 0.4 ml assay buffer (#X065, Arbor Assays) then vortexed thoroughly (2 min). The sample was allowed to rest at room temperature for 5 min before repeating the vortex and rest intervals twice more to solubilize the hormone.

Hormone analysis

Immunoreactive testosterone, progesterone and cortisol were quantified in blubber extracts using commercially available enzyme immunoassay systems (catalogue #ISWE001, ISWE003, ISWE002, respectively; Arbor Assays, Ann Arbor, MI), following the manufacturer's protocols. These bulk-reagent immunoassay kits were developed specifically for measuring hormones and their metabolites in alternative sample matrices from diverse wildlife species. All samples, standards and controls were assayed in duplicate, with the coefficient of variation (CV%) between all duplicates $< 10\%$. Quality control samples of high ($\sim$30%) and low ($\sim$70%) binding were included on each plate, with resulting inter-assay CVs of 1.6% and 3.6% for testosterone ($n = 7$ assays); 6.2%

and 11.4% for progesterone ($n = 7$ assays); and 1.8% and 5.3% for cortisol ($n = 7$ assays). Final results were reported as nanograms of immunoreactive hormone and metabolites per gram of blubber tissue (ng/g), subsequently referred to simply as blubber testosterone, progesterone and cortisol. Antibody cross-reactivity, assay sensitivity and lower limit of detection values are available on the manufacturer's website: www.arborassays.com/products/.

Analytical validations

Blubber from dead whales was used to conduct analytical validations and evaluate both hormone extraction methodologies. These large sections of blubber tissue could be repeatedly subsampled and provided matched pairs of near-identical samples from the same localized region of blubber tissue enabling comparison of extraction techniques.

First, to ensure the selected immunoassays could reliably detect and measure the three hormones of interest in NARW blubber extracts, we conducted the following analytical validations: (i) parallelism; and (ii) accuracy. Parallelism was tested by serially diluting a pool of blubber extracts (from 1:1 (neat) to 1:256) and assessing the resulting dilution curve against the standard curve for differences in slope. Expected results should show no significant difference between the curves (F-test, $P > 0.05$), indicating the assay can reliably detect the hormone of interest (Grotjan and Keel, 1996). Assay accuracy was tested by spiking the standard curve with an equal volume of pooled sample extracts. When plotted, observed versus expected hormone values should be linear (ideal $r^2 > 0.95$) with a slope between 0.7–1.3 (ideal slope = 1.0), demonstrating that the sample matrix does not interfere with antibody binding (Ezan and Grassi, 2000, Grotjan and Keel, 1996).

Next, to evaluate the suitability of using a simplified extraction protocol as an alternative to the widely used extended extraction, we conducted experimental comparisons using both extractions protocols based on: (iii) extraction efficiency; (iv) within-extraction method variation; and (v) comparison of final hormone measurements. Extraction efficiency was tested using a separate set of 10 biopsy-sized blubber subsamples (~0.1 g each) for each individual hormone of interest. Six of these subsamples were placed into individual homogenization tubes and each tube was spiked with a known concentration of hormone at 40 ng in dH_2O, and then left overnight at 4°C to allow the hormone solution to soak into the blubber. The other four subsamples were each placed into homogenization tubes containing dH_2O without added hormone (non-spiked) and left overnight at 4°C. The following day, subsamples were assigned to either the simplified extraction or the extended protocol ($n = 3$ spiked and $n = 2$ non-spiked for the two protocols; $n = 10$ total for each hormone) before immunoassay. Extraction efficiency (%) was calculated as the mean concentration of hormone minus mean background (non-spiked samples), divided by the known amount of hormone added before extraction and multiplied by 100 (Palme, 2019). Within-extraction method variation tested the precision or repeatability of a hormone measurement across multiple extracts generated by each extraction protocol. For this test, blubber was dissected into 20 subsamples that were randomly assigned to extraction using either the simplified protocol ($n = 10$) or extended protocol ($n = 10$). Within-extraction method variation was quantified as the CV% between hormone measurements of 10 replicate extracts per protocol. Finally, we assessed the differences in absolute hormone concentration measured in paired subsamples taken from each of the seven dead whales. For each whale, four blubber subsamples were taken, which allowed for two subsamples to be assigned to each extraction protocol. The resultant extracts were assayed, and hormone concentrations were averaged for each extraction method, with the final measurements compared between the two methods.

To examine concordance of blubber hormone concentrations to faeces (a previously validated and well-studied sample matrix for measuring hormones in NARWs), we used matched blubber and faecal samples that were collected from three dead whales. Faecal samples were processed and analysed for faecal androgens, progestagens and glucocorticoids following methods described by Rolland *et al.* (2005) and Hunt *et al.* (2006). Blubber samples were extracted by the simplified extraction prior to measurement.

Blubber hormone concentrations of NARWs and biological validation

To characterize reproductive and glucocorticoid hormone concentrations in NARW blubber, testosterone, progesterone and cortisol were measured using the validated Arbor Assays immunoassay systems (see *Analytical validations*). Based on validation results, blubber samples from all whales ($n = 28$) were extracted using the simplified extraction protocol and resulting sample extracts were diluted 1:3 in assay buffer (#X065, Arbor Assays) prior to assay. Hormone data were compared across whales of different sexes, age classes, reproductive states and health statuses to evaluate whether blubber sample measurements reflect endocrine profiles expected for whales of known life history states.

Data analysis

Data from analytical validation tests of parallelism, accuracy, extraction efficiency and within-extraction method variation were compared between extraction protocols. A paired *t*-test was used to assess differences in measured hormone concentrations of blubber subsamples extracted following each protocol. Hormone values in matched blubber and faecal samples for three individuals, were graphically presented to observe congruence of trends between these alternative matrices. Descriptive statistics (mean ± SEM) were used to summarize the data set. Hormone concentration data were $\log_{10}$-transformed for the following analyses to meet assumptions of normality and homogeneity of variance, which were tested using Shapiro–Wilk test and Levene's test. Blubber hormone concentrations of live, apparently healthy whales ($n = 20$ out of 21 biopsy samples; one biopsy (from Eg4510) was excluded due to active entanglement) were examined using a univariate general linear model (GLM). A full factorial model was used to analyse the effect of sex, age class (i.e. juvenile or adult) and their interaction on hormone concentrations (dependent variable) of whale blubber samples, with the following equation: $y_i = \beta_0 + \beta_1$ sex$_i$ $+ \beta_2$ age class $_i + \beta_3$ sex × age class$_i$ $+ \epsilon_i$ where y is the response variable, β is the population slope and fixed effect parameters (including β_0 as the population intercept) and ϵ is a random error term associated with the ith observation. To avoid omission of any individual whale due to missing data fields in the GLM, we deliberately classed one female of uncertain age as 'adult'. This decision was grounded on available data that showed this female was older than 7 years of age (based on sighting records) and successfully calved 17 months after sampling—and therefore, this female was presumed to be nearing reproductive maturity when blubber sampling occurred.

To consider the possible effect of abiotic factors on measured hormone variables in the full set of blubber samples ($n = 28$; both live and dead whales), we used a multivariate GLM. Key attributes of sample storage time (i.e. number of years from sample collection until hormone analysis), mass of the analysed sample (measured in grams) and whale survival at time of sampling (i.e. live or dead whale, as associated with biopsy or necropsy sampling) were included as explanatory variables into the model designed to analyse all dependent variables (testosterone, progesterone and cortisol concentrations) simultaneously, with the following equation: z_{ik} = constant $+ c_1$ storage time$_i$ $+ c_2$ sample mass$_i$ $+ c_3$ whale surivival$_i$ where z is the combination of response variables (observation i for the linear combination k) and c is the coefficient measuring the relative contribution of each variable. Univariate between-subjects F-tests that indicated the effect of each factor on each dependent variable were also produced by the GLM framework. All statistical analyses were performed using SPSS (version 25) and significance level was set at 0.05 for all statistical tests.

Results

Analytical validations

For both extraction protocols, serially diluted blubber extracts demonstrated parallelism to the standard curve for testosterone, progesterone and cortisol immunoassays (all $P > 0.05$; Fig. 1 and Table 2). Blubber extracts derived using the simplified method demonstrated reasonable accuracy for all hormones tested and yielded similar results to the extended protocol (all slopes between 0.7 and 1.2, $r^2 > 0.99$; Fig. 1 and Table 2). Analytical validation results indicated that hormone metabolites extracted from NARW blubber by either protocol can be detected by the assay antibody across a range of concentrations (parallelism test) and that substances inherent to the extract matrices do not interfere with accurate hormone measurement (accuracy test).

Extraction efficiency ranged from 61–74% for the simplified protocol and 55–81% for the extended protocol (Table 2). Both protocols had similar overall recoveries across all hormones (mean 68% for both protocols). The simplified protocol resulted in higher recovery of progesterone (70% compared to 55%), but conversely, slightly higher recovery of testosterone was observed for the extended protocol (81% compared to 74%). For cortisol, relatively similar extraction efficiencies were found for both the simplified (61%) and extended extraction protocols (67%). Within-extraction method variability was lower for samples extracted by the simplified protocol (range 6.4–14.9%) compared to the extended method (19.1–35.2%), with the best result for the measurement of cortisol (6.4%) (Table 2).

Overall, hormone measurements from matched subsamples extracted using the two protocols were similar for all hormone types (testosterone: $t_{(6)} = -2.01$, $P = 0.09$; progesterone: $t_{(6)} = -1.69$, $P = 0.14$; cortisol: $t_{(6)} = 0.31$, $P = 0.98$). Generally, testosterone and progesterone concentrations were higher in extracts generated using the simplified extraction protocol (averaging 1.9 and 2.2 times higher, respectively) compared to the extended extraction protocol extracts (Fig. 2). At higher sample concentrations, there was greater variation in resulting hormone values between the simplified and extended protocols (Fig. 2).

Blubber hormone concentrations paralleled faecal hormone patterns for three whales with matched sample types, with hormone concentrations in blubber two or three orders of magnitude lower than faeces (Fig. 3). In both blubber and faeces, the highest concentrations of reproductive hormones (testosterone and progesterone) were observed in the adult female (MME16–249) compared to two juvenile whales. The highest blubber and faecal glucocorticoid concentrations were also measured in whale MME16–249 that died following a severe, chronic entanglement (Table 1; Sharp *et al*., 2019).

Blubber hormone concentrations of NARWs and biological validation

Testosterone, progesterone and cortisol were measurable in all NARW blubber samples following extraction with the simplified protocol. In live, apparently healthy right whales, blubber testosterone concentrations were significantly higher in males (2.02 ± 0.36 ng/g; $n = 12$) than females (0.81 ± 0.15; $n = 8$) ($F_{1,16} = 5.90$, $P = 0.03$). Mean blubber testosterone of adult males (2.54 ± 0.50 ng/g; $n = 7$) was approximately twice as high as juvenile males (1.28 ± 0.32 ng/g; $n = 5$) and over three times greater than adult females (0.74 ± 0.17 ng/g; $n = 5$) (Fig. 4); however, differences associated with age class did not achieve statistical significance ($F_{1,16} = 0.52$, $P = 0.48$; interaction term: $F_{1,16} = 3.7$, $P = 0.07$). Blubber progesterone levels were similar in females (11.80 ± 0.12 ng/g; $n = 8$) and

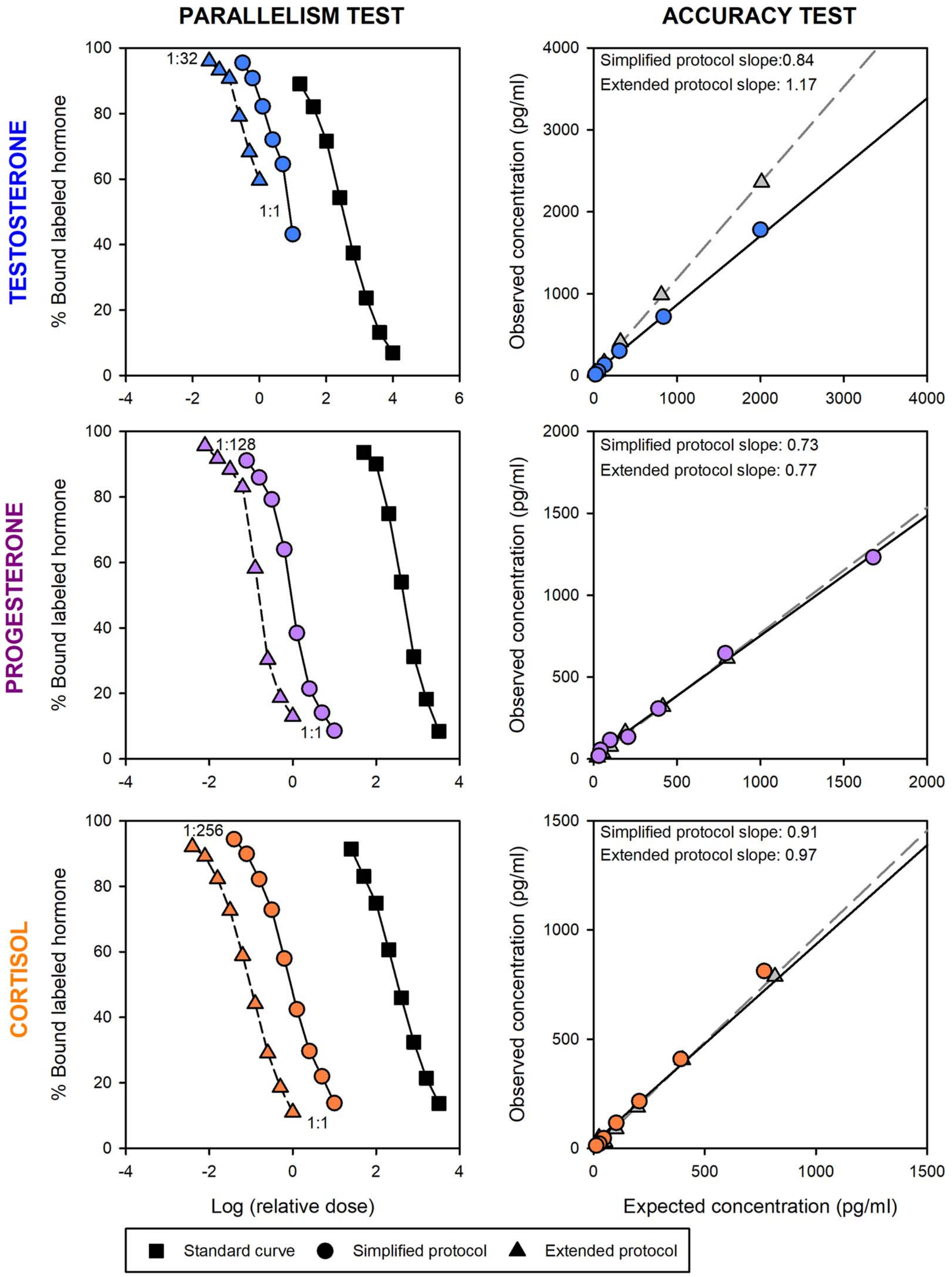


Figure 1: Validation test plots for testosterone (top row), progesterone (middle) and cortisol (bottom) of NARW blubber extracts using the simplified extraction protocol (circles: ● with solid line) or extended extraction (triangles: ▲ with dashed line). Parallelism (left column) was observed between serially diluted sample curves (dilution range reported for each hormone) and standard curves (squares: ■) for both extraction methods across all hormones. [Note: In parallelism graphs, the relative dose (x-axis) of the sample serial dilution curves was displaced to avoid overlap]. Assay accuracy (right column) was demonstrated by the positive linear relationship of expected hormone concentration against observed concentration in spiked samples (simplified extraction protocol: circles ●; extended extraction: triangles▲) and regression line slopes within the acceptable range of 0.7–1.3 (exact value reported on each graph).

Table 2: Analytical validation results (parallelism, accuracy, extraction efficiency and within-extraction method variation) for the simplified and extended extraction protocols.

	Parallelism (F-test$_{(df)}$; *P*-value)		Accuracy test (linear slope)	
Hormone	Simplified extraction	Extended extraction	Simplified extraction	Extended extraction
Testosterone	$F_{(1,9)} = 1.23; P = 0.30$	$F_{(1,8)} = 0.18; P = 0.68$	y = 0.84x + 26.85	y = 1.17x + 15.35
Progesterone	$F_{(1,10)} = 0.65; P = 0.44$	$F_{(1,9)} = 0.37; P = 0.56$	y = 0.73x + 18.70	y = 0.77x—0.43
Cortisol	$F_{(1,12)} = 0.08; P = 0.79$	$F_{(1,12)} = 0.09; P = 0.76$	y = 0.91x + 24.88	y = 0.97x + 0.88
	Extraction efficiency (% recovery)		Within-extraction method variation (mean %CV)	
Hormone	Simplified extraction	Extended extraction	Simplified extraction	Extended extraction
Testosterone	74%	81%	11.4%	21.6%
Progesterone	70%	55%	14.9%	35.2%
Cortisol	61%	67%	6.4%	19.1%

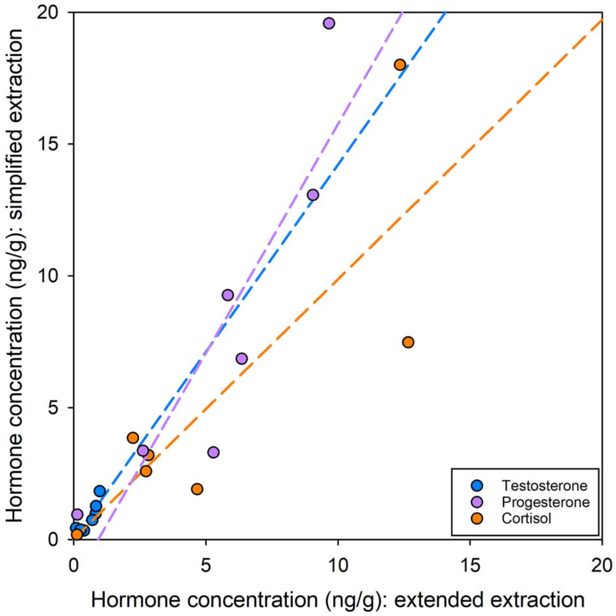


Figure 2: Comparison of hormone measurements (ng/g) in matched blubber subsamples extracted using the extended (x-axis) and simplified (y-axis) protocols. Coloured dotted lines represent the linear regression equation for each hormone type; testosterone (blue): y = 1.42x + 0.02; progesterone (purple): y = 1.74x – 1.60; cortisol (orange): y = 0.98x + 0.03.

males (4.70 ± 0.01 ng/g; *n* = 12) ($F_{1,16} = 0.74$, $P = 0.40$), as well as across age classes ($F_{1,16} = 0.11$, $P = 0.74$; interaction term: $F_{1,16} = 0.54$, $P = 0.47$). However, the highest blubber progesterone concentration (60.30 ng/g) was measured in a confirmed pregnant female (Fig. 4). This value was over 12-fold greater than mean blubber progesterone of non-pregnant females (4.56 ± 0.88 ng/g; *n* = 7).

For live, apparently healthy whales in this study, blubber cortisol concentrations were not significantly different between sexes ($F_{1,16} = 1.70$, $P = 0.21$), age classes ($F_{1,16} = 3.26$, $P = 0.09$), or reproductive groups (interaction term: $F_{1,16} = 0.97$, $P = 0.34$). However, adult males had blubber cortisol levels (0.94 ± 0.27 ng/g; *n* = 7) that averaged two times higher compared to juvenile males (0.37 ± 0.05 ng/g; *n* = 5), juvenile females (0.34 ± 0.07 ng/g; *n* = 3) and adult females (0.44 ± 0.10 ng/g; *n* = 5) (Fig. 4).

In the analysis examining abiotic factors, we found that storage time (Pillai's Trace = 0.24; $F_{3,22} = 2.33$, $P = 0.10$), sample mass (Pillai's Trace = 0.09; $F_{3,22} = 0.75$, $P = 0.53$) and whale survival (Pillai's Trace = 0.76; $F_{3,22} = 2.31$, $P = 0.10$) did not exhibit significant effects on measured hormone concentrations of blubber samples. Univariate tests also showed that storage time (7.7 ± 0.9 years; range: 0.4–12.6 years) and sample mass (0.10 ± 0.003 ng/g; range: 0.07–0.12 ng/g) did not significantly influence blubber testosterone, progesterone or cortisol measurements in this study (all $P > 0.05$). There was no effect of whale survival on reproductive hormone measurements, with similar blubber testosterone concentrations in live (1.48 ± 0.25 ng/g) and dead whales (0.85 ± 0.21 ng/g) ($F_{1,24} = 0.69$, $P = 0.42$), and similar levels of blubber progesterone in live (7.30 ± 2.70 ng/g) and dead whales (8.05 ± 2.47 ng/g) ($F_{1,24} = 2.89$, $P = 0.10$). However, there was a significant influence of whale survival on blubber cortisol concentrations ($F_{1,24} = 6.90$, $P = 0.02$).

Blubber cortisol concentrations of whales that died from anthropogenic causes were significantly greater (5.31 ± 2.28 ng/g; *n* = 7) than living whales (0.72 ± 0.18; *n* = 21), which typically had levels below 1 ng/g (Fig. 5). Notably, however, one live whale had an extreme cortisol concentration (identified as an outlier, Fig. 5) and this individual whale (Eg4510) was actively entangled in fishing line at the time of biopsy collection; whereas, all other live whales were free-swimming and considered apparently healthy. Whale Eg4510 had recently acquired an entanglement (classified as moderate in severity) and her blubber cortisol concentration (3.51 ng/g) was comparable to levels measured in whales that died from acute entanglement (2.88 ± 0.42 ng/g; *n* = 4). One dead whale

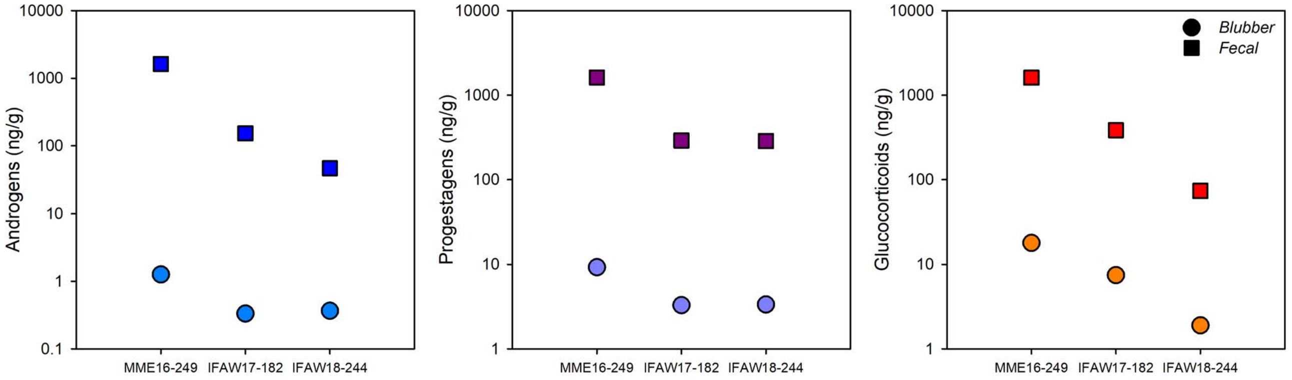


Figure 3: Matched blubber (circle) and faecal (square) hormone values (ng/g) collected from three whales during necropsy procedures. Patterns in blubber hormones showed similar trends to faecal hormones, albeit at concentrations two or three orders of magnitudes lower than in faeces. The y-axis is presented as a log scale.

that sustained a severe, chronic entanglement (MME16–249) had the highest blubber cortisol concentration (18.01 ng/g) measured in this study. Of the two whales that died from injuries related to vessel strikes, one whale (IFAW16–082) that suffered propeller-induced trauma had the lowest measured cortisol value in the study of 0.19 ng/g, whereas the other whale (IFAW17–182) that suffered blunt force trauma had a relatively high cortisol concentration (7.30 ng/g).

Discussion

This study presented a simplified protocol for extracting hormones from cetacean blubber and demonstrated the simplified extraction is a consistent and efficient alternative to a widely used extended protocol (Kellar *et al.*, 2006, 2015) for this essential sample preparation step. We performed and evaluated both extraction protocols (simplified and extended) to obtain comparable data on hormone measurement results for testosterone, progesterone and cortisol, providing a useful reference for future researchers. Moreover, data reported here are the first quantification of reproductive (testosterone and progesterone) and glucocorticoid (cortisol) hormones in NARW blubber tissue and revealed biologically meaningful hormone patterns can be measured in blubber, making it a valuable matrix for assessing reproductive and stress-related states in free-swimming whales, as well as for postmortem investigation.

Analytical validations

The simplified extraction protocol increased the efficiency and reproducibility of blubber hormone measurements and proved to be a reliable extraction technique for cetacean blubber studies. Using the simplified protocol, sample processing time was substantially reduced (>50%) and required fewer steps and hazardous chemicals (i.e. removal of highly volatile diethyl ether), making this simplified blubber hormone extraction technique potentially feasible for laboratories with limited resources (e.g. protective equipment, labour and supply costs). Most importantly, precision of hormone measurements was shown to improve when using the simplified extraction protocol, as all intra-sample CV values for the simplified protocol were near the standards recommended for wildlife endocrinology (i.e. <10%; Grotjan and Keel, 1996), with the best result for the measurement of cortisol (CV of 6.4%). Hormone extraction should be kept as simple as possible because additional steps increase the extent of variation, which could potentially impact accuracy of the final measurement (Burd, 2010, Palme, 2019). We posit that the higher variation measured between replicate samples extracted using the extended protocol may have resulted from inconsistent losses in hormones during repeated supernatant transfer steps. Kellar *et al.* (2006) also found high variation between identical samples when reporting on the use of the extended protocol for progesterone measurement (CV of 18%) but concluded that high variability inherent to this extraction methodology did not impede pregnancy determination. Nonetheless, it is preferable to minimize sources of intra-sample variability, particularly when detecting physiological changes at lower hormone concentration ranges (Millspaugh and Washburn, 2004, Watson *et al.*, 2013). The high variability associated with the extended extraction could be problematic, particularly for stress assessments that may be used in conservation management decisions, clinical diagnostics, or developing endocrine reference ranges for populations.

Extraction efficiency for the two protocols varied across hormone types, however this variation is expected given the range of wash steps and reagents with varying polarities used in each extraction protocol. Furthermore, extraction efficiency calculations that are based on adding exogenous parent steroids to the sample prior to extraction are often considered an artificial measure of true recovery (Palme *et al.*, 2013, Palme, 2019), particularly when hormone metabolites predominate in the tissue, as is the case for blubber (Boggs *et al.*, 2017, Atkinson *et al.*, 2020). Nonetheless, this approach

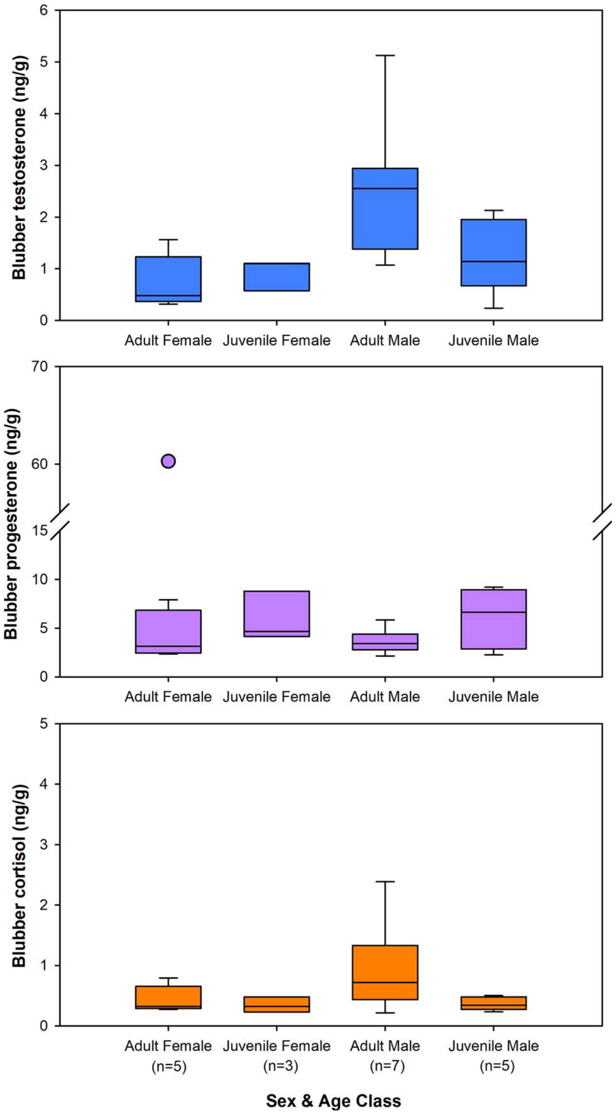


Figure 4: Blubber testosterone (top, blue), progesterone (middle, purple) and cortisol (bottom, orange) of live, apparently healthy NARWs across sexes and age classes. Boxplots encompass first and third quartiles, the line inside the box indicates the median value and whiskers represent the 10th and 90th percentiles. Note: In the progesterone graph, a break was inserted in the y-axis between 15 and 55 ng/g and the value for the pregnant female (denoted by a filled circle) was plotted separately due to its extremely high concentration.

does hold value in the present study for comparing between different extraction protocols. Refinement of the simplified extraction protocol, such as modifying the polarity and/or types of solvents used, may improve extraction efficiency and recovery further.

Successful analytical validation of commercial enzyme immunoassays tested in this study establishes these assays as suitable for measuring testosterone, progesterone, cortisol and associated metabolites in NARW blubber. Concentrations of hormones in NARW blubber were generally low, but comparable to levels measured in blubber of other large whale species (Clark *et al*., 2016, Cates *et al*., 2019, Atkinson *et al*., 2020, Mingramm *et al*., 2020). Studies using LC–MS/MS have established that cetacean blubber contains parent steroids (cortisol, progesterone and testosterone) as well as their metabolites, including cortisone, 17-hydroxyprogesterone, 11-deoxycorticosterone, 11-deoxycortisol and androstenedione (Boggs *et al*., 2017, Galligan *et al*., 2018, Boggs *et al*., 2019, Dalle Luche *et al*., 2019). Analysis of blue whale blubber showed progesterone was present in extracts (5%), although the majority of screened fractions (~67%) were found to be a more polar progesterone metabolite (Atkinson *et al*., 2020). The use of broad-spectrum antibodies in this study permitted the quantification of blubber metabolite concentrations in all samples from NARWs. Future LC–MS/MS analysis of NARW blubber could be used to identify the predominant steroids and metabolites present in this tissue, enabling selection of more targeted immunoassay systems that may offer additional physiological insights from blubber; for example, identifying different stages of pregnancy based on shifts in the predominant steroids and metabolites (Legacki *et al*., 2020).

Blubber hormone concentrations of NARWs and biological validation

Blubber testosterone, progesterone and cortisol in live, apparently healthy right whales followed expected physiologic patterns based on sex and reproductive state and were consistent with well-established faecal hormone patterns for the species (Burgess *et al*., 2017, Hunt *et al*., 2006, Rolland *et al*., 2005, Rolland *et al*., 2017). Adult male NARWs had higher testosterone and cortisol (and/or metabolites) in blubber compared to non-pregnant females and immature animals, presumably related to reproductive activity in males (Rolland *et al*., 2005, Hunt *et al*., 2006, Rolland *et al*., 2017). A confirmed pregnant female was distinguished from non-pregnant animals by extremely high blubber progesterone concentrations (12-fold increase). Such physiological changes associated with pregnancy have also been measured in NARW faeces (Rolland *et al*., 2005) and in the blubber of other large whale species (Kellar *et al*., 2013, Clark *et al*., 2016, Pallin *et al*., 2018, Goertz *et al*., 2019, Atkinson *et al*., 2020). Most adult females in our biopsy sample set were lactating, with only one non-pregnant female considered to be in a resting state. Increasing sample sizes for reproductive females will better delineate the range of progesterone concentrations associated with reproductive cycling and pregnancy in blubber tissue.

Matched faeces and blubber collected from three individuals provided evidence that hormone patterns were similarly reflected in both matrices, though at different quantitative scales. This finding is consistent with bowhead

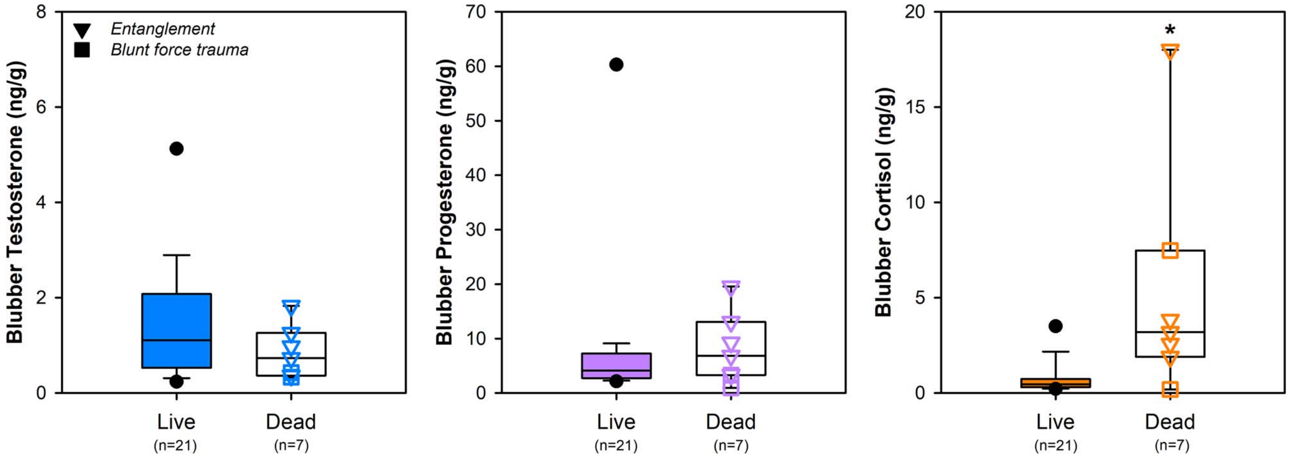


Figure 5: Blubber hormone concentrations for live whales (biopsy samples, $n = 21$) compared to necropsy samples from whales that died from anthropogenic causes ($n = 7$). For live whales, outliers beyond the 5th and 95th percentile are plotted with a circle. For dead whales, individual hormone values are plotted over the boxplot, with whales that died as a result of trauma from entanglement denoted by triangles (▼; $n = 5$) or vessel strike by squares (■; $n = 2$). Asterisk (∗) indicates a significant difference between the live and dead whales at $P < 0.05$.

whale progesterone concentrations that showed concordance among blubber, urine and serum samples (Kellar *et al.*, 2013). Since blood sampling and standard endocrine validations are not possible for most large whales, our preliminary data on matched alternative matrices lends further validity to the use of blubber hormone techniques for physiological assessment. Additionally, blubber hormone measurements may be useful to examine seasonality in free-swimming NARWs, a topic which remains understudied since faecal samples are often not obtainable during annual periods of fasting.

Abiotic factors (including storage time, sample mass and whale survival at time of sampling) should be considered when comparing different sources of tissue and these factors did not appear to hamper interpretation of hormone results in this study. We noted similarities between living and dead whales for both reproductive hormones (testosterone and progesterone), suggesting that carcasses in this study were still viable for hormone measurement. Furthermore, there was a wide variation in cortisol levels among dead whales (spanning the lowest and highest cortisol measurements in this study), suggesting these patterns were not due to tissue decomposition, and instead meaningfully reflect the time course of mortality or injury (similar to NARW faecal glucocorticoid patterns reported in Rolland *et al.*, 2017).

Cortisol data suggest that adrenal activation due to stressful anthropogenic impacts was captured in blubber tissue and the mode by which an animal died (entanglement in fishing gear or vessel strike) was the primary driver of postmortem cortisol levels. Increased blubber cortisol concentrations have been reported in other cetaceans following stressful events, including beach stranding of short-beaked common dolphins (Kellar *et al.*, 2015) and humpback whales (Mingramm *et al.*, 2020), and entrapment of beluga whales in sea ice (Trana *et al.*, 2016). The whale with the highest blubber cortisol measured in this study (MME16–249) died from a severe, chronic entanglement in fishing line that occluded the rostrum and was cinched at the flippers, restricting the ability of the mouth to open for feeding (Sharp *et al.*, 2019) leading to a prolonged decline in health and likely heightened adrenal activation. By contrast, the lowest measure of cortisol came from a whale (IFAW16–082) that died from propeller-induced trauma involving a deep laceration into the abdominal cavity, vertebral shearing and skull fractures (Sharp *et al.*, 2019). The trauma suffered by this individual likely led to a rapid death, with limited time for activating a stress response and/or uptake of hormone into blubber tissue, such that cortisol levels in the blubber of this whale reflected a prior physiological state of an otherwise apparently healthy individual preceding vessel strike. The other whale that sustained blunt force trauma from a vessel strike (IFAW17–182) had somewhat elevated cortisol levels but showed evidence of other pathologies that may have heightened adrenal activity in this individual prior to death (Sharp *et al.*, 2019). All four dead whales that were classified as acute entanglement cases showed intermediate cortisol levels, with evidence that two of these whales drowned (potentially an acute death) as a result of their entrapment in fishing gear (Sharp *et al.*, 2019). Blubber levels are likely a function of total cortisol production, with a lag time before accumulating in this peripheral tissue (possibly on the order of weeks to months for large whales, based on progesterone signal dynamics in pregnant bowhead whales (Kellar *et al.*, 2013)). Ultimately, using blubber glucocorticoid measurements for stress assessment in large whales may be most applicable for assessing threats sustained over longer period (weeks to months) rather than shorter term impacts (hours to days).

Conclusions

This study presents a useful and practical contribution towards advancing blubber hormone assessments for marine mammal populations by developing and validating a reliable, simplified hormone extraction protocol and then applying it to evaluate blubber hormone concentrations in well-studied NARWs. Optimization of blubber hormone measurements has the potential to expand the reach and reliability of this approach, benefitting researchers and management agencies studying vulnerable marine mammal populations. Using a small mass of blubber, we were able to measure and compare three different hormone types for reproductive and stress assessment of a large whale. Many blubber studies using immunoassays have focused on measuring a single hormone. However, the capacity to examine a suite of hormones is valuable for interpreting physiologic patterns, particularly because factors such as reproductive state can influence other hormone measures (e.g. adrenal hormones) (Hunt *et al*., 2006, Sheriff *et al*., 2011). Additional hormone types, such as thyroid hormones and aldosterone could also be explored in marine mammal blubber, as these data may be beneficial for more detailed physiological assessment. The hormone values reported here are important for establishing reference ranges of physiological information to which we can compare in future studies, especially given the increasing impact of human activities on the ocean (Maxwell *et al*., 2013, Fleishman *et al*., 2016) and animal welfare concerns (Moore and van der Hoop, 2012, Rolland *et al*., 2017, Papastavrou *et al*., 2017). Physiologic profiles measured in blubber are valuable for assessing the lethal and sublethal effects of major anthropogenic threats, including entanglements in fishing gear and vessel strikes, on NARWs as well as other vulnerable marine mammal populations.

Funding

This work was supported by Fisheries and Oceans Canada: Ocean Ecology Section (contract # F5211–180767).

Acknowledgements

The authors greatly appreciate the consistent and dedicated survey and biopsy sampling efforts of the New England Aquarium Right Whale Team and the Canadian Whale Institute, in particular Dr. Moira Brown, without whom this work would not have been possible. Thank you to Misty Niemeyer and team at the International Fund for Animal Welfare for providing the necropsy blubber samples used in this study, and to the necropsy teams who conducted sampling. The authors are grateful to the North Atlantic Right Whale Consortium data contributors for use of identification, sightings and necropsy reports that helped inform this study. Gratitude to Philip Hamilton, Kelsey Howe, Heather Pettis and Monica Zani for assistance with whale identification and life history data. We would also like to thank Dr. Hilary Moors-Murphy and Dr. Andrew Wright for facilitating project funding.

References

Atkinson S, Gendron D, Branch TA, Mashburn KL, Melica V, Enriquez-Paredes LE, Brownell RL Jr (2020) Pregnancy rate and biomarker validations from the blubber of eastern North Pacific blue whales. *Mar Mamm Sci* 36: 6–28.

Boggs AS, Ragland JM, Zolman ES, Schock TB, Morey JS, Galligan TM, Dalle Luche G, Balmer BC, Wells RS, Kucklick JR (2019) Remote blubber sampling paired with liquid chromatography tandem mass spectrometry for steroidal endocrinology in free-ranging bottlenose dolphins (*Tursiops truncatus*). *Gen Comp Endocrinol* 281: 164–172.

Boggs AS, Schock TB, Schwacke LH, Galligan TM, Morey JS, McFee WE, Kucklick JR (2017) Rapid and reliable steroid hormone profiling in *Tursiops truncatus* blubber using liquid chromatography tandem mass spectrometry (LC-MS/MS). *Anal Bioanal Chem* 409: 5019–5029.

Booth CG, Sinclair RR, Harwood J (2020) Methods for monitoring for the population consequences of disturbance in marine mammals: a review. *Front Mar Sci* 7: 115. doi: 10.3389/fmars.2020.00115.

Brown MW, Kraus SD, Gaskin DE (1991) Reaction of North Atlantic right whales (*Eubalaena glacialis*) to skin biopsy sampling for genetic and pollutant analysis. In GP Donovan, ed, *Report of the International Whaling Commission: Special Issue Volume 13*. International Whaling Commission, Cambridge, p. 9.

Burd EM (2010) Validation of laboratory-developed molecular assays for infectious diseases. *Clin Microbiol Rev* 23: 550–576.

Burgess EA, Hunt KE, Kraus SD, Rolland RM (2016) Get the most out of blow hormones: validation of sampling materials, field storage and extraction techniques for whale respiratory vapour samples. *Conserv Physiol* 4: cow24. doi: 10.1093/conphys/cow024.

Burgess EA, Hunt KE, Kraus SD, Rolland RM (2017) Adrenal responses of large whales: integrating fecal aldosterone as a complementary biomarker to glucocorticoids. *Gen Comp Endocrinol* 252: 103–110.

Burgess EA, Hunt KE, Kraus SD, Rolland RM (2018) Quantifying hormones in exhaled breath for physiological assessment of large whales at sea. *Sci Rep* 8: 10031. doi: 10.1038/s41598-018-28200.

Carone E, Pardo MA, Atkinson S, Mashburn K, Pérez-Puig H, Enríquez-Paredes L, Gendron D (2019) Sex steroid hormones and behavior reveal seasonal reproduction in a resident fin whale population. *Conserv Physiol* 7: coz059. doi: 10.1093/conphys/coz059.

Cates KA, Atkinson S, Gabriele CM, Pack AA, Straley JM, Yin S (2019) Testosterone trends within and across seasons in male humpback whales (*Megaptera novaeangliae*) from Hawaii and Alaska. *Gen Comp Endocrinol* 279: 164–173.

Champagne CD, Kellar NM, Trego ML, Brendan D, Rudy B, Wasser SK, Booth RK, Crocker DE, Houser DS (2018) Comprehensive endocrine response to acute stress in the bottlenose dolphin from serum, blubber, and feces. *Gen Comp Endocrinol* 266: 178–193.

Clark CT, Fleming AH, Calambokidis J, Kellar NM, Allen CD, Catelani KN, Robbins M, Beaulieu NE, Steel D, Harvey JT (2016) Heavy with child? Pregnancy status and stable isotope ratios as determined from biopsies of humpback whales. *Conserv Physiol* 4: cow050. doi: 10.1093/conphys/cow050.

Corkeron P, Hamilton P, Bannister J, Best P, Charlton C, Groch KR, Findlay K, Rowntree V, Vermeulen E, Pace RM (2018) The recovery of North Atlantic right whales, *Eubalaena glacialis*, has been constrained by human-caused mortality. *R Soc Open Sci* 5: 180892. doi: 10.1098/rsos.180892.

Dalle Luche G, Bengtson Nash S, Kucklick JR, Mingramm FM, Boggs AS (2019) Liquid chromatography tandem mass spectrometry for the quantification of steroid hormone profiles in blubber from stranded humpback whales (Megaptera novaeangliae). *Conserv Physiol* 7: coz030. doi: 10.1093/conphys/coz030.

Ezan E, Grassi J (2000) Optimization. In J Gosling, ed, *Immunoassays: A Practical Approach*. Oxford University Press, Oxford, pp. 187–210.

Fleishman E *et al.* (2016) Monitoring population-level responses of marine mammals to human activities. *Mar Mamm Sci* 32: 1004–1021.

Frasier T, Gillett R, Hamilton P, Brown M, Kraus S, White B (2013) Postcopulatory selection for dissimilar gametes maintains heterozygosity in the endangered North Atlantic right whale. *Ecol Evol* 3: 3483–3494.

Frasier TR, Rastogi T, Brown MW, Hamilton PK, Kraus SD, White BN (2006) Characterization of tetranucleotide microsatellite loci and development and validation of multiplex reactions for the study of right whale species (genus *Eubalaena*). *Mol Ecol Notes* 6: 1025–1029.

Galligan TM, Schwacke LH, Houser DS, Wells RS, Rowles T, Boggs ASP (2018) Characterization of circulating steroid hormone profiles in the bottlenose dolphin (*Tursiops truncatus*) by liquid chromatography–tandem mass spectrometry (LC–MS/MS). *Gen Comp Endocrinol* 263: 80–91.

Geraci JR, Lounsbury VJ (2005) *Marine Mammals Ashore: A Field Guide for Strandings*. National Aquarium in Baltimore, Baltimore, pp. 176–178.

Goertz CE, Burek-Huntington K, Royer K, Quakenbush L, Clauss T, Hobbs R, Kellar NM (2019) Comparing progesterone in blubber and serum to assess pregnancy in wild beluga whales (Delphinapterus leucas). *Conserv Physiol* 7: coz071. doi: 10.1093/conphys/coz071.

Grotjan HE, Keel BA (1996) Data interpretation and quality control. In EP Diamandis, TK Christopoulos, eds, *Immunoassay*. Academic Press, San Diego, pp. 51–95.

Hamilton PK, Knowlton AR, Marx MK (2007) Right whales tell their own stories: The photo-identification catalog. In SD Kraus, RM Rolland, eds, *The Urban Whale: North Atlantic Right Whales at the Crossroads*. Harvard University Press, Cambridge, pp. 73–102.

Hamilton PK, Knowlton AR, Marx MK, Kraus SD (1998) Age structure and longevity in North Atlantic right whales *Eubalaena glacialis* and their relation to reproduction. *Mar Ecol Prog Ser* 171: 285–292.

Harcourt R, van der Hoop J, Kraus S, Carroll EL (2019) Future directions in Eubalaena spp.: comparative research to inform conservation. *Front Mar Sci* 5: 530. doi: 10.3389/fmars.2018.00530.

Hunt KE, Lysiak NS, Moore MJ, Rolland RM (2016) Longitudinal progesterone profiles in baleen from female North Atlantic right whales (Eubalaena glacialis) match known calving history. *Conserv Physiol* 4: cow014. doi: 10.1093/conphys/cow014.

Hunt KE, Lysiak NS, Robbins J, Moore MJ, Seton RE, Torres L, Buck CL (2017) Multiple steroid and thyroid hormones detected in baleen from eight whale species. *Conserv Physiol* 5: cox061. doi: 10.1093/conphys/cox061.

Hunt KE *et al.* (2013) Overcoming the challenges of studying conservation physiology in large whales: a review of available methods. *Conserv Physiol* 1: cot006. doi: 10.1093/conphys/cot006.

Hunt KE, Rolland RM, Kraus SD, Wasser SK (2006) Analysis of fecal glucocorticoids in the North Atlantic right whale (*Eubalaena glacialis*). *Gen Comp Endocrinol* 148: 260–272.

Hunt KE, Stimmelmayr R, George C, Hanns C, Suydam R, Brower H Jr, Rolland RM (2014) Baleen hormones: a novel tool for retrospective assessment of stress and reproduction in bowhead whales (Balaena mysticetus). *Conserv Physiol* 2: cou030. doi: 10.1093/conphys/cou030.

Inoue S, Yasunaga G, Pastene LA (2019) Comparison of progesterone concentrations in blubber and plasma among female antarctic minke whales of known reproductive status. *Fish Sci* 85: 971–977.

Kellar NM, Catelani KN, Robbins MN, Trego ML, Allen CD, Danil K, Chivers SJ (2015) Blubber cortisol: a potential tool for assessing stress response in free-ranging dolphins without effects due to sampling. *PLoS One* 10: e0115257. doi: 10.1371/journal.pone.0115257.

Kellar NM, Keliher J, Trego ML, Catelani KN, Hanns C, George JC, Rosa C (2013) Variation of bowhead whale progesterone concentrations across demographic groups and sample matrices. *Endanger Species Res* 22: 61–72.

Kellar NM, Trego ML, Marks CI, Chivers SJ, Danil K, Archer FI (2009) Blubber testosterone: a potential marker of male reproductive status in short-beaked common dolphins. *Mar Mamm Sci* 25: 507–522.

Kellar NM, Trego ML, Marks CI, Dizon AE (2006) Determining pregnancy from blubber in three species of delphinids. *Mar Mamm Sci* 22: 1–16.

Knowlton AR, Robbins J, Landry S, McKenna HA, Kraus SD, Werner TB (2015) Effects of fishing rope strength on the severity of large whale entanglements. *Conserv Biol* 30: 318–328.

Kraus SD, Moore KE, Price CA, Crone MJ, Watkins WA, Winns HE, Prescott JH (1986) The use of photographs to identify individual North Atlantic right whales (*Eubalaena glacialis*). In RL Brownell Jr, PB Best, JH Prescott, eds, *Report of the International Whaling Commision: Special Issue Volume 10*. International Whaling Commission, Cambridge, p. 7.

Legacki EL, Robeck TR, Steinman KJ, Conley AJ (2020) Comparative analysis of steroids in cyclic and pregnant killer whales, beluga whales and bottlenose dolphins by liquid chromatography tandem mass spectrometry. *Gen Comp Endocrinol* 285: 113273. doi: 10.1016/j.ygcen.2019.113273.

Mansour AAH, Mkay DW, Lien J, Orr JC, Banoub JH, Ølen N, Stenson G (2002) Determination of pregnancy status from blubber samples in minke whales (*Balaenoptera acutorostrata*). *Mar Mamm Sci* 18: 112–120.

Maxwell SM *et al.* (2013) Cumulative human impacts on marine predators. *Nat Commun* 4: 2688. doi: 10.1038/ncomms3688.

McLellan WA, Rommel SA, Moore MJ, Pabst DA (2004) Right whale necropsy protocol. In *U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Office of Protected Resources*. Silver Spring.

Mello D, Colosio A, Marcondes M, Viau P, Oliveira C (2017) Feasibility of using humpback whale blubber to measure sex hormones. *J Exp Mar Biol Ecol* 486: 32–41.

Meyer-Gutbrod EL, Greene CH (2017) Uncertain recovery of the North Atlantic right whale in a changing ocean. *Global Change Biol.* 24: 455–464.

Millspaugh JJ, Washburn BE (2004) Use of fecal glucocorticoid metabolite measures in conservation biology research: considerations for application and interpretation. *Gen Comp Endocrinol* 138: 189–199.

Mingramm F, Keeley T, Whitworth D, Dunlop R (2020) Blubber cortisol levels in humpback whales (*Megaptera novaeangliae*): a measure of physiological stress without effects from sampling. *Gen Comp Endocrinol* 117: 104606. doi: 10.1016/j.ygcen.2020.113436.

Moore MJ, Knowlton AR, Kraus SD, McLellan WA, Bonde RK (2004) Morphometry, gross morphology and available histopathology in North Atlantic right whale (*Eubalaena glacialis*) mortalities (1970-2002). *J Cetacean Res Manage* 6: 199–214.

Moore MJ, van der Hoop JM (2012) The painful side of trap and fixed net fisheries: chronic entanglement of large whales. *J Mar Sci* 2012: 230653. doi: 10.1155/2012/230653.

Noren DP, Mocklin JA (2012) Review of cetacean biopsy techniques: factors contributing to successful sample collection and physiological and behavioral impacts. *Mar Mamm Sci* 28: 154–199.

Pallin L, Robbins J, Kellar N, Bérubé M, Friedlaender A (2018) Validation of a blubber-based endocrine pregnancy test for humpback whales. *Conserv Physiol* 6: coy031. doi: 10.1093/conphys/coy031.

Palme R (2005) Measuring fecal steroids: guidelines for practical application. *Ann N Y Acad Sci* 1046: 75–80.

Palme R (2019) Non-invasive measurement of glucocorticoids: advances and problems. *Physiol Behav* 199: 229–243.

Palme R, Touma C, Arias N, Dominchin MF, Lepschy M (2013) Steroid extraction: get the best out of faecal samples. *Wien Tierarztl Monatsschr* 100: 238–246.

Papastavrou V, Leaper R, Lavigne D (2017) Why management decisions involving marine mammals should include animal welfare. *Mar Policy* 17: 19–24.

Pettis HM, Rolland RM, Hamilton PK, Knowlton AR, Burgess EA, Kraus SD (2017) Body condition changes arising from natural factors and fishing gear entanglements in North Atlantic right whales *Eubalaena glacialis*. *Endanger Species Res* 32: 237–249.

Richard JT, Robeck TR, Osborn SD, Naples L, McDermott A, LaForge R, Romano TA, Sartini BL (2017) Testosterone and progesterone concentrations in blow samples are biologically relevant in belugas (*Delphinapterus leucas*). *Gen Comp Endocrinol* 246: 183–193.

Right Whale Consortium (2019) North Atlantic Right Whale Consortium Identification, Sightings, and Genetics Databases. In *Anderson Cabot Center for Ocean Life at the New England Aquarium*, Boston.

Rolland RM, Graham KM, Stimmelmayr R, Suydam RS, George JC (2019) Chronic stress from fishing gear entanglement is recorded in baleen from a bowhead whale (*Balaena mysticetus*). *Mar Mamm Sci* 35: 1625–1642.

Rolland RM, Hunt KE, Kraus SD, Wasser SK (2005) Assessing reproductive status of right whales (*Eubalaena glacialis*) using fecal hormone metabolites. *Gen Comp Endocrinol* 142: 308–317.

Rolland RM, McLellan WA, Moore MJ, Harms CA, Burgess EA, Hunt KE (2017) Fecal glucocorticoids and anthropogenic injury and mortality in North Atlantic right whales (*Eubalaena glacialis*). *Endanger Species Resear* 34: 417–429.

Rolland RM, Moore MJ (2018) Health Assessment of Large Whales. In FMD Gulland, LA Dieruf, KL Whitman, eds, *CRC Handbook of Marine Mammal Medicine*, EdEd 3. CRC Press, Boca Raton, pp. 835–848.

Sharp SM *et al.* (2019) Gross and histopathologic diagnoses from North Atlantic right whale *Eubalaena glacialis* mortalities between 2003 and 2018. *Dis Aquat Org* 135: 1–31.

Sheriff MJ, Dantzer B, Delehanty B, Palme R, Boonstra R (2011) Measuring stress in wildlife: techniques for quantifying glucocorticoids. *Oecologia* 166: 869–887.

Trana MR, Roth JD, Tomy GT, Anderson WG, Ferguson SH (2015) Influence of sample degradation and tissue depth on blubber cortisol in beluga whales. *J Exp Mar Biol Ecol* 462: 8–13.

Trana MR, Roth JD, Tomy GT, Anderson WG, Ferguson SH (2016) Increased blubber cortisol in ice-entrapped beluga whales (*Delphinapterus leucas*). *Polar Biol* 39: 1563–1569.

Trego ML, Kellar NM, Danil K (2013) Validation of blubber progesterone concentrations for pregnancy determination in three dolphin species and a porpoise. *PLoS One* 8: e69709. doi: 10.1371/journal.pone.0069709.

Vu ET, Clark C, Catelani K, Kellar NM, Calambokidis J (2015) Seasonal blubber testosterone concentrations of male humpback whales (*Megaptera novaeangliae*). *Mar Mamm Sci* 31: 1258–1264.

Wasser SK, Hunt KE, Brown JL, Cooper K, Crockett CM, Bechert U, Millspaugh JJ, Larson S, Monfort SL (2000) A generalized fecal glucocorticoid assay for use in a diverse array of non-domestic mammalian and avian species. *Gen Comp Endocrinol* 120: 260–275.

Watson R, Munro C, Edwards KL, Norton V, Brown JL, Walker SL (2013) Development of a versatile enzyme immunoassay for non-invasive assessment of glucocorticoid metabolites in a diversity of taxonomic species. *Gen Comp Endocrinol* 186: 16–24.

Attachment C

• Center for Biological Diversity • Conservation Law Foundation •
• Defenders of Wildlife • Humane Society of the United States •
• Humane Society Legislative Fund • Natural Resources Defense Council •

Via Electronic Mail

February 19, 2021

National Marine Fisheries Service
Northeast Regional Office
55 Great Republic Drive
Gloucester, MA 01930
nmfs.gar.fisheriesbiopfeedback@noaa.gov

RE: Comments on the Draft Batch Biological Opinion and Conservation Framework

On behalf of the Center for Biological Diversity, Conservation Law Foundation, Defenders of Wildlife, the Humane Society of the United States, Humane Society Legislative Fund, Natural Resources Defense Council, and our millions of members and supporters, we submit these comments to the National Marine Fisheries Service ("NMFS") on its Draft "Endangered Species Act Section 7 Consultation on the: (a) Authorization of the American Lobster, Atlantic Bluefish, Atlantic Deep-Sea Red Crab, Mackerel/Squid/Butterfish, Monkfish, Northeast Multispecies, Northeast Skate Complex, Spiny Dogfish, Summer Flounder/Scup/Black Sea Bass, and Jonah Crab Fisheries and (b) Implementation of the New England Fisheries Management Council's Omnibus Essential Fish Habitat Amendment 2, Consultation No. GARFO-2017-00031" (hereinafter "Draft BiOp").

NMFS's Draft BiOp is fatally flawed in numerous ways. The Draft BiOp fails to properly define the agency actions under review; arbitrarily defines the environmental baseline; improperly relies on uncertain, unproven, and future mitigation measures; is not based on the best available scientific data; employs an unlawful jeopardy analysis; reaches conclusions contrary to the evidence before the agency; and fails to include a proper incidental take statement, among other shortcomings. The agency's Draft BiOp and related "North Atlantic Right Whale Conservation Framework for Federal Fisheries in the Greater Atlantic Region" (hereinafter "Framework") represent a gross dereliction of the agency's legal obligations under the Endangered Species Act ("ESA"), 16 U.S.C. §§ 1531–1544, to the critically endangered North Atlantic right whale and other ESA-listed large whale species. If finalized without substantial, fundamental changes, the Draft BiOp will only further imperil ESA-listed species, including right whales already struggling to survive in the face of ongoing entanglements in commercial fishing gear and vessel strikes in U.S. and Canadian waters.

The Draft BiOp's inadequacies with respect to right whales are particularly egregious. As NMFS is well aware, entanglements in the ropes used in commercial fisheries have become the leading cause of documented right whale deaths and serious injuries in recent years.[1] Entanglements can also increase a whale's stress hormone levels, leading to infections; make it more vulnerable to other sources of mortality like vessel strikes; and impede its ability to feed.[2] Additionally, the trauma suffered during an entanglement can reduce the chances a whale will reproduce.[3] Females that have suffered a severe entanglement "are significantly less likely to calve again."[4]

As NMFS has recognized, both the rate and severity of entanglements have increased in recent years.[5] For example, NMFS determined in 2018 that 26 percent of the right whale population is entangled each year, that the risk of an entanglement is increasing at a rate of 6.3 percent per year, and that the impacts of entanglement events on individual whales have become more severe over the last few years as U.S. fisheries have moved further offshore.[6] The increase in the frequency and severity of entanglements has coincided with the sharp population decline, reduced calving rates, and an Unusual Mortality Event unprecedented in modern times.[7] Deaths now outpace births three to two.[8]

According to the Draft BiOp, an astonishing 201 right whales were killed from 2010–2019. Draft BiOp at 225.[9] But the true death toll is likely even higher, according to a recently-

---

[1] NMFS, 2017–2021 North Atlantic Right Whale Unusual Mortality Event, https://www.fisheries.noaa.gov/national/marine-life-distress/2017-2021-north-atlantic-right-whale-unusual-mortality-event (updated Feb. 17, 2021).

[2] *See, e.g.*, Julie M. van der Hoop, Douglas P. Nowacek, Michael J. Moore, M. S. Triantafyllou. 2017. Swimming kinematics and efficiency of entangled North Atlantic right whales. Endang. Species Res. Vol. 32: 1–17, 2017, doi: 10.3354/esr00781; Julie van der Hoop, Peter Corkeron and Michael Moore. 2016. Entanglement is a costly lifehistory stage in large whales. Ecology and Evolution, 7: 92–106, doi:10.1002/ece3.2615; Cassoff R.M., Moore K.M., McLellan W.A., Barco S.G., Rotstein D.S., Moore M. 2011. Lethal entanglement in baleen whales. Dis. Aquat. Org. 96: 175−185.

[3] *See, e.g.*, Julie van der Hoop, et al. 2016.

[4] *Id.*

[5] Hayes S.A., Gardner S., Garrison L., Henry A., Leandro L. 2018. North Atlantic right whales - Evaluating their recovery challenges in 2018. NOAA Tech Memo NMFS NE. 247; 24 p. at 2, 8–9 (hereinafter "Right Whale Recovery Tech Memo"); *see also* Kraus, S., R. Kenney, C. Mayo, W. McLellan, M Moore and D. Nowacek. 2016 Recent Scientific Publications Cast Doubt on North Atlantic Right Whale Future. Frontiers in Marine Science. Opinion. August 17, 2016.

[6] Right Whale Recovery Tech Memo at 1, 2, 4, 10.

[7] NMFS, 2017–2021 North Atlantic Right Whale Unusual Mortality Event.

[8] Anderson Cabot Center, Right Whale Consortium Releases 2020 Report Card Update (Nov. 9, 2020), https://www.andersoncabotcenterforoceanlife.org/blog/2020-narwc-report-card; Pettis, H.M., Pace, R.M. III, Hamilton, P.K. 2021. North Atlantic Right Whale Consortium 2020 Annual Report Card. Report to the North Atlantic Right Whale Consortium.

[9] *See* Pace, R. M. III et al. 2021. Cryptic mortality of North Atlantic right whales. Conservation Science and Practice. e346.

published study that concludes only 29% of right whale mortalities were detected from 2010–2017. As that study also finds—and as NMFS has also acknowledged in the Draft BiOp—unobserved mortalities are far more likely to have resulted from entanglements than from vessel strikes.

Entanglements in commercial fishing gear are no longer simply impeding the recovery of this critically endangered species but are actively driving it towards extinction at an accelerating rate. The right whale's dire status and the increasing frequency and severity of entanglements have led NMFS to declare that protecting every individual is a top priority, and that the species "extinction is almost certain in the immediate future" absent swift intervention to reduce threats to the species.[10]

Yet the Draft BiOp fails to conduct the careful, probing analysis required or require adequate mitigation measures that the ESA demands. The Draft BiOp—and the inadequate proposed amendments to the Atlantic Large Whale Take Reduction Plan ("ALWTRP" or "Plan") that the Draft BiOp purports to analyze—will, if finalized as written, deprive right whales of important protections to which they are legally entitled and desperately need.

At the very least, NMFS must use its emergency rulemaking authority under the Marine Mammal Protection Act, 16 U.S.C. § 1387(g), to implement immediate measures to protect right whales from suffering further deaths and serious injuries from entanglements in commercial fishing gear while NMFS works to develop a long-term solution to the entanglement problem afflicting this species. Indeed, new information that has come to light in the short time since NMFS issued the Draft BiOp, including an observed serious injury of a right whale off Georgia due to an entanglement, only highlights the urgent need for NMFS to act as the law requires and the species' plight demands.

I. The Draft BiOp Improperly Limits the Agency Action, the Action Area, and the Effects of the Action under Review

The Draft BiOp fails to appropriately define the agency action, the action area, and the effects of the action under review. Each of these failures means that the draft has not properly evaluated the impacts of the full suite of actions requiring consultation on ESA-listed species, particularly the right whale. NMFS must address and rectify these errors before finalizing the biological opinion.

A. The Draft BiOp Improperly Defines the Agency Action

The Draft BiOp's definition of the agency action under consultation manages to be simultaneously overinclusive and underinclusive. As a result, the Draft BiOp fails undertake

---

[10] NMFS, Immediate Action Needed to Save North Atlantic Right Whales, July 3, 2019, https://www.fisheries.noaa.gov/leadership-message/immediate-action-needed-save-north-atlantic-right-whales; NMFS, Species in the Spotlight, https://www.fisheries.noaa.gov/topic/endangered-species-conservation#species-in-the-spotlight (last visited Feb. 3, 2021).

the meaningful, data-driven analysis of the full scope of the effects of these actions that the ESA requires.

The ESA's implementing regulations define "action" as:

> [A]ll activities or programs of any kind authorized, funded, or carried out, in whole or in part, by Federal agencies in the United States or upon the high seas. Examples include, but are not limited to:
>
> > (a) actions intended to conserve listed species or their habitat;
> > (b) the promulgation of regulations;
> > (c) the granting of licenses . . . [or] permits []; or
> > (d) actions directly or indirectly causing modifications to the land, water, or air.

50 C.F.R. § 402.02.

The Draft BiOp identifies three separate components of the "proposed action."

First: the authorization of ten federal fisheries NMFS authorizes and manages under the Atlantic Coastal Fisheries Cooperative Management Act ("ACA"), 16 U.S.C. §§ 5101–5108, and the Magnuson-Stevens Fishery Conservation and Management Act ("MSA"), *id.* §§ 1801–1884, including (1) American lobster, (2) Atlantic bluefish, (3) Atlantic deep-sea red crab, (4) Jonah crab, (5) mackerel/squid/butterfish, (6) monkfish, (7) Northeast multispecies, (8) Northeast skate complex, (9) spiny dogfish, and (10) summer flounder/scup/black sea bass. Draft BiOp at 22.

As part of the effects analysis for this first component of the proposed action, NMFS includes (a) the effects of changes in the operations of these federal fisheries in federal waters only as modified by the proposed ALWTRP measures, and (b) the effects of vessels transiting through state and federal waters to the federal fishing grounds. *Id.*

Second: the Framework that establishes a schedule of rulemakings, of which the current proposal to amend the ALWTRP is the first, to take place over the next decade "to further reduce M/SI in the federal fisheries." *Id.* at 23–26.

Third: the post hoc consultation on the New England Fishery Management Council Omnibus Essential Fish Habitat Amendment 2 ("Habitat Amendment") and related measures. *Id.* at 27–29.

NMFS has framed these actions (and, as a result, the action area and effects of the action) unlawfully. First, it is improper and overinclusive for NMFS to characterize its action under the Marine Mammal Protection Act ("MMPA") as the ten-year Framework for three to four phases of rulemaking, of which the current proposed ALWTRP amendments are only the first phase. Second, it is improper and underinclusive for NMFS to exclude the effects the Plan as proposed to be amended in state waters, where NMFS regulates state fisheries subject to the Plan under the MMPA.

As shown below, properly framed, the three actions that NMFS must analyze in this biological opinion are: (1) the Plan as amended by the proposed measures as implemented in both state and federal waters to regulate commercial fishing for the protection of marine mammals pursuant to the MMPA; (2) NMFS's ongoing authorization and management of federal fisheries, as modified by the proposed ALWTRP measures; and (3) the already-finalized Habitat Amendment.[11]

1. The Agency Action is Overinclusive Because the Framework Itself Is Not an Agency Action and Cannot Form the Basis for a Reasoned No Jeopardy Conclusion on the North Atlantic Right Whale

The Draft BiOp improperly defines the Framework as one of the three agency actions under consultation. NMFS characterizes the proposed ALWTRP amendments as the first of the agency's projected three to four phases of separate rulemakings over the next five to ten years that will purportedly reduce the annual average of mortality and serious injury ("M/SI") in the federal fisheries to ensure against jeopardy do not jeopardize the right whale. Draft BiOp at 23–25; *see id.* at 23 ("The Framework will further modify how the federal fixed gear fisheries operate and, as such, these changes are considered as part of the proposed action.").

But the Framework is not itself an agency action. It sets only timeframes for future rulemakings and targets for the success rates these rulemakings must achieve to bring NMFS into compliance with the ESA—which, as it admits explicitly, the proposed ALWTRP measures on the table now cannot do:

> Once the ALWTRP measures are implemented, NMFS estimates that, without further action, the federal fisheries are anticipated to result in the death of approximately an annual average of 2.2 right whales (22 right whales over a 10-year period). Our analyses indicate that further reductions in entanglements and M/SI in the federal fisheries under this Conservation Framework are needed to ensure the fisheries will not appreciably reduce the likelihood of the survival and recovery of the species as required by the ESA.

Framework at 3; *see also id.* at 4 ("With no further reduction in M/SI [above that from the proposed ALWTRP measures], our analyses indicate the federal fisheries are impacting the survival and recovery of right whales."). But NMFS cannot substitute the Framework as the action under analysis and presume future benefits from future actions simply because it cannot otherwise avoid a jeopardy conclusion on the proposed action actually in front of it.

---

[11] For the first action, the Greater Atlantic Regional Fisheries Office ("GARFO"), through its Protected Resources Division, is the "action agency" for ESA section 7(a)(2) purposes, while GARFO's Sustainable Fisheries Division is the "action agency" for the second and third actions. For all three actions, GARFO's Protected Resources Division is the "consulting agency."

Distilled to its essence, the Framework consists of two elements: (1) a schedule for future rulemakings, and (2) a projection of the necessary quantitative reductions in right whale M/SI in the federal fisheries that NMFS states it must achieve to avoid jeopardy. But neither the schedule of rulemakings nor the presumed future benefits of these rulemakings is sufficiently certain to occur. (And as explained below NMFS may not lawfully exclude M/SI in state fisheries regulated by the ALWTRP from its jeopardy analysis anyway.)

First, despite its statement of "commitment," NMFS cannot guarantee that rulemakings for Phases 2 through 4 will occur at all, let alone occur on the Framework's schedule. The Framework, developed in the last administration (as was this Draft BiOp), does not bind the present administration to follow through on this "commitment" to implement a Phase 2 rule on gillnet fisheries in 2023. Nor can the Framework bind the next two administrations that will hold office from 2025–2029 and 2029–2033 when Phase 3 and 4 rulemakings are scheduled to occur.

Even assuming the Framework could commit NMFS to a rulemaking schedule, the history of the ALWTRP belies the notion that the agency will actually meet the schedule's deadlines. In the current rulemaking alone, every time the agency has publicly represented that it would complete this rulemaking by a date certain, it has not even come close. The same is true for past ALWTRP rulemakings, which dragged on for years until litigation forced the agency to act, as illustrated by the 2007 and 2014 Plan Amendments. And even when NMFS has ultimately issued final ALWTRP amendments, it often establishes extended timeframes before regulatory changes take effect, meaning there are often no changes on the water until many months after the rule is published. NMFS is in no position to promise completed rulemakings by dates certain, let alone assume any benefits from future rulemakings will accrue soon enough to meet the agency's scheduled evaluation periods.[12]

Second, NMFS's projected risk reduction targets to be achieved from Phases 2 through 4 are no more than wishful thinking. The Framework presents no information to undergird its conclusions that future rulemakings can, in fact, hit their risk reduction targets. As NMFS repeatedly states, the Framework does not establish specific measures for each rulemaking to prescribe how each will modify fixed gear fisheries in any way that this consultation can analyze meaningfully, let alone make a rational connection between those future rulemakings and the specified risk reduction targets.[13]

---

[12] Indeed, the 2014 Biological Opinion stated that it would not expect to see effects in the right whale population estimates of the 2009 sinking groundline ALWTRP amendments and the 2008 vessel speed rule for some time and predicted it would take at least five more years to see any benefit from the 2014 vertical line rule. 2014 Biological Opinion at 147–48. It is pure fantasy here for NMFS to assume that it will have any meaningful data of the effectiveness of this proposed rulemaking and the 2023 gillnet rulemaking available by 2023–2024 sufficient to ensure the 2025 rulemaking—only four years away—meets the agency's risk reduction target.

[13] *See, e.g.*, Draft BiOp at 23 ("The Framework identifies the level of reductions in mortalities and serious injuries (M/SI) that NMFS is committed to achieve in order to meet its mandates (Table 2). At this time, the Framework does not specify particular measures to allow NMFS to consider input on these measures."); *id.* at 230–32 (identifying "general measure"); Framework, at 1 ("The Conservation

The history of the ALWTRP shows that NMFS's track record in predicting risk reductions to be achieved by past ALWTRP amendments justifies no confidence in its ability to predict that future amendments will achieve their risk reduction goals. In 2014, for example, a paper published by NMFS scientists at the Northeast Fisheries Science Center evaluating the effectiveness of ALWTRP from 1999 to 2009 found "no evidence to suggest that the frequency of entanglements or entanglement-related mortality substantially abated" over that time period; indeed, entanglement events became more frequent through the study period.[14]

In its 2014 Biological Opinion on the federal fisheries as modified by the 2014 Plan Amendments, based on data from 2007–2011, NMFS predicted that M/SI from entanglements in U.S. fisheries or fisheries of unknown origin presumptively attributed to the U.S. would be no more than 3.25 right whales on a five-year average basis.[15] It also assumed that it would take at least five years following the 2014 rule to start seeing the benefits of the trawling-up requirements. Seven years later, the current Draft BiOp now attributes an annual average of 6.724 M/SI to U.S. fisheries from 2010 to 2019, even only attributing half of entanglements in gear of unknown origin to the U.S. Draft BiOp at 225–26. Even the accuracy of this new estimate is now suspect given the best available data that rates of cryptic mortality over this time period were higher than previously thought.

Not only was the 2014 Biological Opinion wrong in predicting that risk reductions from the 2014 Rule would start to show up in the data by 2019, but as we now know, M/SI attributable to U.S. fisheries over that time period was much higher than the agency's previous assumption. NMFS has no credible basis to assert that the Framework's future rulemakings will have any better success in hitting the agency's stated targets than its past rules have.

Moreover, where the Framework's 60% risk reduction target for the current rulemaking is already demonstrably inadequate to the task of bringing M/SI below PBR and avoiding jeopardy, the Framework's risk reduction targets for future rulemakings are meaningless. The proposed ALWTRP amendments explain that NMFS established the 60% risk reduction target for premised on a PBR of 0.9 and on assigning 50% of the observed entanglements of unknown origin from 2009—2018 to the U.S. fisheries. 85 Fed. Reg. 86,878, 86,880 (Dec. 31,

---

Framework does not specify particular measures but identifies the level of reductions in mortalities and serious injuries (M/SI) that NMFS is committed to achieve in order to meet its ESA mandates."); *id.* at 4 ("The Conservation Framework describes the targets to be achieved and the dates by which they must be implemented to ensure the Framework's goals are achieved. At this time, the Conservation Framework does not specify the specific measures that will be implemented. When developing measures at each phase, we will be able to consider gear innovations, ALWTRT actions, fishing and shipping changes, and evidence of impacts of U.S. and Canadian right whale conservation."); *id.* at 7 ("As described above, this Conservation Framework specifies targets rather than particular measures to be implemented.").

[14] Pace, R.M. III, et al. 2014. Incremental fishing gear modifications fail to significantly reduce large whale serious injury rates. Endang Species Res. Vol. 26:115-126, doi: 10.3354/esr00635.

[15] NMFS, Endangered Species Act Section 7 Consultation on the Continued Implementation of Management Measures for the American Lobster Fishery, Consultation No. NER-2014-11076 (July 31, 2014) at 145.

2021). The Draft Environmental Impact Statement further explains the assumptions underlying this risk reduction target,[16] including an estimate that 40% of mortalities between 2010 and 2018 were unobserved.[17]

The newly-published Pace et al. 2021 paper, however, finds that 71% of mortalities between 2010 to 2017 were unobserved. And as NMFS is well aware, PBR is now officially 0.8 as per the final 2019 Stock Assessment Report and actually 0.7 as per the most recent data on the population estimate.[18] The 60% risk reduction targets the Framework establishes for Phases 1 and 2 are thus terminally outdated. By contrast, NMFS does not explain how it derived the risk reduction targets for Phases 3 and 4, but to the extent they rely on the outmoded 60% risk reduction target for the first two phases, they too are unreliable.

This illustrates the problem of establishing quantitative risk reduction targets years in advance of developing and implementing appropriate management measures, when the science and data are moving faster than the agency's risk reduction target-focused rulemaking process can keep up with. Nearly two years after the April 2019 ALWTRT meeting at which NMFS established the 60% risk reduction target for the current rulemaking to meet, with months to go before the agency finalizes the Plan amendments and more months still before they take effect, it is painfully clear that NMFS is still trying to navigate forward by looking only in the rearview mirror. NMFS has no credible basis to assert that the Framework's risk reduction targets established now for future rulemakings will be adequate to the task as shown by future science and data, let alone build an entire jeopardy analysis around them.

Finally, unlike the proposed ALWTRP amendments, the ongoing authorization and management of the ten federal fisheries, and the Habitat Amendment, the Framework does not "propose" to do anything now with respect to Phases 2 through 4 that will change the operations of fisheries in state and federal before those rulemaking phases actually occur. Nothing in Phases 2 through 4 currently has effects that are "reasonably certain to occur." *See* 50 C.F.R. § 402.02 ("effects of the action" are consequences caused by the proposed action that are reasonably certain to occur); *see also id.* § 402.17(b) ("[a] conclusion of reasonably certain to occur must be based on clear and substantial information"). Only if and when NMFS actually proposes new amendments to the ALWTRP in Phases 2 through 4 will it propose "actions" that may affect listed species and will require full formal consultations of their own.

In sum, NMFS may not bootstrap the Framework's aspirational goals of reducing M/SI to right whales to specified levels in future rulemakings over the next decade into an "action" with specific "effects" that incorporates the proposed ALWTRP measures as simply Phase 1 of a four-phase plan, thereby minimizing and offsetting the effects of the proposed ALWTRP measures and the ongoing operations of the fisheries themselves. The Draft BiOp's entire

---

[16] NMFS, Draft Environmental Impact Statement for Amending the Atlantic Large Whale Take Reduction Plan: Risk Reduction Rule, Dec. 30, 2020, Vol. I, at 2-37—2-40 (hereinafter "DEIS").

[17] *Id.* at 2-39 (citing Pace, R., pers. comm).

[18] NMFS, Stock Assessment Report: North Atlantic Right Whale, Apr. 2020 at 22; Colleen Coogan, NMFS, Presentation to the Atlantic Large Whale Take Reduction Team, Jan. 2021.

jeopardy analysis is premised on a fiction. NMFS must revise the Draft BiOp to omit the Framework entirely and focus as the ESA requires it to do only the only proposed actions on the table—the authorization of the federal fisheries, the proposed ALWTRP amendments (across all relevant state and federal fisheries), and the Habitat Amendment, and do so based on the best available scientific data.

2. *The Agency Action is Underinclusive Because It Does Not Consider the ALWTRP, Including the Proposed Amendments, as an Action with Effects in Both State and Federal Waters*

With respect to fisheries impacts on right whales, the Draft BiOp improperly limits the agency action to NMFS's authorization of ten federal fisheries and disclaims any responsibility for state fisheries: "As NMFS does not authorize, fund, or carry out fishing activities in state waters, these activities are not considered part of the proposed action in this Opinion. Consequently, this Opinion is evaluating effects from fishing activities (i.e., entanglement/bycatch) by vessels with federal permits in federal waters only." Draft BiOp at 22.

Similarly, with respect to the proposed rule to amend the ALWTRP, the Draft BiOp states that only "[c]hanges in the operation of these [federal] fisheries resulting from the proposed ALWTRP measures are included in our analysis in this Opinion." *Id.* For the proposed ALWTRP amendments, NMFS considers these changes to be part of the proposed action only insofar as "how the proposed measures will alter the [federal] fisheries in this opinion." *Id*. at 25.

The Draft BiOp's unduly narrow definition of the agency action improperly excludes the proposed ALWTRP measures that will govern the operations of the northeast commercial lobster and crab trap/pot fisheries in both state and federal waters. *See* 85 Fed. Reg. 86,878 (Dec. 31, 2020). But the final regulation amending the ALWTRP is an independent agency action and the agency must consult on the full range of its effects irrespective of whether they occur in state or federal waters. Similarly, NMFS's ongoing management and authorization of other state fisheries that are subject to the ALWTRP, but not subject to the proposed Plan amendments, are also ongoing agency actions on which NMFS must consult.

Section 118 of the MMPA requires NMFS to develop a "take reduction plan" for Category I and II fisheries that interact with "strategic stocks," including ESA-listed marine mammals. 16 U.S.C. §§ 1387(f)(1), 1362(19)(C). Each take reduction plan must contain regulatory measures to reduce fishery-related mortality and serious injury to below the species' potential biological removal level ("PBR")[19] within six months of the plan's implementation. *Id.* § 1387(f)(2), (f)(5)(A), (f)(7)(F).[20] The MMPA plainly does not limit the application of take

---

[19] "Potential biological removal" means "the maximum number of animals, not including natural mortalities, that may be removed from a marine mammal stock while allowing that stock to reach or maintain its optimum sustainable population." 16 U.S.C. § 1362(20).

[20] The "long-term goal" of the plan must be to reduce bycatch levels to the "zero mortality and serious injury rate" within five years. *Id.* § 1387(f)(2). The MMPA requires NMFS to amend a take reduction plan as necessary to meet these goals.

reduction plan regulation to federal fisheries. The statute's take prohibition applies to any person or vessel subject to the jurisdiction of the United States irrespective of whether the take occurs in federal or state waters or on the high seas. *Id.* §§ 1372(a)(1), (a)(2)(A). NMFS has exclusive jurisdiction to authorize the incidental take of marine mammals in commercial fisheries, irrespective of whether those fisheries are prosecuted in state or federal waters. *Id.* §§ 1371(a)(5)(E), 1387(f).

The proposed ALWTRP measures are clearly actions "intended to conserve listed species."[21] By the plain language of the ESA's implementing regulations, NMFS is not excused from complying with section 7(a)(2) in promulgating or amending a take reduction plan simply because the plan is expected to reduce mortality of an endangered marine mammal. *See* 50 C.F.R. § 402.02 (defining action); *see also Cooling Water Intake Structure Coal. v. EPA*, 905 F.23d 49, 81 (2d Cir. 2018) ("Consistent with the ESA's goal of 'conserv[ing] endangered species and threatened species, 16 U.S.C. § 1531(c)(1), the relevant inquiry is whether the action causes jeopardy or adverse modification, period—not whether it provides 'incremental improvements' that make conditions 'slightly less harmful' to a species but still reduce the likelihood of survival and recovery for that species." (citing *Alcoa v. BPA*, 175 F.3d 1156, 1162 n.6 (9th Cir. 1999)).

The proposed ALWTRP measures also constitute regulations promulgated by NMFS to authorize incidental take of marine mammals by Category I and II commercial fisheries in U.S. waters (both state and federal). NMFS may not exclude the proposed ALWTRP measures to be implemented in state waters from the scope of the consultation based on a convenient fiction that its federal fisheries authorities restrict it solely to regulating only that incidental take of ESA-listed marine mammals that occurs in federal waters by federally-permitted vessels. Although NMFS generally lacks jurisdiction to regulate state fisheries in state waters under the ACA[22] or the MSA, the MMPA gives NMFS full authority to promulgate fishing regulations to regulate

---

[21] Table 1, Draft BiOp at 19, on the history of formal consultations completed on fishery management plans or marine mammal take reduction plans, indicates that NMFS has only ever completed formal consultation on the ALWTRP once, in 1997. NMFS's past failures to complete formal consultation on its actions amending the ALWTRP notwithstanding, NMFS may not avoid its obligation to do so here.

[22] Note, however, that NMFS regulates fishing federal limited access permits issued pursuant to the American Lobster Fishery Management Plan under ACA in both state and federal waters. Federal fisheries regulations, including those of the ALWTRP, are binding on federal permit holders regardless of whether they fish in federal or state waters, although these permit holders remain subject to applicable state and local requirements as well. 50 C.F.R. § 697.4(b) (citing 50 C.F.R. pt. 229). If federal or state management measures differ, the more restrictive applies. *Id.* Thus, even considering only its ACA authority to authorize and manage lobster fishing in federal waters, NMFS must include within the scope of its action fishing in state waters by vessels with federal limited access lobster permits.

marine mammal incidental take that apply to commercial fisheries regardless of where they are prosecuted.[23,24]

Under the MMPA, NMFS authorizes marine mammal incidental take by vessel owners participating in any Category I or II commercial fishery who have duly registered[25] and who comply with applicable take reduction plan regulations. *Id.* §§ 1387(c)(2)(A); 1387(c)(3); 50 C.F.R. § 229.4(a)(1), (b). Additionally, each owner must comply with reporting requirements and "any applicable take reduction plan and emergency regulations" established by NMFS. 16 U.S.C. § 1387(c)(3)(A)(iii)–(iv); 50 C.F.R. § 229.4(f), (k). These requirements apply to all fishing vessels in the commercial fishery to which the Plan applies, irrespective of whether the fishing vessel operates in state waters, federal waters, or both, unless the applicable Plan explicitly exempts them. *See, e.g.*, 50 C.F.R. § 229.32(a)(2)(i) (applying ALWTRP regulations to all U.S. waters in the Atlantic except for areas exempted in paragraph (a)(3)).

The ALWTRP regulations specify how, where, and when fishing vessels and operators subject to the Plan may fish in both state and federal waters. *See, e.g.*, 50 C.F.R. §§ 229.32(b) (establishing gear marking schemes for different areas); 229.32(c) (establishing general, area-specific, and seasonal gear restrictions). Both the MMPA and its implementing regulations prohibit fishing in violation of these restrictions, 16 U.S.C. § 1372(a)(5), 50 C.F.R. § 229.3(i), or even owning, operating, or being on board a vessel subject to the ALWTRP unless that vessel and its gear comply with those regulations. 50 C.F.R. § 229.3(h).

---

[23] NMFS's current position that it lacks authority to regulate fishing in state waters, Draft BiOp at 22, flatly contradicts its previous statements in first promulgating the ALWTRP in 1997. There, NMFS specifically rejected an argument that its authority to regulate the incidental take of marine mammals in commercial fisheries is limited to federally licensed and regulated marine fisheries:

> The MMPA grants legal authority to NMFS to regulate any vessel allowed to engage in commercial fishing in all U.S. waters, including both state and Federal waters. . . . The MMPA's legal authority applies without regard to whether a fishery occurs in state waters or Federal waters. Section 118 of the MMPA does not make a distinction between Federal or state fisheries but applies to any fishery that interacts with marine mammal stocks.

62 Fed. Reg. 39,157, 39,170 (July 22, 1997).

[24] The ESA also provides NMFS with authority to regulate fishing in state waters for the protection of listed species. 16 U.S.C. § 1540(f). For example, NMFS promulgated the ALWTRP regulations governing the state and federal waters in the Southeast Restricted Area, 50 C.F.R. § 229.32(f), under the authority of both the ESA and the MMPA. 79 Fed. Reg. 36, 586, 36,610 (June 27, 2014).

[25] *See* NMFS, Marine Mammal Authorization Program, available at https://www.fisheries.noaa.gov/national/marine-mammal-protection/marine-mammal-authorization-program ("If you own a commercial fishing vessel or non-vessel gear that operates in a ***Category I or II fishery***, you must obtain a marine mammal authorization certificate each year from NOAA Fisheries or its designated agent. This certificate legally authorizes you to incidentally take a marine mammal in a commercial fishery.").

The proposed ALWTRP measures will prescribe additional restrictions on how, where, and when lobster vessels may fish in state waters, irrespective of whether they are also permitted to fish in federal waters. *See id*. § 229.32 (ALWTRP); *see also* 85 Fed. Reg. at 86,891–900 (proposed measures); Draft BiOp at 185 ("The regulatory component of the Plan includes a combination of broad fishing gear modifications and time area restrictions . . . . Revisions are made to the Plan by implementing regulations as new information and technology becomes available."); *id.* at 185–87 (summarizing Plan regulatory measures). Because NMFS "authorizes" via the Marine Mammal Authorization Program ("MMAP") fishing activities in state waters under the ALWTRP, it therefore must consult on the proposed amendments to the Plan as well as its ongoing authorization of other fisheries via the existing Plan regulations and MMAP.[26]

In NMFS's recent 2021 List of Fisheries, it maintains the listing of the Northeast/Mid-Atlantic American lobster trap/pot fishery as a single Category I fishery. 86 Fed. Reg. 3028, 3046 (Jan. 14, 2021). NMFS explicitly addressed and rejected comments from the Maine Lobstermen's Association seeking to separate out and reclassify the Maine lobster fishery, *id.* at 3035–36; it treated a similar request from the Massachusetts Division of Marine Fisheries for Massachusetts state waters the same way. *Id.* at 3037–38.

Just as NMFS denied requests from state fishing interests and a state fishery management agency to separate out and recategorize their respective state fisheries, it must also recognize that it cannot separate out the federal components of this Category I fishery as regulated by the proposed amendments to the ALWTRP for separate analysis at the behest of federal fisheries managers. The ALWTRP is a single set of federal regulations governing the activities of this Category I fishery in both state and federal waters and must be recognized and analyzed as such. Similarly, NMFS cannot separate out its ongoing authorization of other fisheries in state waters under the ALWTRP and MMAP for the same reason.

Take reduction plan regulations promulgated under 16 U.S.C. § 1387(f) are no different than regulations or authorizations issued under 16 U.S.C. §§ 1371(a)(5)(A)(i), 1387 (a)(5)(D), or 1387(a)(5)(E). Under both sections, NMFS may authorize the incidental take of marine mammals, provided certain standards are met and subject to permissible methods of taking. Under both sections, whenever such authorizations may affect ESA-listed species, NMFS must comply with its ESA section 7(a)(2) obligations.

The Draft BiOp here (and the agency's past biological opinions that consistently failed to consult on ALWTRP amendments as agency actions in their own right) stands in marked contrast to NMFS's practice in consulting on ESA regulations governing the incidental take of sea turtles in

---

[26] It is irrelevant that NMFS has not previously authorized the lethal incidental take of ESA-listed large whales such as the North Atlantic right whale and will not do so here either. Through the MMAP program, NMFS authorizes the incidental take of the Gulf of Maine DPS of humpback whale and the Canadian east coast stock of minke whale by vessels engaged in the Category I fishery who register and comply with the ALWTRP requirements. This authorization therefore triggers the ESA consultation requirement for all listed species and critical habitats in state waters potentially affected by fishing activities subject to regulation by the proposed ALWTRP measures.

shrimp trawls and the authorization and management of shrimp fisheries in the southeast. In the most recent (but soon to be superseded) biological opinion, completed in 2014, NMFS consulted on the continuation of two actions: (1) conserving sea turtles via its sea turtle conservation regulations, that exempt incidental take under specific conditions; and (2) authorizing shrimp trawling under the federal South Atlantic and Gulf of Mexico Shrimp FMPs under the MSA.[27] That consultation did not limit itself to the effects of the sea turtle conservation regulations in the federal fisheries, however, but analyzed their effects in state waters as well:

> NMFS's sea turtle conservation regulations under the ESA apply to all shrimp trawlers, wherever they occur. They apply in federal waters (i.e., the Gulf and South Atlantic EEZ), where NMFS authorizes shrimp trawling via two federal fishery management plans under the MSFCA, and in state waters, where fisheries are authorized by respective state agencies. Unlike NMFS's authority to manage fisheries under the Magnuson Stevens Act, NMFS's authority to conserve listed species under the ESA is not restricted to federal waters. . . . Thus, although NMFS does not authorize state fisheries, NMFS, in implementing the sea turtle conservation regulations, does mandate that those state-authorized fisheries comply with the sea turtle conservation regulations [affecting how shrimp trawlers may fish] and provides an exemption from the Section 9 prohibitions that would otherwise apply to sea turtle species.[28]

There is no meaningful distinction between ESA sea turtle conservation regulations and MMPA take reduction plan regulations. Both regulate how state and federal fisheries subject to their requirements may operate and receive authorization to take federally-protected species irrespective of where the fishery operates or which agency has jurisdiction over the management of the fishery resource itself. NMFS must treat the proposal to amend the ALWTRP and its ongoing authorization of state and federal fisheries under the ALWTRP and MMAP the same way—by consulting on it as an agency action.

No matter how longstanding, NMFS's crabbed view of its authority to regulate commercial fishing in state waters under the MMPA is inconsistent with the law and its own statements, both past and present.[29] NMFS must correct this legal error—and all of the legal errors that flow from

---

[27] *See* NMFS, Reinitiation of Endangered Species Act (ESA) Section 7 Consultation on the Continued Implementation of the Sea Turtle Conservation Regulations under the ESA and the Continued Authorization of the Southeast U.S. Shrimp Fisheries in Federal Waters under the Magnuson-Stevens Fishery Management and Conservation Act (MSFMCA), Consultation No. SER-2013-12255 (Apr. 18, 2014), https://media.fisheries.noaa.gov/dam-migration/shimpbo_2014.pdf.

[28] *Id.* at 35 (defining action area as both Gulf and South Atlantic EEZ and adjacent marine and tidal state waters).

[29] The agency's outreach guides, published to assist fisheries participants subject to the ALWTRP understand how the regulations apply to them, demonstrate the specifics of ALWTRP requirements in various state waters. *See, e.g.*, NMFS, Atlantic Large Whale Take Reduction Plan, Northeast Trap/Pot

it—before concluding formal consultation and issuing a final biological opinion by defining the proposal to amend the ALWTRP as an agency action to be consulted on and by considering the full range of the effects of this proposal in both state and federal waters.

B. The Draft BiOp Arbitrarily Limits the Action Area and Effects of the Action to Federal Waters

Because NMFS has improperly restricted the scope of the action subject to consultation, it has also improperly defined the action area. Draft BiOp at 68 ("For the purposes of this Opinion, the action area encompasses the area in which the ten [federal] fisheries operate, broadly defined as all U.S. EEZ waters from Maine through Key West, Florida. This includes state waters (0 to 3 nautical miles) as vessels fishing in the federal fishery transit to the fishing grounds through these waters.").

As explained above, NMFS must consult on the full range of the effects the proposed measures to amend the ALWTRP and its ongoing management and authorization of other fisheries subject to the ALWTRP in both state and federal waters. Therefore, it must redefine the action area to encompass not only the federal waters in which federal fisheries operate but also the state waters in which NMFS regulates fisheries subject to the ALWTRP's requirements. Here, because NMFS's proposed MMPA action is to amend the ALWTRP regulations that govern the northeast commercial lobster and crab trap/pot fisheries in both state and federal waters, all state waters in which these fisheries operate are part of the action area. Additionally, because NMFS continues to authorize and manage other fisheries subject to the ALWTRP in both state and federal waters, all state waters in which these fisheries operate are also part of the action area. Relatedly, NMFS must consult on the effects of fishing vessel transits and the risks of vessel strikes from both federally permitted vessels transiting to the federal fishing grounds and vessels regulated by the ALWTRP operating only in state waters.

Similarly, NMFS has improperly limited the "effects of the action," or "all consequences to listed species or critical habitat that are caused by the proposed action," 50 C.F.R. § 402.02, section of its analysis. It has inappropriately failed to consider the effects of fishing in state waters that will be regulated by the proposed ALWTRP amendments as well as the effects of fishing in state waters under the unchanged aspects of the Plan as part of the effects of the action.

The Draft BiOp acknowledges that right whales are susceptible to entanglement in pot/trap and gillnet gear, and that any part of the gear (buoy line, groundline, floatline, and surface system line) creates an entanglement risk that can injure or kill a right whale. *See, e.g.*, Draft BiOp at 168. The Draft BiOp estimates that right whales are killed or seriously injured every year in state fisheries, yet it fails to consider these impacts as part of the effects of the action. *Id.* at 169 (emphasis added); *see also id.* ("There are state fishery components of the Northeast sink gillnet, Northeast/mid-Atlantic lobster trap/pot, and the Atlantic mixed species pot/trap."). As

---

Fisheries Requirements and Management Areas, https://media.fisheries.noaa.gov/dam-migration/northeast_trap_pot___2018_alwtrp.pdf; NMFS, Atlantic Large Whale Take Reduction Plan, Supplements, https://media.fisheries.noaa.gov/dam-migration/all_supplements_2018_alwtrp.pdf.

NMFS manages and authorizes these fisheries under the ALWTRP and MMAP,[30] NMFS must appropriately categorize them in the baseline and describe their effects under effects of the action rather than cumulative effects.

After correcting its description of the agency action and the action area, NMFS must revise its effects of the action analysis to include the effects of the proposed ALWTRP measures and its continuing authorization of other fisheries under the existing ALWTRP regulations and MMAP on listed species and critical habitat in both state and federal waters to which these measures will apply.[31]

II. NMFS Must Use the Best Available Scientific Data on the Effects of the Fisheries in Both State and Federal Waters

NMFS is obligated to use the best available scientific data in describing and evaluating the effects of entanglements on right whales. The Draft BiOp's effects description is incomplete and does not apply the best available scientific data. As a result, its effects analysis and integration/synthesis of effects are irredeemably flawed and cannot be carried forward to the final biological opinion.

First, as a matter of law, NMFS may not lawfully exclude right whale entanglements in state fisheries that are subject to the ALWTRP's requirements. *See supra*, Section I; Draft BiOp at 216, 227. Further, as a matter of scientific data, the entire MMPA section 118 process for categorizing the Category I and II fisheries in both state and federal waters that are subject to the ALWTRP makes no such arbitrary distinctions because NMFS recognizes that it cannot distinguish by political jurisdiction the risks posed by trap/pot fisheries. In the 2021 List of Fisheries ("LOF"), NMFS found that gear used in the state and federal lobster trap/pot fishery in the northeast and mid-Atlantic is functionally equivalent; that the "sample size of recovered gear from entanglements is small and much of the retrieved gear is unmarked and cannot be attributed to a particular location;" that current gear marking systems are wholly inadequate to determine relative entanglement risks in state vs. federal fisheries; that it is likely that entanglements occur in areas where they have not yet been observed or reported; that "entanglement data indicate that the gear used across this fishery remains a risk to right whales." 86 Fed. Reg. at 3036–37.

It is fundamentally irrational for NMFS to determine on the one hand that the data available on entanglements cannot be used to exclude particular state fisheries from the overall Category I

---

[30] *See, e.g.*, NMFS, Atlantic Large Whale Take Reduction Plan: Mid-Atlantic Trap/Pot Fisheries Requirements and Management Areas at 4, available at https://media.fisheries.noaa.gov/dam-migration/mid_atlantic_trap_pot_2018_alwtrp.pdf.

[31] Among many other fatal flaws in the jeopardy analysis, as described below, it was arbitrary for NMFS not to include the effects of the state fisheries as managed by the ALWTRP in the "without fisheries" scenario of its state-space mark-recapture model projecting population trajectories under scenarios with and without the proposed action. Draft BiOp at 330–38. Regardless, the entire modeling exercise was purely academic because it was built on unlawful definitions of the proposed action, unfounded assumptions about the efficacy of the proposed ALWTRP measures and the Framework, and outdated data on estimated M/SI in the U.S. fisheries.

determination for section 118 purposes, but on the other to apply the Decision Support Tool—that does not take into account all the uncertainties on the origins of entanglements that NMFS points out in the LOF—to apportion M/SI entanglements in U.S. trap/pot gear between state and federal fisheries on a 73/27 percentage split.[32] The final biological opinion must fully account for 100% effects of all right entanglements in state and federal fisheries managed by the ALWTRP and may not relegate state fisheries impacts to the cumulative effects section.

Second, in estimating future lethal right whale entanglements, the Draft BiOp relies on data from 2010 to 2019 of 112 confirmed right whale entanglements, 49 of which resulted in M/SI. *Id.* at 222. But the Draft BiOp then counts only entanglements that result in mortality or serious injury determinations, *id.* at 223, excluding all observed entanglements that were not determined to have resulted in M/SI. This decision arbitrarily contradicts NMFS's own statements in the 2021 List of Fisheries "there have been a number of life-threatening entanglements since 2010 that have resulted in a non-serious injury due to disentanglement intervention. (Henry *et al*., 2019)." 86 Fed. Reg. at 3036. These cases "that would have been serious injuries prior to disentanglement are not counted against PBR in the SAR, but they are included in the recorded takes for the LOF and associated management measures." *Id.* It is arbitrary and irrational for the agency to include these cases for purposes of the LOF but exclude them for purposes of the ESA consultation where the only difference is that in the non-M/SI cases a right whale was lucky enough to be sufficiently disentangled by a response team. The Draft BiOp's approach is in fact the opposite of "provid[ing] the benefit of the doubt to the species and a more conservative estimate of total right whale entanglements." Draft BiOp at 223.

Third, NMFS's estimates of total (observed + cryptic) mortalities between 2010 and 2019 in both Canada and the US from all causes, Draft BiOp at 225, and the calculations reflected in Row 5 of Table 57[33] must be recalculated in light of the best available data from the recently-published Pace et al. 2021 study on cryptic mortality. The Draft BiOp's total right whale mortality estimate of 201 whales from 2010 to 2019 includes 90.04 observed mortalities and an estimated 110.96 unobserved mortalities. The Draft BiOp thus assumes that 45% of mortalities were observed and 55% were unobserved.

---

[32] This is especially true given that NMFS has never established reporting requirements for the federal lobster fishery, Draft Biop at 29, rendering it "difficult" to define fishing effort, *id.* at 33, and to determine the number of lines fished in federal waters. It is also irrational for NMFS to state, without support, that Canadian snow crab gear is "more lethal than most U.S. fishing gear." Draft BiOp at 224. One, as NMFS has reiterated many times, only a tiny fraction of entangling gear is ever recovered, and only a tiny fraction of recovered gear is ever able to be identified definitively to a fishery. Second, the U.S. lobster fishery has steadily shifted northwards and offshore, Right Whale Recovery Tech Memo at 4–5, where "[o]ffshore U.S. gear may be equivalent in risk of injury and mortality given the large diameter of the rope fished and the long and heavy trawls." DEIS at 2-39. That snow crab gear is more readily identifiable when taken off a whale says nothing about relative lethality, only about relative identifiability in the face of wholly inadequate gear marking requirements.

[33] We assume that the caption for Table 57 stating that the data comes from 2010 to 2018 (rather than 2019) is in error and should read 2010 to 2019.

In Pace et al. 2021, however, the authors determined based on data from 2010–2017 that the observed mortality detection rate was only 29% of total mortality, leaving 71% of mortalities undetected. NMFS must update its entire effects analysis to explain what this means for its calculations for unobserved cryptic mortalities of unknown cause and unknown country to update the total and annual average M/SI entanglements attributed to U.S. fisheries from 2010–2019. (Draft BiOp at 225–26, Table 57, rows 5 and 6). For now, every calculation in the Draft BiOp's effects analysis from p. 225 on based on the estimate of 6.724 annual average M/SI attributable to U.S. fisheries cannot be carried forward into the final biological opinion.

Even when NMFS updates that calculation, however, the Draft BiOp's effects analysis is so incomplete and unfounded that it cannot be fixed by rejiggering a few numbers in a table. NMFS cannot exclude the M/SI entanglements in state fisheries regulated by the ALWTRP from its effects analysis. *Id.* at 223. It cannot assume that the stated 60% risk reduction target for the current ALWTRP amendments is the appropriate goal. *Id.* at 228. It cannot assume the currently proposed measures will even achieve the 60% risk reduction target. *Id.* at 228–30. It cannot assume its future risk reduction targets for Framework Phases 2 through 4 are appropriate or achievable. *Id.* at 230–32. Its entire jeopardy analysis and no jeopardy determination for the right whale, Draft BiOp at 326–42, including the population projection model, rests on assumptions that are neither legally tenable nor factually supportable.

III. The Draft BiOp Improperly Defines the Environmental Baseline

NMFS's definition of the environmental baseline is unlawful in two distinct ways. First, it fails to properly examine whether the right whale is already in jeopardy. Second, it arbitrarily includes operations of the fisheries as part of the environmental baseline thus ignoring ongoing jeopardy risks.

A. NMFS Fails to Evaluate Whether the Right Whale Is Already in Jeopardy

NMFS's Draft BiOp fails to analyze whether the right whale's risk of extinction is already sufficiently high to qualify as jeopardy. This is arbitrary.

It is critical that NMFS explain whether the right whale is already at jeopardy. This is because if a species is already at jeopardy, additional action that "causes some deterioration in the species' pre-action condition" is prohibited. *Nat'l Wildlife Fed'n*, 524 F.3d at 930 ("[W]here baseline conditions already jeopardize a species, an agency may not take action that deepens the jeopardy by causing additional harm."). In other words, "if baseline conditions are already dire, then even a small additional impact due to [takes caused by the action under review] may require a jeopardy determination." *Oceana v. Pritzker*, 75 F. Supp. 3d 469, 491 (D.D.C. 2014); *see also Am. Rivers v. Fed. Energy Regulatory Comm'n*, 895 F.3d 32, 46–47 (D.C. Cir. 2018) (holding biological opinion unlawful where agency failed to take degraded baseline conditions caused by two decades of dam operations into account).[34]

---

[34] NMFS recently enacted amendments to its longstanding regulations implementing section 7 of the ESA that purport to overturn the standard articulated by the Ninth Circuit in *Nat'l Wildlife Fed'n v. Nat'l Marine Fisheries Service*. However, those regulatory changes are inconsistent with the statute and

NMFS itself has recognized the right whale as one whose "extinction is almost certain in the immediate future" if existing threats are not dramatically reduced;[35] that anthropogenic threats appear to be worsening; and that death, serious injuries, and other harmful impacts from entanglements are currently the primary driver behind the species' dire status. *See, e.g.*, Draft BiOp at 94–95. Given the species' existing status, NMFS has concluded that "its resilience to future perturbations is expected to be very low," and "the species may decline towards extinction if prey conditions worsen, and anthropogenic mortalities are not reduced." *Id.* at 95.

Yet the Draft BiOp contains no analysis of whether the right whale is already in jeopardy. NMFS's failure stems, at least in part, from its reliance on the Trump administration's 2019 unlawful amendments to longstanding regulations implementing section 7 of the ESA. In enacting these amendments, the agency advanced a new interpretation of "appreciably" in the definition of "jeopardize the continued existence of." *See* 50 C.F.R. § 402.02. Specifically, the agency asserted that a species cannot be "in jeopardy," "in peril," or "jeopardized" by baseline conditions, and that any other interpretation would be inconsistent with the ESA. 84 Fed. Reg. 44,976, 44,987 (Aug. 27, 2019); 83 Fed. Reg. 35,178, 35,182–83 (July 25, 2018). To the contrary, NMFS's interpretation is inconsistent with the protections of section 7(a)(2) and the overall purposes of the ESA. The agency itself has previously recognized that, "[t]he very concept of 'jeopardy' is that a Federal agency should not authorize, fund, or carry out an action that would injure a listed species' chances for survival to the point that recovery is not attainable." 51 Fed. Reg. 19,926, 19,934 (June 3, 1986).

NMFS's unlawful interpretation allows it to take actions that perpetuate or worsen existing conditions, even when doing so will mean that a species will never recover, undermining one of the primary purposes of the ESA "to ensure the recovery of endangered and threatened species, not merely the survival of their existing numbers." *Alaska Oil & Gas Ass'n v. Jewell*, 8145 F.3d 544 (9th Cir. 2016) ("the goal of species recovery is paramount" under the statute). NMFS's approach renders the prohibition on actions that jeopardize a protected species meaningless in the very situation where species need them the most. *See* 51 Fed. Reg. at 19,934 ("Congress intended that the 'jeopardy' standard be the ultimate barrier past which Federal actions may not proceed…").

---

unlawful. The regulatory changes are the subject of several lawsuits, and the Biden administration has included the regulations on a list of actions it is reviewing. *See, e.g.*, *Ctr. for Biological Diversity, et al. v. Bernhardt, et al.*, Case No. 4:19-cv-05206 (filed N.D. Cal. Aug. 21, 2019); *State of California, et al. v. Bernhardt, et al.*, Case No. 4:19-cv-06013 (filed N.D. Cal. Sept. 25, 2019); *Animal Legal Defense Fund v. Bernhardt, et al.*, Case No. 4:19-cv-06812 (filed N.D. Cal. Oct. 22, 2019); White House, Fact Sheet: List of Agency Actions for Review, Jan. 20, 2021, https://www.whitehouse.gov/briefing-room/statements-releases/2021/01/20/fact-sheet-list-of-agency-actions-for-review/.

[35] NMFS, Immediate Action Needed to Save North Atlantic Right Whales, July 3, 2019, https://www.fisheries.noaa.gov/leadership-message/immediate-action-needed-save-north-atlantic-right-whales; NMFS, Species in the Spotlight, https://www.fisheries.noaa.gov/topic/endangered-species-conservation#species-in-the-spotlight (last visited Feb. 3, 2021).

Indeed, that is just what is happening with right whales. Decades of entanglements in fishing gear and other stressors have devastated the population and contributed to its current steep decline. While NMFS has proposed amendments to the ALWTRP, they cannot support the agency's failure to examine whether the right whale is already in jeopardy. In other words, "the species already stands on the brink of extinction, and the incremental improvements pale in comparison to the requirements for survival and recovery," *Aluminum Co. of America v. Bonneville Power Admin.*, 175 F.3d 1156, 1162 n.6 (9th Cir. 1999), particularly where, as described below, the measures on which NMFS relies are largely unproven and uncertain.

B. NMFS Improperly Includes Ongoing Activities as Part of the Environmental Baseline

NMFS's Draft BiOp improperly includes operations of the fisheries in state and federal waters as managed and authorized by NMFS under the ACA, MSA, and MMPA that are (or should be) the subject of the Draft BiOp as part of the environmental baseline. Courts have rejected biological opinions that categorize "ongoing agency activities" as part of the environmental baseline, rather than as part of "the effects of the action," as inconsistent with the ESA. *See Nat'l Wildilfe Fed'n*, 524 F.3d at 926–29. For example, in *National Wildlife Federation*, NMFS incorporated the ongoing impacts of a dam operation into the environmental baseline by claiming that ongoing operations were "non-discretionary." *Id.* at 928. The court held the biological opinion unlawful because the ESA does not permit agencies to "ignore potential jeopardy risks by labeling parts of an action non-discretionary." *Id*. Such an approach undermines the precautionary nature of the ESA and the purpose and protections that section 7(a)(2) consultations are supposed to provide.

The same is true here. NMFS cannot sweep the impacts of the fisheries analyzed in the Draft BiOp under the rug by including them in the environmental baseline. That the agency has previously consulted on the fisheries is irrelevant. The "effects of the action" include *all* effects of an ongoing federal agency action over which the agency has discretionary involvement or control—regardless of whether consultation was previously conducted on the action.

NMFS's approach is especially arbitrary here for two reasons. First, none of the agency's prior consultations on the ongoing operation of the fisheries at issue in the Draft BiOp have properly defined the agency action under review, the relevant action area, or the effects of that action on the right whale and other ESA-listed whales or included a proper ITS. For example, the agency's prior consultations have always arbitrarily narrowed the scope of the agency action under review to the agency's authorization of federal permits under applicable fishery management plans, ignoring its authorization and management of the fisheries in both state and federal waters under the MMPA; arbitrarily narrowed the scope of the effects of the action by focusing on only entanglements that cause death or serious injury; and unlawfully failed to contain an ITS authorizing and mitigating the extent of permitted take.

Second, NMFS's new regulatory definition of the environmental baseline (already the subject of several lawsuits) specifies that "ongoing agency activities or existing agency facilities **that are not within the agency's discretion to modify** are part of the environmental baseline." *See* 50 C.F.R. § 402.02 (emphasis added). Yet NMFS has the authority to modify the operations of the federal fisheries that are the subject of this opinion under the MSA and the ACA and has the authority under the MMPA to modify—or halt altogether—the operations of all commercial fisheries subject to the ALWTRP in both state and federal waters.

That NMFS is proposing to change how the American lobster and Jonah crab fisheries operate to reduce risk to right whales does not change the equation. A decision to continue an ongoing action—even if modified to be slightly less harmful than it was previously—is as much a decision to carry forward the harmful effects as it is a decision to continue the action in a slightly less detrimental fashion. *See* 50 C.F.R. § 402.02 (defining agency "action" as anything a Federal agency authorizes, funds, or carries out).

IV. The Draft BiOp Improperly Relies on Unproven, Uncertain, Future Mitigation Measures to Reduce the Impacts of the Fisheries

The ESA prohibits NMFS from relying on unproven, uncertain, or future mitigation measures in reaching a no-jeopardy determination. Yet that is just what NMFS has done in the Draft BiOp. Indeed, nearly the entire draft opinion—including the agency's key finding that operation of Atlantic fisheries will not jeopardize the continued existence of critically endangered North Atlantic right whales—is based on unproven or future measures from the Framework and the current proposed ALWTRP rulemaking. This approach violates a basic tenet of the ESA that the risk that mitigation measures may not occur or may be ineffective "must be borne by the project, not by the endangered species," *Sierra Club v. Marsh*, 816 F.2d 1376, 1386 (9th Cir. 1987), and renders NMFS's Draft BiOp unlawful as written.[36]

As courts have made clear, an agency cannot rely on "unapproved and undefined mitigation measures" in reaching a no jeopardy conclusion. *Ctr. for Biological Diversity v. Bernhardt*, 982 F.3d 723, 744 (9th Cir. 2020). Rather, "mitigation measures supporting a [biological opinion's] no jeopardy or no adverse modification conclusion must be 'reasonably specific, certain to occur, and capable of implementation; they must be subject to deadlines or otherwise-enforceable obligations; and most important, they must address the threats to the species in a way that satisfies the jeopardy and adverse modification standards.'" *Ctr. for Biological Diversity v. Salazar*, 804 F. Supp. 2d 987, 1001 (D. Ariz. 2011) (quoting *Ctr. for Biological Diversity v. Rumsfeld*, 198 F. Supp. 2d 1139, 1152 (D. Ariz. 2002)). Mitigation measures that may eventually be developed under the MMPA, such as new ALWTRP amendments, "do[] not change this analysis because . . . [the] MMPA . . . does not alter the agency's obligations under Section 7 of the ESA." *Ctr. for Biological Diversity v. Bernhardt*, 982 F.3d at 747.

The Draft BiOp violates this fundamental premise in multiple ways. First, even if the Framework were appropriately before NMFS for consultation as a legitimately-proposed agency action—which it is not—the Draft BiOp would still be arbitrary in relying on future Framework

---

[36] To the extent NMFS is relying on the recent changes to its regulations implementing section 7 of the ESA that provide the agency can rely on future mitigation promises "as proposed" without requiring "specific binding plans or a clear, definite commitment of resources," 84 Fed. Reg. at 44,979–80, 45,017, such reliance is unlawful because the new regulatory language violates section 7 of the ESA. *See* 16 U.S.C. § 1536(a)(2), (b)(3)(A), (b)(4)(A); *see also NWF v. NMFS*, 524 F.3d at 935–36.

rulemakings to avoid a jeopardy finding.[37] NMFS relies on the Framework as the action under consultation to perform its jeopardy analysis and rationalize its no jeopardy conclusion. *See, e.g.*, Draft BiOp at 330 (no jeopardy conclusion relying on the fact "implementation of the Framework will reduce M/SI by at least 60% in gillnet and other pot/trap fisheries in 2023, reduce M/SI by at least an additional 60% in fixed gear in federal waters in 2025, and by an additional 87% in fixed gears in federal waters in 2030"). The Framework's purported actions "include the current ALWTRP rulemaking and anticipates three additional rulemakings *over the next ten years*." Framework at 5 (emphasis added).

Yet the Framework consists of nothing but unproven, uncertain, future mitigation measures as demonstrated above. By its terms, the Framework "**does not specify particular measures.**" *Id.* at 1 (emphasis added). Instead, it sets a series of goals to reduce risk in federal fisheries over the next ten years by certain percentages, with no mention of what those measures will entail, when they would go into effect in the water, or how NMFS is justified in assuming the measures will actually hit the intended risk reduction targets. Thus, the entire Framework is nothing more than "'general commitment[s] to future improvement' [that] are insufficient under Section 7." *Ctr. for Biological Diversity v. Bernhardt*, 982 F.3d at 747 (citing *Nat'l Wildlife Fed. v. Nat'l Marine Fisheries Serv.*, 524 F.3d 917, 935–36 (9th Cir. 2008)). That notion resonates particularly strongly here, where the agency is allowing fisheries to continue during the pendency of the purported development of the Framework rulemakings that NMFS candidly admits are necessary to avoid jeopardy. *See Nat'l Wildlife Fed'n. v. Nat'l Marine Fisheries Serv.*, 184 F. Supp. 3d 861, 908 (D. Or. 2016) ("Reliance on a 'commitment' to achieve a certain percent increase in salmon survival does not relieve [NMFS] of the requirement to rely only on those actions that are reasonably certain to occur." (citation omitted)).

Second, the Draft BiOp relies on measures in the current proposed rule to amend the ALWTRP that are unproven and therefore not guaranteed to hit the projected risk reduction goal. For example, the agency's no jeopardy conclusion relies on its claim that the current proposed rule to amend the ALWTRP "will reduce M/SI in U.S. waters by at least 60% across lobster and Jonah crab fisheries." Draft BiOp at 330. This assumption is based, in large part, on the use of weak rope or weak insertions. But the assumption of the efficacy of weak rope or weak contrivances for reducing serious injuries and mortalities is just that—an assumption—that is largely theoretical and has never been tested in the field. Lower-pound breaking strength ropes will not necessarily reduce or avoid mortality or serious injury or longer-term sublethal impacts depending on the complexity and specifics of an entanglement event. For example, even so-called weak rope could wrap around a whale's mouth and damage its baleen, thereby impeding its ability to feed, leading to weight loss and starvation. Even if that weight loss is not fatal in and of itself, in females it can contribute to delayed reproduction. Moreover, right whale calves and juveniles are likely not strong enough to break 1700-lb rope. Indeed, the single paper on which the concept of weak rope as a mitigation measure was developed is based on the "suggest[ion]" that "**adult** right whales . . . can break free from [] weaker ropes and thereby

---

[37] Additionally, as explained above, the Framework also unlawfully excludes consideration of take in state waters.

avoid a life-threatening entanglement."[38] The study's authors have admitted that younger right whales have a much lower force output than adult right whales,[39] meaning young whales are less likely to be able to break even lower-pound breaking strength rope.

The agency's reliance on weak rope to reduce risk, especially in offshore areas is particularly inappropriate where (1) lobstermen use a large number of pots per trawl, and thus may not be able to safely use weak rope, contrivances, or toppers; (2) the area is of particularly high risk for right whales due to the heavier line and increased number of traps; and (3) there is no evidence that whales diving to the bottom in search of copepods and entangled near the seafloor (where there is no weak link and the line is heavier) can break free. Indeed, NMFS itself acknowledges that vast majority of mortality and serious injury risk from entanglements is from fisheries in federal waters. *E.g.*, Draft BiOp at 220.

Moreover, while the ALWTRP is focused on reducing mortality and serious injury, the jeopardy analysis under the ESA must look at *all* impacts of entanglements, including those that do not lead to serious injury or mortality, such as impaired reproductive ability, among other negative impacts. *See infra*, Section V. In light of these sublethal impacts, weak rope will continue to be a source of morbidity.

Third, the Draft BiOp relies on uncertain measures to be developed by states in New England. This is improper. To the extent NMFS wants to rely on measures enacted by a state, it can and must add those measures to the ALWTRP via its authority under the MMPA. Otherwise, NMFS has no way to ensure that such measures will actually be enacted or will not be subsequently amended in a way that would increase risk to right whales. For example, while the Draft BiOp relies on various risk reduction measures proposed by the state of Massachusetts, *see* Draft BiOp at 26, not all of those measures were ultimately enacted. The state chose not to adopt (1) the closure of state waters between February 1 and April 30 south of the Massachusetts Restricted Area or (2) the prohibition on fishing singles for vessels greater than 29 feet.[40]

NMFS's reliance on unproven, uncertain, future mitigation measures is especially arbitrary in light of the long, beleaguered history of the ALWTRP. Despite its existence for over two decades and several significant, substantive amendments, documented mortality and serious injury for right whales has continued to exceed the right whale's PBR—often by significant levels—and vastly exceeds insignificant levels approaching a zero-mortality rate. In fact, since

---

[38] Knowlton, A. et al. 2016. Effects of fishing rope strength on the severity of large whale entanglements. Conservation Biology. Vol. 30:2, 318–328 (emphasis added).

[39] Amy Knowlton, Tim Werner and Scott Kraus, *Whale Release Ropes*, Presentation at the Consortium for Wildlife Bycatch Reduction, https://www.mmc.gov/wp-content/uploads/Knowlton2_Marine-Mammal-Commission-Knowlton2-VERSION-2.pdf at 7.

[40] Sean Horgan, Fish panel bans inshore lobstering during whale migration, Gloucester Times, Jan. 28, 2021 https://www.gloucestertimes.com/news/fish-panel-bans-inshore-lobstering-during-whale-migration/article_761e98de-6196-11eb-b9f6-c3c00dd2aecc.html; MA DMF, February 19, 2021, "New Protected Species Regulations Finalized for Fixed Gear Fisheries and Industry Outreach on Required Gear Modifications," https://content.govdelivery.com/accounts/MADMF/bulletins/2c2930d.

the most recent round of amendments to the ALWTRP, right whale mortality and serious injury from entanglement in commercial fishing gear has **increased**, while the population has **plummeted**.

In other words, there is no rational basis for the agency's speculative assumption that future risk reduction measures will be successful, particularly where the agency continues to enact the very types of measures that a 2007 scientific review panel has deemed ineffective at reducing risk:

> In general, [NMFS] should set higher standards of protection and place greater reliance on the ability of industry to adapt to those standards, rather than continuing to depend on a complex, shifting, inefficient, and ineffective network of regulatory measures to protect the whales. The guiding principle should be to separate high-risk human activities from right whales, in both space and time, to the maximum extent feasible.[41]

Studies issued since then only reinforce this point. For example, a 2014 study by agency scientists concluded that incremental gear modifications under the ALWTRP from 1999 to 2009 were "generally ineffective in abating whale deaths from entanglements in fishing gear."[42] In October 2018, NMFS' Technical Memorandum observed that, starting in 1997 when the original Plan was put in place, including the 2009 sinking groundline and 2014 vertical line rules, data from 2000 through 2017 showed that "absolute entanglements appear to be on the rise."[43] The same document noted the "unintended consequences" of the 2015 vertical line rule that required trawling up, potentially contributing to the increased severity of entanglements.[44]

From the very outset of the ALWTRP more than two decades ago, NMFS recognized that reducing entanglement risk for right whales would be especially difficult and that "extensive closures of large areas of the ocean to lobster and gillnet fishermen . . . would guarantee reduction of entanglements causing serious injury and mortalities." 62 Fed. Reg. 39,157, 39,159 (July 22, 1997). Yet the agency has continued to fail to enact these necessary measures, despite the dire status of the right whale and its legal to do so.

V. The Draft BiOp Downplays the Sublethal Effects of Entanglements

The Draft BiOp arbitrarily downplays the sublethal impacts of entanglements on right whales. These effects are clearly "consequences to" right whales "that are caused by the proposed

---

[41] Reeves, R.R., A.J. Read, L. Lowry, S.K. Katona, and D.J. Boness. 2007. Report of the North Atlantic right whale program review, 13-17 March 2006, Woods Hole, Massachusetts. Marine Mammal Commission, Bethesda, MD.

[42] Pace, R. M. III et al. 2014.

[43] Right Whale Recovery Tech Memo at 8.

[44] *Id.*; *see also* Kenney, R. 2018. What if there were no fishing? North Atlantic right whale population trajectories without entanglement mortality. Endangered Spec. Res. 37:233 ("[d[espite legal requirements to reduce fishery-related mortality, little or no real progress has been made over the last 2 decades").

action—a wealth of scientific information indicates that the impacts of sublethal entanglements affect the survival and recovery of right whales within the meaning of the ESA. *See* 50 C.F.R. §§ 402.02 (defining "effects of the action;" "jeopardize the continued existence of" and "recovery"), 402.14(h)(1)(iii) (biological opinion must contain a "detailed discussion of the effects of the action on listed species").

To be clear, the Draft BiOp acknowledges sublethal effects. It recognizes, for example, that "entanglement in fishing gear appears to have substantial health and energetic costs that affect both survival and reproduction (Hayes et al. 2018a, Hunt et al. 2016, Lysiak et al. 2018, Pettis et al. 2017, Robbins et al. 2015, Rolland et al. 2017, van der Hoop et al. 2017a)." Draft BiOp at 95, 220-221. It also states that "[t]he sublethal stress of entanglements can have a serious impact on individual health and reproductive rates (Lysiak et al. 2018, Pettis et al. 2017, Robbins et al. 2015). *Id.* at 146.

However, the Draft BiOp fails to properly consider sublethal impacts in the effects of the action or its jeopardy analysis. Instead, it dismisses them on the basis that "there is no further evidence to make the conclusion that sublethal effects from fishing gear entanglement alone causes a decline in large whale health" and that NMFS supposedly "cannot quantify the degree to which entanglements are affecting calving rates." *See id.* at 221, 338. This is improper. For example, as explained in more detail below, *see infra* Section VIII, NMFS's jeopardy analysis must consider not just the impacts from the proposed action in isolation, but the effects of the action in light of all the other stressors acting on the population. Thus, the fact that there is allegedly no information that sublethal impacts alone cause a decline in whale health is immaterial to agency's obligation to include sublethal effects in its jeopardy analysis. Moreover, NMFS cannot dismiss impacts from sublethal entanglements simply because it cannot quantify them. *See* BiOp at 220–221. NMFS's failure to properly consider the impacts of sublethal entanglements on the ability of animals to successfully reproduce is particularly concerning given its conclusion in prior biological opinions that "[h]ealthy reproduction is critical for the recovery of the North Atlantic right whale."[45]

Any reliance in the jeopardy analysis on the Linden model to dismiss the threat of the impacts from sublethal entanglements is flawed. *See* Draft BiOp at 326, 329, 330. Rather than address the sublethal impacts quantitatively, this model addresses them qualitatively and assumes that the effects are all consumed by calving rates. *Id.* This analysis ignores the effects that go beyond mortality—such sickness and injury—that would decrease the fitness of an individual animal but not necessarily kill it (although it could make them more vulnerable to a fatal vessel strike).

It is well established that right whales are negatively impacted by entanglement, not only through a reduction in the numbers of individuals through serious injuries and mortalities, but also

---

[45] *See, e.g.*, NMFS, Endangered Species Act Section 7 Consultation on the Continued Implementation of Management Measures for the American Lobster Fishery, Consultation No. NER-2014-11076 (July 31, 2014) at 33.

through increasing a whale's stress hormone levels, leading to infections; making them more vulnerable to other sources of mortality like vessel strikes; and impeding their ability to feed.[46]

For example, studies have concluded that "[p]rotracted entanglement in fishing gear often leads to emaciation through reduced mobility and foraging ability, and energy budget depletion from the added drag of towing gear for months or years."[47] Additionally, the "chronic effects of entanglement in free-swimming individuals include systemic infection and debilitation from extensive tissue damage . . . More common in protracted cases is severe emaciation due to the inability to cope with a negative energy budget, driven by the combined effects of reduced mobility and foraging ability, and increased energetic demand imposed by towing accessory gear for months to years."[48]

The best available scientific data also indicates that even a single line increases drag on a whale; extra energy demand may affect body condition to the point that individual females' reproductive capacities could be impaired. Indeed, scientific studies have concluded that poor body condition that may result from chronic entanglement in right whales is a serious limitation to reproductive success.[49] Studies have also found that "[r]eproductive females seen alive and carrying gear or with severe wounds from entanglement had a significantly lower chance of calving again. Females that experienced moderate or severe entanglement wounds between calvings had a significantly longer calving interval than females that experienced minor or no entanglement wounds;"[50] that "females that have suffered a severe entanglement are

---

[46] *See, e.g.*, Julie M. van der Hoop, Douglas P. Nowacek, Michael J. Moore, M. S. Triantafyllou. 2017. Swimming kinematics and efficiency of entangled North Atlantic right whales. Endang. Species Res. Vol. 32: 1–17, 2017, doi: 10.3354/esr00781; Julie van der Hoop, Peter Corkeron and Michael Moore. 2016. Entanglement is a costly lifehistory stage in large whales. Ecology and Evolution, 7: 92–106, doi:10.1002/ece3.2615; Cassoff RM, Moore KM, McLellan WA, Barco SG, Rotstein DS, Moore MJ. 2011. Lethal entanglement in baleen whales. Dis. Aquat. Org. 96: 175−185; Moore, M. and van der Hoop, J. 2012. The Painful Side of Trap and Fixed Net Fisheries: Chronic Entanglement of Large Whales. Journal of Marine Biology. Volume 2012, Article ID 230653, doi.org/10.1155/2012/230653.

[47] Julie van der Hoop, et al. 2014. Behavioral impacts of disentanglement of a right whale under sedation and the energetic cost of entanglement. Marine Mammal Science. Vol. 30:1, pp. 282–307.

[48] *Id.*

[49] Miller, C. , D. Reeb, P. Best, A. Knowlton, M.Brown and M.Moore. 2011. Blubber thickness in right whales (Eubalaena glacialis) and (Eubalaena australis) related with reproduction, life history status and prey abundance. Marine Ecology Progress Series. Vol. 438, pp. 267–283.

[50] Knowlton, A., P. Hamilton, M. Marx, H. Pettis, and S. Kraus. 2012. Monitoring North Atlantic right whale (Eubalaena glacialis) entanglement rates: a 30 yr retrospective. Marine Ecology Progress series. Vol. 466, pp 293–302; Knowlton, A., P. Hamilton, and H. Pettis. 2012. Status of Reproductive Females in the North Atlantic Right Whale Population and Impacts of Human Activities on their Reproductive Success. Report Submitted to Woods Hole Oceanographic Institution.

significantly less likely to calve again;"[51] and that "[h]uman impacts are reducing the reproductive success of this population."[52]

Other studies have concluded that entanglements contribute to poor body condition in juvenile right whales, adults, and lactating females, "which could be suppressing their growth, survival, age of sexual maturation and calving rates."[53] Moreover, the poor condition of lactating females, may cause a reduction in calf growth rates, "potentially lead[ing] to a reduction in calf survival or an increase in female calving intervals."[54] As such, "the poor body condition of individuals within the NARW population is of major concern for its future viability."[55]

Thus, entanglement is likely one of the major determinants of reproductive failure in right whales, and probably all large whales. NMFS cannot conduct an adequate jeopardy analysis without properly considering these and the other sublethal impacts of entanglements.

VI. The Draft BiOp Otherwise Omits Key Factors from Consideration Downplays Stressors, and Ignores the Best Available Scientific Data

In the "Effects of the Proposed Action" (Section 7), NMFS fails to consider many consequences of the proposed actions (improperly defined and unduly narrowed, as described above) on the critically endangered right whale. And although NMFS claims it will afford the "benefit of the doubt" to the species when uncertainties are present, Draft BiOp at 214 (quoting House of Representatives Conference Report No. 697, pg. 1442, 96th Congress, Second Session, 12 (1979)), it fails to do so by downplaying the consequences of ongoing and future fishing in both state and federal waters as well as reopening thousands of square miles of ocean waters in Southern New England to expanded gillnet fishing, in addition to the consequences of many other non-fishing stressors on the right whale population.

A. <u>The Draft BiOp Unreasonably Relies on the Vessel Speed Rule that NMFS has Recently Acknowledged Is Insufficient to Reduce the Likelihood that Fishing Vessels in State and Federal Waters Will Hit a Whale</u>

The Draft BiOp makes a determination that right whales are not likely to be adversely affected by fishing vessels operating in the action area under the proposed action, Draft BiOp at 237. This conclusion relies on the ship speed restriction rule implemented in 2008 (50 C.F.R. § 225.105)

---

[51] Julie van der Hoop, et al. 2016.

[52] *Id.*

[53] Christiansen, F., Dawson, S.M., Durban, J.W., Fearnbach, H., Miller, C.A., Bejder, L., Uhart, M., Sironi, M., Corkeron, P., Rayment, W., Leunissen, E., Haria, E., Ward, R., Warick, H.A., Kerr, I., Lynn, M.S., Pettis, H.M., & Moore, M.J. 2020. Population comparison of right whale body condition reveals poor state of the North Atlantic right whale. Marine Ecology Progress Series. Vol. 640, pp. 1–16.

[54] *Id.*

[55] *Id.*

that may have reduced the risk of vessel strikes and the number of mortalities, Draft BiOp at 187–192, 237 (based on data from 2009–2018). However, any reliance on this rule to ensure no jeopardy in the final batched biological opinion would be misplaced. While the Draft BiOp denotes the "rarity" of ship strikes and makes the conclusory statement that "it seems extremely unlikely and discountable that a fishing vessel would strike a whale, even during transiting," *id*. at 237, there have been at least four documented right whale deaths and serious injuries due to vessel strikes in U.S. waters since January 1, 2020, all due to confirmed or suspected recreational fishing vessels less than 65 feet.[56]

As NMFS recently acknowledged in its North Atlantic Right Whale Vessel Speed Rule Assessment (June 2020) ("Assessment"), the current rule does not sufficiently protect right whales from getting run over or killed by ships and many of the components of the rule are voluntary, rather than mandatory. NMFS cannot rely on unenforceable or ineffectual measures in its jeopardy analysis. *See, e.g.*, *Rumsfeld*, 198 F. Supp. 2d at 1152.

Specifically, the Assessment concludes that "[s]ince the speed rule was implemented, there has been a decline in the total number of documented right whale vessel strike mortalities but an increase in serious and non-serious injuries." Assessment at 35. It notes that "certain discrete areas of poor compliance stand out," *id.*, the continuing level of vessel collisions including those by boats smaller than 65 feet, and the "gravity of the whales' heath and population status," NMFS made several recommendations to strengthen the current rule including: (1) consideration of a new Seasonal Management Area (in which speed limits would be mandatory) south of Martha's Vineyard and Nantucket because "right whale foraging activity has steadily increased in this area;" (2) regulating vessels less than 65 feet in acknowledgement that smaller vessels have killed and injured right whales; and (3) modification or even termination of the Dynamic Management Area ("DMA") program because compliance with voluntary speed limits is low. *See* Assessment at 36–37.[57]

B. The Draft BiOp Ignores the Best Available Scientific Data Demonstrating Right Whales Use Southern New England Year-Round as Foraging Habitat

When discussing important foraging habitat for right whales, the Draft BiOp identifies the "continental Shelf south of New England" as new foraging habitat, yet it makes no mention of year-round use of the area. Draft BiOp at 195 (describing use as "seasonal"); 196 (describing a habitat shift out of the Great South Channel and Bay of Fundy and into Southern New England in "fall and winter," and describing right whales as "moving through the action area" but "foraging in northern parts of the action area"); 218 (describing high use in winter through early spring); 229 (proposing seasonal closure to trap/pot fishing south of Nantucket).

---

[56] Aidan Cox, North Atlantic right whale found dead on Florida beach, CBC News, Feb. 17, 2021, https://www.cbc.ca/news/canada/new-brunswick/right-whale-death-1.5917363.

[57] NMFS's inclusion of federal vessel operations in the environmental baseline is puzzling in light of its new regulation that specifies the environmental baseline includes "consequences to listed species or designated critical habitat from ongoing agency activities . . . that are not within the agency's discretion to modify," *see* 50 C.F.R. § 402.02, and NMFS has the authority to regulate vessels under the MMPA and ESA as its ship speed rule demonstrates.

This runs counter to a recent NMFS Technical Memorandum authored in 2020 by the agency's North Atlantic right whale "Expert Working Group" that describes the area "South of the Islands" as "core" North Atlantic right whale foraging habitat during the Winter/Spring/Summer/Fall."[58]

As noted, right whale distribution and habitat use has shifted since 2010 in response to climate change-driven shifts in prey availability.[59] Draft BiOp at 222. The best available scientific information, including aerial surveys,[60] acoustic detections,[61] stranding data,[62] a series of DMAs declared by NMFS pursuant to ship strike rule,[63] and prey data,[64] all indicate that right whales

---

[58] Oleson, E.M., Baker, J., Barlow, J., Moore, J.E., and Wade, P., "North Atlantic Right Whale Monitoring and Surveillance: Report and Recommendations of the National Marine Fisheries Service's Expert Working Group." NOAA Technical Memorandum NMFS-OPR-64 (August 2020), at Fig. 1. Available at: https://www.fisheries.noaa.gov/resource/document/north-atlantic-right-whale-monitoring-and-surveillance-report-and-recommendations.

[59] Record, N., Runge, J., Pendleton, D., Balch, W., Davies, K., Pershing, A., Johnson, C., Stamieszkin, K., Ji, R., Feng, Z. and Kraus, S. 2019. Rapid Climate-Driven Circulation Changes Threaten Conservation of Endangered North Atlantic Right Whales. Oceanography. Vol. 32, pp. 162–169.

[60] Kraus, S.D., Leiter, S., Stone, K., Wikgren, B., Mayo, C., Hughes, P., Kenney, R.D., Clark, C.W., Rice, A.N., Estabrok, B., and Tielens, J. 2016. Northeast large pelagic survey collaborative aerial and acoustic surveys for large whales and sea turtles. Final Report. OCS Study, BOEM 2016-054, pp. 118; Leiter, S.M., Stone, K.M., Thompson, J.L., Accardo, C.M., Wikgren, B.C., Zani, M.A., Cole, T.V.N., Kenney, R.D., Mayo, C.A., and Kraus, S.D. 2017. North Atlantic right whale *Eubalaena glacialis* occurrence in offshore wind energy areas near Massachusetts and Rhode Island, USA. Endangered Species Research. Vol. 34, pp. 45–59; Quintana, E., "Monthly report No. 3: May 2017," Report prepared for the Massachusetts Clean Energy Center by the New England Aquarium, pp. 26 (May 15, 2017).

[61] Kraus, et al. 2016; Davis, G.E., Baumgartner, M.F., Bonnell, J.M., Bell, J., Berchick, C., Bort Thorton, J., Brault, S., Buchanan, G., Charif, R.A., Cholewiak, D., 2017. Long-term passive acoustic recordings track the changing distribution of North Atlantic right whales (*Eubalaena glacialis*) from 2004 to 2014. Scientific Reports. Vol. 7, p. 13460.

[62] Asaro, M.J., Update on US Right Whale Mortalities in 2017, NMFS, November 30, 2017, available at: https://www.greateratlantic.fisheries.noaa.gov/protected/whaletrp/trt/meetings/2017%20Nov/asaro_usstrandings_nov2017.pdf.

[63] NMFS Interactive DMA Analyses: https://www.nefsc.noaa.gov/rcb/interactive-monthly-dma-analyses/.

[64] Pendleton, D.E., Pershing, A., Brown, M.W., Mayo, C.A., Kanney, R.D., Record, N.R., and Cole, T.V.N. 2009. Regional-scale mean copepod concentration indicates relative abundance of North Atlantic right whales. Marine Ecology Progress Series. Vol. 378, pp. 211–225; NOAA Northeast Fisheries Science Center, "Ecology of the Northeast US Continental Shelf – Zooplankton," available at https://www.nefsc.noaa.gov/ecosys/ecosystem-ecology/zooplankton.html.

now heavily rely on Southern New England waters.[65] In January 2019, an aggregation representing a quarter of the population—100 whales—was seen in this area[66] engaged in both foraging and social activities, demonstrating that it is clearly more than just a migratory corridor. Southern New England is important to all life history stages. Of 196 individual whales identified in the area between January 1, 2010 and June 30, 2015, 35 percent were females, 58 percent were males, and the remainder were of unknown sex. Of the 188 individuals that were assigned an age class, almost two thirds were adults and one third juveniles. Six individuals were classified as calves at the time of their sighting.[67] There were 34 different reproductive females identified, eight of which had only been documented in Southern New England since the start of 2010.[68]

As discussed above, large, consistent aggregations of right whales in all four seasons, have led scientists to describe Southern New England as a year-round foraging "hotspot."[69] Several other scientific data sources demonstrate that right whales use these waters year-round. Further, a recent presentation at the North Atlantic Right Whale Symposium discussed new evidence showing that 11 out of 15 newly catalogued whales identified south of Cape Cod have never been sighted further north in the Bay of Fundy of the Gulf of St. Lawrence,[70] and suggesting this area may represent an end-point of the northern migration for some portion of the population.

In addition to year-round use of the area, the relative abundance in the area has increased. For example, there is evidence of a broader temporal shift in distribution resulting in greater densities off Rhode Island and Massachusetts later in the year, through May and into the summer months.[71] April appears to be particularly important for females of reproductive age.[72] Inter-annual and inter-seasonal variability in aerial and acoustic detections imply that there are no

---

[65] Although there are challenges in the use of opportunistic sightings data (no area systematically surveyed, effort not corrected for, and potential for counting an individual whale more than once), they are a proxy for habitat used by North Atlantic right whales, as validated by NMFS' management actions based on these data, including the implementation of DMAs.

[66] NMFS, Voluntary Vessel Speed Restriction Zone in Effect South of Nantucket to Protect Right Whales (Jan. 28, 2019), https://www.fisheries.noaa.gov/feature-story/voluntary-vessel-speed-restriction-zone-effect-south-nantucket-protect-right-whales.

[67] Leiter et al. 2017, at 52–54.

[68] *Id.*

[69] Oleson, E.M., Baker, J., Barlow, J., Moore, J.E., and Wade, P., 2020. North Atlantic Right Whale Monitoring and Surveillance: Report and Recommendations of the National Marine Fisheries Service's Expert Working Group. NOAA Technical Memorandum NMFS-OPR-64, at Fig. 1.

[70] Hamilton, P., "North Atlantic Right Whale Catalog Update, Recent Genetic Findings and Whale Naming Results," Presentation at the North Atlantic Right Whale Consortium Annual Meeting (Oct. 29, 2020).

[71] Davis, G. E., et al. 2017.

[72] Leiter et al. 2017.

clear spatial patterns of habitat use across SNE and right whales should be expected to be encountered equally across the region.[73] Several scientific data sources demonstrate that right whales use these waters year-round.[74] Right whales should therefore be expected to be present in Southern New England in increasing numbers year-round and the Draft BiOp's characterization of their use of the area as "seasonal" minimizes the risks of entanglement and vessel strikes in that region.

C. The Draft BiOp Downplays Foraging Displacement Caused by Offshore Wind Development in Southern New England

While the Draft BiOp mentions numerous MMPA incidental harassment authorizations ("IHA") and letters of authorization issued pursuant to section 101(a)(5) of the MMPA for a variety of activities, its jeopardy analysis is silent on the effects that foraging displacement caused by offshore wind projects could have on the survival and recovery of right whales. *See* Draft BiOp at 165. NMFS has openly acknowledged that ocean noise associated with surveying for and constructing these projects may cause foraging displacement in IHAs for the projects proposed in the Massachusetts and Rhode Island wind energy areas. A recently published IHA reiterates this point and illuminates the agency's assumptions:

> North Atlantic right whales may temporarily avoid the immediate area but are not expected to permanently abandon the area. NMFS does not anticipate North Atlantic right whales takes that would result from the proposed project would impact annual rates of recruitment or survival.

See Proposed IHA for Vineyard Wind, 86 Fed. Reg. 8490, 8533 (Feb. 5, 2021).

We now know that several offshore wind projects have been unwittingly sited within a critical foraging hotspot for right whales. *See supra*, Section VI.B.

The need for right whales to forage and socialize undisturbed, where and when food is available, cannot be downplayed. Scientists have concluded that "right whales acquire their energy in a relatively short period of intense foraging; even moderate changes in their feeding behavior or their prey energy density are likely to negatively impact their yearly energy budgets and therefore reduce fitness substantially."[75] North Atlantic right whales are already experiencing significant food-stress: juveniles, adults, and lactating females have significantly poorer body condition relative to Southern right whales, and the poor condition of lactating

---

[73] *Id.*; DMAs; Redfern, J., Pendleton, D., O'Brien, O., Ganley, L., Hodge, B. and McKenna, K., "Tools to identify and minimize risk to marine mammals," Presentation to the Massachusetts Habitat Working Group (Dec. 11, 2020).

[74] Kraus, S.D. 2016; Davis, G.E., et al. 2017; NMFS Interactive DMA Analyses.

[75] Van der Hoop, J., Nousek-McGregor, A.E., Nowacek, D.P., Parks, S.E., Tyack, P., and Madsen, P, "Foraging rates of ram-filtering North Atlantic right whales," *Functional Ecology*, published online May 11, 2019.

females may cause a reduction in calf growth rates.[76] The Draft BiOp provides no scientific support for NMFS's assertions in its IHAs that right whales will not permanently abandon certain areas once construction begins or that even temporary avoidance will not impact recruitment and survival of the species.

In addition to the energetic costs to right whales of avoiding increasingly noisy ocean waters, another potential consequence of this habitat displacement is displacement into nearby shipping lanes, thus increasing the risk of a ship strike. In the final biological opinion, NMFS should consider these additional risks; especially given that any additional stressor could further exacerbate population-level impacts. The difficulty in obtaining empirical data on these kind of population-level impacts demands a precautionary approach.

D. The Draft BiOp Downplays the Effects of Gillnet Entanglements on Right Whales

The Draft BiOp estimates that 1.25 right whales were entangled in gillnet gear in U.S. fisheries (based on data from 2010–2019). Draft BiOp at 227, 233. Even given the new uncertainty as to the validity of this estimate given the need to recalculate total estimates based on Pace et al. 2021, the assignment of all presumed U.S. entanglements in unknown gear based solely on the huge proportion of vertical trap/pot lines, *id.* at 224, resulting in a total estimate of annual average 0.125 M/SI, *id.* at 227, downplays the effects of gillnet entanglements on right whales by ignoring the disproportionate risk of entanglement in a gillnet end-line. Perhaps more importantly, NMFS and the take reduction team have not even begun to discuss or analyze the effects of gillnet entanglements (sublethal or lethal) on right whales, much less recommend immediate protections, having spent the last four years focused on the lobster fishery.

End-lines in the northeast sink gillnet fisheries present a disproportionate risk of entangling a right whale. The presence of one or more nets (up to 300 feet long each) strung together and held up by floats, presents a much bigger target area for whales foraging throughout the water column, as compared to vertical trap/pot buoy lines without net in between. The Draft BiOp contains no discussion of the disproportionate impact of the significantly larger target area that could entangle a whale. Further, its limited analysis of gillnet fishing in critical foraging grounds in Southern New England waters is flawed and fails to rely on the best available scientific data, as discussed below.

While the Draft BiOp generally concludes that it is unlikely that gillnet fishing effort will shift much across the region, it provides little specificity or support. *See* Draft BiOp at 308, 312, 315, 317, 318. For example, there is no analysis of the likelihood that the number of fishing vessels could change. Similarly, there is no analysis of the likelihood that latent fishing effort could change. And while noting that numerous management actions have increased fishing opportunities in gillnet fisheries—including by allowing extra-large mesh-size sector exemptions, modifying the management uncertainty buffer in the monkfish fishery, adding an additional skate species to the skate fishery management plan, and increasing quota allocations and trip limits for certain target stocks, *see, e.g.*, Draft BiOp at 44–52, 306—there is no

---

[76] Christiansen, et al. 2020.

justification for the BiOp's conclusion that these additional opportunities will result in increased efficiency rather than increased amount of gear in the water.

By ignoring the effects of this increased gillnet fishing effort on right whales, NMFS's jeopardy analysis cannot accurately address the short or long-term impacts of the continued operation of these fisheries on right whales. NMFS's final biological opinion must therefore incorporate these threats into its analysis. *See, e.g., Pac. Coast Fed'n of Fishermen's Ass'ns v. Nat'l Marine Fish. Serv*, 265 F.3d 1028, 1037–38 (9th Cir. 2001) (invalidating biological opinion due to agency's failure to consider relevant factors).

E. The Draft BiOp Downplays the Entanglement Risk of Aquaculture Facilities

The Draft BiOp acknowledges that aquaculture increases the entanglement risk, the likelihood of a vessel strike, and ocean noise:

> Aquaculture has the potential to impact ESA-listed species through entanglement and/or other interaction with aquaculture gear (e.g., buoys, nets, and vertical lines), introduction or transfer of pathogens, increased vessel traffic and noise, impacts to habitat and benthic organisms, and water quality (Clement 2013, Lloyd 2003, Price and Morris 2013, Price et al. 2017).

Draft BiOp at 151. NMFS tries to avoid carefully analyzing such impacts, stating that known interactions are "rare," but it is well documented that fewer than 1% of entanglements are attributed to the activity of origin. *Id.* The Draft BiOp also acknowledges that aquaculture in the Northeast has been and continues to expand (state and federal waters). *Id.* at 152. In fact, at least one active project in right whale critical habitat (in federal waters eight miles off Rockport, MA) has plans to dramatically increase the number of longlines lines (from 3 lines to 120 lines) in waters where right whales are known to forage. *See id.* ("surface longlines consist of horizontal longline suspended on/near the surface of the water with buoy lines or poles at each end"). Yet, despite at least 299 projects in the Northeast, *see id.* at Table 49, regulation by NMFS is unclear at best and the Draft BiOp contains no descriptions of completed consultations or discussion of the effects of these projects on the survival and recovery of right whales.

F. The Draft BiOp Downplays the Impacts of Noise Pollution from Vessels and Military Activities along the Atlantic Seaboard

The Draft BiOp notes that "NMFS has completed consultations on individual Navy and USCG activities," Draft BiOp at 166, but provides *no* discussion of the impact of these activities on right whales in the U.S. Atlantic. Likewise, NMFS mentions that the maritime industry "has the potential to interact with ESA-listed species," but does not address noise pollution as a potential impact. *Id.* at 178. This is a significant omission as the best available scientific data demonstrate that the noise generated by these activities and other vessel activity can negatively impact right whales in numerous ways.

NMFS fails to even acknowledge its rule issued under the MMPA that allows the Navy to harass right whales **hundreds** of times **each year** over the next seven years incidental to testing and training activities conducted in the Atlantic Fleet Training and Testing Study Area. *See* 84 Fed. Reg. 70,712, 70,763 (authorizing 471 instances of Level B harassment of right whales from December 2019 through November 2025). Instead, the Draft BiOp's description of these activities focuses solely on take of other species of whales and sea turtles via "**harm** due to exposure to impulsive and non-impulsive acoustic stressors annually." Draft BiOp at 166 (emphasis added).

While the agency provides no explanation for its decision to ignore impacts to right whales, it appears to have done so because the activities will supposedly not "harm" right whales within the meaning of the ESA. This is improper. The ESA prohibits not just actions that "harm" or "kill" right whales, but also those that "harass" the whales. 16 U.S.C. § 1532(19). And the agency regularly applies the MMPA's broad definition of harassment when analyzing impacts to ESA-listed marine mammals under the ESA.[77]

Moreover, the environmental baseline includes not just those activities that cause "harm" or otherwise "take" right whales within the meaning of the ESA, but rather includes:

> the past and present **impacts** of all Federal, State, or private actions and other human activities in the action area, the anticipated *impacts* of all proposed Federal projects in the action area that have already undergone formal or early section 7 consultation, and the *impact* of State or private actions which are contemporaneous with the consultation in process.

50 C.F.R. § 402.02 (emphasis added); *cf.*, 16 U.S.C. § 1532(19) (defining take to mean "to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect," or attempt to do so). NMFS has no authority to exclude impacts to listed species from various activities simply because the agency believes such impacts do not rise to the level of take under the ESA. Yet that is just what NMFS has done in the Draft BiOp. In doing so, NMFS has failed to conduct the comprehensive jeopardy analysis required by law. *See, e.g.*, *Am. Rivers v. U.S. Army Corps of Eng'rs*, 271 F. Supp. 2d 230, 255 (D.D.C. 2003) ("The ESA requires that all impacts of agency action . . . be addressed in the consultation's jeopardy analysis.").

Noise from the Navy's and USCG's activities and the maritime industry will certainly "impact" right whales. For example, scientific research reveals that chronic stress in North Atlantic right whales is associated with exposure to low frequency noise from ship traffic.[78] Specifically, "the adverse consequences of chronic stress often include long term reductions in fertility and decreases in reproductive behavior; increased rates of miscarriages; increased vulnerability to diseases and parasites; muscle wasting; disruptions in carbohydrate metabolism; circulatory

---

[77] *See, e.g.*, NMFS, Endangered Species Act (ESA) Section 7(a)(2) Biological Opinion Liberty Oil and Gas Development and Production Plan Activities, Beaufort Sea, Alaska, NMFS Consultation Number at 134 AKR-2018-9747 (July 31, 2018).

[78] Rolland, R, et al. 2012. Evidence that ship noise increases stress in right whales. Proc. R. Soc. B. 279: 2363–2368.

diseases; and permanent cognitive impairment."[79] As such, "over the long term, chronic stress itself can reduce reproduction, negatively affect health, and even kill outright."[80] In addition, right whales will experience temporary threshold shifts, behavioral response, and stress throughout the Atlantic from Navy sonar and other transducers.[81] Vessel and navy training activities can also impact important communications, including those between mothers and calves.[82]

G. The Draft BiOp Downplays the Consequences of Opening Longstanding Closures in Southern New England to Gillnet Fishing via the Habitat Amendment

The Draft BiOp contains the court-ordered ESA section 7 consultation on the Omnibus Essential Fish Habitat Amendment 2 ("Habitat Amendment"). *See* Draft BiOp at 284-85; *see also Conservation Law Foundation v. Ross*, 422 F. Supp. 3d 12, 31 (Oct. 28, 2019). Despite noting that that closures benefit ESA-listed species such as right whales "due to elimination of active gear in areas where ESA-listed species are present," Draft BiOp at 193, the Draft BiOp concludes that reopening the court-ordered closures of the Nantucket Lightship Closure Area and Closure Area 1 to gillnet fishing is not likely to adversely affect right whales. *Id.* at 323. This determination is legally flawed for several reasons.

First, the consultation's risk analysis ignores new scientific data on increasing abundance and year-round use of Southern New England waters where the court-ordered closures occur. *See supra*, Section VI.B. The process to assess risk to ESA-listed species is described as follows: "To assess risk, we take into consideration our analysis of effort pre-and post-Amendment, ESA-

---

[79] Rolland, R.M., K.E. Hunt, G.J. Doucette, L.G. Rickard, and S.K. Wasser. 2007. The inner whale: hormones, biotoxins and parasites. In: Kraus S.D. and R.M. Rolland, (eds.). The Urban Whale: North Atlantic Right Whales at the Crossroads. Harvard University Press, Cambridge, MA.

[80] *Id.*; *see also* Mayo, C.S., Page, M., Osterberg, D., and Pershing, A., "On the path to starvation: the effects of anthropogenic noise on right whale foraging success," North Atlantic Right Whale Consortium: Abstracts of the Annual Meeting (2008) (finding that decrements in North Atlantic right whale sensory range due to shipping noise have a larger impact on food intake than patch-density distribution and are likely to compromise fitness).

[81] *See, e.g.*, NMFS, Biological and Conference Opinion on U.S. Navy Atlantic Fleet Training and Testing and the National Marine Fisheries Service's Promulgation of Regulations Pursuant to the Marine Mammal Protection Act for the Navy to "Take" Marine Mammals Incidental to Atlantic Fleet Training and Testing (Nov. 2018) at 508.

[82] *See, e.g.*, NMFS, Biological Opinion on the Bureau of Ocean Energy Management's Issuance of Five Oil and Gas Permits for Geological and Geophysical Seismic Surveys off the Atlantic Coast of the United States, and the National Marine Fisheries Services' Issuance of Associated Incidental Harassment Authorizations (Nov. 2018) at 87 ("North Atlantic right whales shift calling frequencies, particularly those of upcalls, and increase call amplitude over both long and short term periods due to exposure to vessel sound, which may limit their communication space by as much as 67 percent compared to historically lower sound conditions").

listed species distribution (see Status of the Species), and documented interactions. This informs the degree of overlap between listed species and fisheries in each region. We then identify which gears pose a risk to listed species." Draft BiOp at 287. However, the consultation analysis repeatedly refers to a seasonal closure of the Southern New England waters and ignores the best available scientific data demonstrating that right whales use Southern New England waters all of the year and at higher abundance, and thus entanglement risk could increase there. *See id.* at 323 (listing the criteria evaluated and stating: "interaction risks with listed species are strongly associated with the quantity of gear in the water (e.g., number of vertical lines, gillnets, trawls), gear soak/tow duration, and the temporal and spatial overlap of the gear and protected species.").

Second, the conclusion that effort is "not likely" to shift if these closures are reopened is not reasonable. *See* Draft BiOp at 301 (Closed Area 1), 312 (Nantucket Lightship). To assess whether shifts in effort are likely to occur, the Draft BiOp first makes a series of caveated conclusory statements without support regarding the "potential to result in a shift" and the purported poor health of target stocks within the closure (while alternatively claiming fishermen fish the edges now for "spillover effects"). *Id.* Next it analyzes and compares pre-Amendment (September 1, 2016, through March 31, 2018) Vessel Trip Reports ("VTR") data to post-Amendment (April 1, 2018, through October 31, 2019) VTR data, in specified regions and by gear types. Draft BiOp at 286. Given that court-ordered closures were effective November 1, 2019, the agency's use of the limited data set obtained from a 572-day period on either side of March 31, 2018 is arbitrary, ignores the spatial and temporal aspects of the several gillnet fisheries operating there, *see* Draft BiOp at 53, 56, 57, and ignores the circumstances related to opening thousands of square miles of ocean waters to gillnet fishing that had been closed between 17 and 27 years. Draft BiOp at 288.

Third, the fisheries interaction risk analysis does not consider the impact of the increasing quotas for target stocks in the sink gillnet fisheries operating in that area or of potential latent effort in the gillnet fisheries. *See supra*, Section VI.D.

Until additional analysis is done, the ALWTRT meets to recommend gillnet measures across the Category I and II fisheries, and all relevant rulemaking is completed, all closures (ALWTRP and court-ordered) should remain in place.

H. The Conclusion that the Relevant Fisheries are Not Likely to Adversely Affect Critical Habitat for Right Whales Ignores the Best Available Scientific Data

The Draft BiOp concludes that the proposed action is not likely to adversely affect critical habitat for right whales. *See*, *e.g.*, Draft BiOp at 71, 83, Table 40. For this determination, the boundaries of the action area are defined as existing boundaries of current critical habitat designations. *Id*. at 84. For two independent reasons, this conclusion is flawed: (1) in critical habitat designated specifically as foraging habitat, the presence of vertical line diminishes the value of the foraging habitat thus adversely modifying it such that it cannot serve its intended purpose; and (2) fishing gear could interfere with prey availability in this critical habitat.

1. *The Best Available Scientific Data Demonstrate that the Conservation Value of Right Whale Foraging Habitat As a Whole Is Diminished by Lines in the Water*

The Draft BiOp concludes that line in the water has no impact on critical habitat, stating:

> Fixed fishing gear also does not block the entire water column or form a wall preventing access. Vertical buoy lines supporting the fixed gear may extend throughout the water column, however, the Gulf of Maine critical habitat feeding area is vast and not constricted by geological or physical barriers, therefore whales are free to move through and around these gears to reach their feeding resources. The impact of entanglements on individual animals as they access their feeding resources is addressed in section 7.2 of this analysis, but is not considered an impact to whales accessing or moving within critical habitat.

Draft BiOp at 87. This ignores the best available scientific data. The sheer number and the concentration of vertical lines in the Gulf of Maine, *see* Draft BiOp at 289–92, appreciably diminish the value of this critical habitat as a whole for the conservation (i.e., survival and recovery) of right whales. The area may be "vast," but it is a relatively small proportion of the species' total range and by definition it was established precisely to protect areas critical to foraging. It is disingenuous to state that right whales are "free to move through and around these gears," implicitly characterizing a right whale's movement through areas with fishing gear as the whale's choice rather than appropriately recognizing that fishing gear constitutes a barrier to unimpeded foraging that is imposed on the whale. The data is clear not only that right whales are more likely to get entangled when feeding because their mouths are wide open but also that there is no absolutely evidence to suggest that whales can detect or avoid fishing gear in the water column.[83] Thus, the value of the critical habitat established to protect the whale's access to prey resources is appreciably diminished by the life-threatening risks of entanglement right whales must assume when foraging in critical habitat.

In addition, NMFS's consideration unduly narrows the effects of the action by considering only the impacts of federal fisheries on critical habitat, not fishing in state waters as regulated and authorized by NMFS under the ALWTRP.

---

[83] *See, e.g.*, Leiter et al. 2017; Moore, M. 2019. How we can all stop killing whales: a proposal to avoid whale entanglement in fishing gear. ICES Journal of Marine Science. 76(4): 781–786; Baumgartner, M. et al. 2007. Enormous Carnivores, Microscopic Food, and a Restaurant That's Hard to Find. In: Kraus S.D. and R.M. Rolland, (eds.). The Urban Whale: North Atlantic Right Whales at the Crossroads. Harvard University Press, Cambridge, MA at 140; Anderson Cabot Center, About the North Atlantic Right Whale, https://www.andersoncabotcenterforoceanlife.org/rightwhales/right-whales/about-right-whales/ (last visited Feb. 18, 2021); Sharp, S., W. McLellan, D. Rotstein, A. Costidis, S. Barco, K. Durham, T. Pitchford, P.-Y. Daoust, T. Wimmer, E. Couture, L. Bourque, T. Frasier, B. Frasier, D. Fauquier, T. Rowles, P. Hamilton and M. Moore. 2019. Gross and histopathologic diagnoses from North Atlantic right whale Eubalaena glacialis mortalities between 2003 and 2018. Dis. Aq. Org. 135:1-31.

2. *The Best Available Scientific Data Demonstrates that Fishing has an Effect on Prey Availability*

In concluding that the operation of the fisheries will have no adverse effects on the availability of prey because they pass through rather than are captured by fishing gear, Draft BiOp at 237, the agency has ignored the best available scientific data suggesting that fishing activity can have an effect on prey availability for right whales, and thus affect the conservation value of critical habitat.

Right whales select foraging areas based on a relatively high threshold of copepod density. *Id.* Notably, foraging areas with suitable prey density are limited relative to the overall distribution of North Atlantic right whales,[84] meaning that unrestricted and undisturbed access to suitable areas, when they exist, is extremely important for the species to maintain its energy budget. Scientific information on right whale functional ecology also shows that the species employs a "high-drag" foraging strategy that enables them to selectively target high-density prey patches, but is energetically expensive.[85] Thus, if access to prey is limited in any way, the ability of the whale to offset its energy expenditure during foraging is jeopardized.

The Draft BiOp dedicates several pages of Section 4 (Status of the Species), *see* Draft BiOp at 85–88, to explaining exactly how fishing (including using trap/pot and gillnet gear) might inhibit copepod aggregation.[86] Specifically, it states: "fixed fishing gear, such as gillnets and trap/pots, may also temporarily disturb local aggregations of copepods during the setting and hauling of gear due to turbidity caused by the sediment disturbance as the gears are set or dragged over the bottom during retrieval (Northeast Region Essential Fish Habitat Steering Committee 2002)." Draft BiOp at 87. Yet, ultimately, it concludes:

> we have determined that the effects of the fishing gears and vessels used by the fisheries in this Opinion on the availability of copepods for foraging right whales are **likely so small that they cannot be meaningfully measured, detected, or evaluated, and, therefore, insignificant**.

Id. at 88 (emphasis added). Given the declining prey availability for right whales due to climate change, *id*. at 95, these effects should not be discounted so readily. NMFS itself apparently recognizes that these prey disturbances should and could be minimized because it relies on the Massachusetts Restricted Area to "further minimize" such disturbances stating:

---

[84] *Id.*

[85] Van der Hoop, J., Nousek-McGregor, A.E., Nowacek, D.P., Parks, S.E., Tyack, P., and Madsen, P, "Foraging rates of ram-filtering North Atlantic right whales," *Functional Ecology*, published online May 11, 2019.

[86] The Conservation Law Foundation submitted at least two public comment letters to the New England Fishery Management Council and NMFS regarding the need for a section 7 consultation on the impacts of fishing on critical habitat in the Great South Channel. That consultation has not happened.

> Localized disturbance to dense copepod aggregations by these gear types is further minimized by MMPA gillnet and trap/pot closure areas that exist in temporal and spatial areas where these dense concentrations are expected to trigger foraging behavior (e.g., Massachusetts Bay Restricted Area). 50 CFR 229.23).

Draft BiOp at 87.

VII. The Draft BiOp Fails to Properly Analyze the Effects of the Action on the Recovery of Right Whales

The Draft BiOp fails to properly evaluate how the (improperly defined) actions under consultation will affect the recovery of the critically endangered right whale. Instead, the Draft BiOp largely assumes that because the fisheries will not impact the survival of the right whale, they will not impact its recovery either. In so doing, NMFS arbitrarily conflates the analysis of whether the proposed actions will jeopardize the right whale's survival with the distinct analysis of whether they will jeopardize the right whale's recovery.[87]

To "jeopardize the continued existence of" a species means "to engage in an action that reasonably would be expected, directly or indirectly, to reduce appreciably the likelihood of both the *survival and recovery* of a listed species in the wild by reducing the reproduction, numbers, or distribution of that species." 50 C.F.R. § 402.02 (emphasis added). As courts have explained, "[t]he only reasonable interpretation of the jeopardy regulation requires NMFS to consider recovery impacts as well as survival." *Nat'l Wildlife Fed'n*, 524 F.3d at 933; *see also Gifford Pinchot Task Force v. U.S. Fish and Wildlife Serv.*, 378 F.3d 1059, 1070–71 (9th Cir. 2004) (requiring consideration of recovery in evaluation of effects on critical habitat). Recovery is a more stringent jeopardy standard than survival because "a species can often cling to survival even when recovery is far out of reach" and an agency could find jeopardy based on "injury to recovery prospects alone." *Nat'l Wildlife Fed'n*, 524 F.3d at 931–32. As such, a "singular focus on survival violate[s] the ESA." *Id.* at 932 (citation omitted).

Thus, as part of its jeopardy analysis, NMFS must identify a benchmark—a tipping point precluding recovery—against which it can gauge an action's impacts. *Wild Fish Conservancy v. Salazar*, 628 F.3d 513, 527 (9th Cir. 2010). *See also Nat'l Wildlife Fed'n*, 524 F.3d at 936 (wildlife agency must "know roughly at what point survival and recovery will be placed at risk before it may conclude no harm will result"); *Nat'l Wildlife Fed'n v. Nat'l Marine Fisheries Serv.*, 184 F. Supp. 3d at 892.

The Draft BiOp contains no detailed analysis of how the agency actions being consulted on will impact the right whale's recovery. Such failure is particularly glaring considering the right whale is already nearing extinction. Instead, it only focuses on the effects of the proposed action on the whale's survival. *See e.g.*, Draft BiOp at 343 ("Above, we determined that the mortality of North Atlantic right whales associated with the proposed action is not reasonably expected to cause an appreciable reduction in the likelihood of survival of the species, and we do

---

[87] NMFS compounds this error by narrowly defining the agency action, as described above.

not expect the proposed action to have consequential effects on NARW population potential for recovery.").

In addition, the Draft BiOp contains no analysis of the "rough point" recovery will be at risk or establish any "tipping point" metrics against which to assess the species' recovery prospects. *Nat'l Wildlife Federation*, 524 F.3d at 936. These failures are particularly troubling given NMFS's other findings in the Draft BiOp, including, for example, that the right whale "faces a high risk of extinction" and "anthropogenic threats appear to be worsening;" the right whale's "resilience to future perturbations is expected to be very low;" and the right whale "may decline towards extinction if prey conditions worsen, and anthropogenic mortalities are not reduced." Draft BiOp at 95, 326–27; *see also* 73 Fed. Reg. at 60,175 (population models "indicate that preventing the death of even one adult female could significantly affect the population's trend."); 73 Fed. Reg. 60,173, 60,176 (Oct. 10, 2008) (NMFS's statement, when the population was near what it is today, that "the population can sustain **no deaths or serious injuries** due to human causes if its recovery is to be assured." (emphasis added)). This concern is only heightened because of the agency's improper exclusion of the effects of ALWTRP-regulated state fisheries and improper inclusion of the "benefits" of the ten-year Framework in its effects analysis.

VIII. The Draft BiOp Fails to Aggregate the Effects of the Action to the Baseline and Cumulative Effects

NMFS's Draft BiOp employs an unlawful jeopardy analysis. In evaluating whether the actions under consultation will jeopardize endangered right whales and other protected species, NMFS cannot simply compare the effects of the agency action on the species to other threats—it must consider the status of the species, the impacts of the proposed action **added to** the environmental baseline **added to** cumulative effects and whether these effects **in the aggregate** are likely to jeopardize a species' survival and recovery. *See* 50 C.F.R. § 402.14(g)(3), (4), (h)(1); 16 U.S.C. § 1536(b)(3), (4).

In other words, the proper analysis "is not the proportional share of responsibility the federal agency bears for the decline in the species, but what jeopardy might result from the agency's proposed action in the present and future human and natural contexts." *Pac. Coast Fed'n of Fishermen's Ass'ns v. U.S. Bureau of Recl.*, 426 F.3d 1082, 1093 (9th Cir. 2005) (citations omitted). Were it otherwise, "a listed species could be gradually destroyed, so long as each step on the path to destruction is sufficiently modest." *Nat'l Wildlife Fed'n*, 524 F.3d at 930. But "[t]his type of slow slide into oblivion is one of the very ills the ESA seeks to prevent." *Id.*; *see also Pac. Coast Fed'n of Fishermen's Ass'ns v. Nat'l Marine Fisheries Serv.*, 265 F.3d 1028, 1036–37 (9th Cir. 2001) (holding that if "individual projects are diluted to insignificance and not aggregated," then NMFS's "assessment . . . is tantamount to assuming that no project will ever lead to jeopardy of a listed species.").

The Draft BiOp fails to conduct this required aggregate analysis.[88] For example, NMFS "compare[s] the population trajectory with no impact from the proposed action (i.e., no entanglements in federal waters) to the population trajectory that includes the anticipated impacts from the action (i.e., entanglements in federal waters)." Draft BiOp at 331. NMFS then uses this analysis to conclude that "even in the absence of the U.S. federal fisheries, the female right whale population will decline," and the fisheries therefore will not jeopardize the species. *Id.* at 332–33. And fatally, the entire modeling exercise is rendered meaningless by NMFS's improper definitions of the proposed action, which assumes the full mitigating effects if all four Framework rulemakings are implemented in the federal fisheries on schedule and are fully effective, while excluding the effects of ALWTRP-regulated fishing in state waters.

Put simply, NMFS impermissibly based its "no jeopardy" conclusions on the view that, because the right whale's prospects for survival are dismal either way, mortality, serious injury, and other impacts from federal fisheries will not leave the whales that much worse off, comparatively speaking. The ESA forbids this approach. *See Nat'l Wildlife Fed'n*, 524 F.3d at 930 (rejecting the Fisheries Service's approach where only if the effects of the action "are 'appreciably' worse than baseline conditions must a full jeopardy analysis be made").

IX. The No Jeopardy Conclusion Is Contrary to the Evidence Before the Agency

Even if the Draft BiOp used the appropriate jeopardy analysis (which it did not), the agency still has to "articulate[ ] a rational connection between the facts found and the [conclusion] made." *Pac. Coast Fed'n of Fishermen's Ass'ns v. Nat'l Marine Fisheries Serv.*, 265 F.3d at 1034. The Draft BiOp's no jeopardy conclusion does not meet this standard.

For example, NMFS's Draft BiOp states that "[t]he North Atlantic right whale population faces a high risk of extinction. The population size is small enough for the death of any individuals to have measurable effects in the projections on its population status, trend, and dynamics." Draft BiOp at 326. It further states that "[t]he species has low genetic diversity . . . and the species['] resilience to future perturbations is expected to be very low;" and that "entanglement in fishing gear appears to have had substantial health and energetic costs that affect both survival and recovery of right whales." *Id.* at 327. The agency's no jeopardy conclusion is impossible to square with these findings.

Other evidence before the agency—including numerous statements from the agency itself—also demonstrates the arbitrary nature of its conclusion. For example, in 2019, NMFS assigned the right whale "a recovery priority #1," meaning its "extinction is almost certain in the immediate future because of rapid population decline or habitat destruction, and its survival conflicts with construction, development, or economic activity."[89] Also in 2019, NMFS stated that the right whale's situation presents "an urgent conservation crisis;" that "protecting every individual is a top priority;" and that "[r]ight whales cannot withstand continued losses of mature females—

---

[88] Moreover, as discussed above, NMFS excluded state waters in its jeopardy analysis. Further, the "action" it consulted on was the Framework, not just the proposed ALWTRP amendments. This analysis is fundamentally flawed to begin with.

[89] NMFS, Species in the Spotlight.

we have reached a critical point."[90] And in July 2020, the International Union for the Conservation of Nature ("IUCN") reclassified the North Atlantic right whale from "endangered" to "critically endangered"—the last category before "extinct in the wild."[91] Additionally, following the death of the first known calf of the 2020–2021 breeding season, NMFS stated that "each new right whale calf brings so much hope for this critically endangered species, and losses like this have a substantial impact on their recovery."[92] Indeed, one of the agency's own scientists recently published a paper concluding that known right whale deaths—which represent only a fraction of actual right whale deaths—"suggest that the recovery of North Atlantic right whales is in serious jeopardy . . . unless substantial mitigation measures that reduce mortality and serious injury from human activities are instituted immediately."[93]

Further, because of the low population size, the PBR of the right whale is 0.7.[94] The MMPA specifies that the PBR calculations require a 0.1 recovery factor for species listed under the ESA to assure no more than a ten percent delay in recovery time. 50 C.F.R. § 229.2. If takes occur at a rate at or above the PBR, the recovery rate for the stock will be impeded by definition.[95]

Moreover, while the Draft BiOp states that entanglement in commercial fishing gear is a leading cause of right whale serious injury and mortality, it also recognizes many other activities that currently pose a threat, or will do so in the future, in its analysis of the environmental baseline and cumulative effects. These threats include vessel strikes, plastic pollution, and exposure to harmful algal blooms, among others. Draft BiOp at 143–79.

---

[90] NMFS, Immediate Action Needed to Save North Atlantic Right Whales.

[91] IUCN, Almost a third of lemurs and North Atlantic Right Whale now Critically Endangered – IUCN Red List, (July 9, 2020), https://www.iucn.org/news/species/202007/almost-a-third-lemurs-and-north-atlantic-right-whalenow-critically-endangered-iucn-red-list; IUCN Red List, North Atlantic Right Whale, https://www.iucnredlist.org/species/41712/162001243 (last assessed Jan. 1, 2020).

[92] NMFS, First Known North Atlantic Right Whale Calf of the Season Washes Up Dead off North Carolina (Nov. 23, 2020), https://www fisheries.noaa.gov/feature-story/first-known-north-atlantic-right-whale-calf-season-washesdead-north-carolina.

[93] Pace, R. M. III, et al. 2021.

[94] *See, e.g.*, Colleen Coogan Presentation to the Atlantic Large Whale Take Reduction Team, Jan. 2021. While the new right whale PBR has not gone through peer review, that is irrelevant as the ESA requires NMFS to base its biological opinion on the best *available* scientific data. *See, e.g.*, *Sw. Ctr. for Biological Diversity v. Babbitt*, 215 F.3d 58, 60 (D.C. Cir. 2000) (under the best available science standard of the ESA, "[e]ven if the available scientific and commercial data were quite inconclusive, [NMFS] may—indeed must—still rely on it.").

[95] The MMPA defines PBR as "the maximum number of animals, not including natural mortalities, that may be removed from a marine mammal stock while allowing that stock to reach or maintain its optimum sustainable population;" and defines "optimum sustainable population" as the number of animals which will result in the maximum productivity of the population or the species, keeping in mind the carrying capacity of the habitat and the health of the ecosystem of which they form a constituent element," 16 U.S.C. § 1362(9), (22), which is comparable to the recovery goals of the ESA.

Yet, despite the plethora of threats faced by right whales and NMFS's express recognition that these threats have a negative impact on recovery, *see, e.g.*, *id.* at 203, the Draft BiOp contradictorily concludes that the operation of the fisheries is not likely to jeopardize the right whale's continued existence. It is hard to see how the effects of the fisheries—which NMFS estimates will result in the lethal and sublethal entanglement of over 11% of the population each year in the federal fisheries alone (improperly excluding entanglements in ALWTRP-regulated state fisheries)—when added to these other threats that NMFS finds negatively impact recovery in and of themselves can have no appreciable effect on the survival or recovery of the species. *See, e.g.*, 50 C.F.R. §§ 402.02, 402.14(g) (effects of the action must be added to the environmental baseline and cumulative effects in light of the status of the species); *see also Nat'l Wildlife Fed'n*, 524 F.3d at 930. The Draft BiOp certainly provides no answer.

Indeed, the Draft BiOp's conclusions are impossible to reconcile with its findings and scientific studies referenced earlier in the opinion that if none of the observed fishery-related mortality or serious injury occurred, the right whale population in 2016 would have been more than 12% higher—totaling 506 individuals. Draft BiOp at 95. Similarly, the Draft BiOp also acknowledges that eliminating all mortalities from fisheries, including cryptic mortality, could have resulted in a 2016 population more than 24% higher—to 562 individuals, and possibly as high as 600 individuals in 2018. *Id.*[96] Other studies have reached similar conclusions, determining for example, that "the population should continue to grow even with poor prey availability and only fails to do so when whale mortalities reach 8 to 10 per year."[97] Right whale mortalities are well above that level.

X. The Draft BiOp Fails to Include a Proper Incidental Take Statement and Cannot Authorize Any Take of ESA-Listed Large Whales

The language of the ESA and its implementing regulations make clear that a biological opinion must include an incidental take statement ("ITS") if NMFS concludes that the action is likely to result in the incidental take of listed species. 16 U.S.C. § 1536(b)(4); 50 C.F.R. § 402.14(g)(7). Where the take of an endangered marine mammal is involved, NMFS cannot issue an ITS unless and until it has first issued an MMPA take authorization under section 101(a)(5) of that statute. 16 U.S.C. § 1536(b)(4)(C). Despite the bind that that puts NMFS in here, NMFS is never excused from its mandatory duty to issue an ITS with a biological opinion because it cannot also authorize incidental take of an endangered marine mammal under the standards established in MMPA section 101(a)(5). Indeed, a federal court recently held that NMFS's prior biological opinion on the American lobster fishery was unlawful for failing to include an ITS despite recognizing that the fishery would result in the death or serious injury of 3.25 right whales per year even where the agency pled impossibility. *Ctr. for Biological Diversity v. Ross*, No. 18-112-JEB, 2020 U.S. Dist. LEXIS 62550 (D.D.C. Apr. 9, 2020).

---

[96] While the paper the Draft BiOp cites for this proposition considered M/SI from both U.S. and Canadian fisheries, the paper supports the notion that there would be more right whales if entanglements in U.S. fisheries ceased.

[97] Right Whale Recovery Tech Memo at 6.

The only circumstance when a biological opinion does not need to include an ITS is where the consulting agency determines that the proposed action **will not** result in any incidental takes of any listed species. *Az. Cattle Growers' Ass'n v. U.S. Fish and Wildlife Serv.*, 273 F.3d 1229, 1242 (9th Cir. 2001). In the Draft BiOp, NMFS does not conclude that an ITS is not required—nor could it—as NMFS does not determine that operation of the fisheries will not result in the incidental take of any listed species. To the contrary, NMFS concludes that both lethal and non-lethal entanglement of ESA-listed whales in the federal fisheries will continue to occur (which again unreasonably excludes take in state fisheries).

Specifically, NMFS estimates that operation of the U.S. fisheries will take an average of 15.125% of the North Atlantic right whale population per year via entanglements, an estimate that includes both lethal entanglements of 6.724 per year as well as sublethal entanglements. Draft BiOp at 226–27. After improperly excluding entanglements in ALWTRP-regulated state fisheries, *id.* at 227, and unrealistically assuming that the proposed ALWTRP measures will reduce M/SI in the federal fisheries to an annual average of 2.2, *id.* at 230, the ITS then purports to authorize sublethal take of 11.04% of the right whale population, *id.* at 392, even though NMFS explicitly assumes that this percentage will include the 2.2 average M/SI per year that will continue to occur, *id.* at 227. The Draft BiOp also estimates that the fisheries will take 1.89 fin whales per year, one sei whale per year, and one sperm whale per year via entanglements. *Id.* at 392.

Nevertheless, while NMFS's ITS purports to authorize the non-lethal take of right whales and other ESA-listed whales from entanglement in fishing gear used in federal fisheries, it does not explicitly authorize the lethal take of right whales "because the lethal incidental take of ESA-listed whales has not been authorized under section 101(a)(5) of the MMPA." Draft BiOp at 390. NMFS noted that "[f]ollowing the issuance of such authorizations, NMFS may amend this Opinion to adjust lethal incidental take allowance for these species, as appropriate." *Id.*

This approach is arbitrary for numerous reasons. First, the Draft BiOp does not include an ITS for the deaths and serious injuries of ESA-listed large whales that NMFS acknowledges will occur by operation of the fisheries in both federal and state waters. NMFS's "failure to include an ITS . . . after finding that the [fisheries have] the potential to harm the North Atlantic right whale at more than three times the sustainable rate is about as straightforward a violation of the ESA as they come." *Ctr. for Biological Diversity v. Ross*, 2020 U.S. Dist. LEXIS 62550, at *28. NMFS's approach is especially arbitrary here considering its express recognition that the level of sublethal take of right whales it purports to authorize—11.04% of the population each year—**includes "[e]ntanglements in the U.S. federal fisheries anticipated to result in M/SI."** Draft BiOp at 227 (emphasis added).

That the ITS specifies the extent of non-lethal take, contains reasonable and prudent measures ("RPMs"), and specifies terms and conditions cannot save the agency's draft ITS—"[a]ny non-ITS substitute, even one that fulfills one of several functions of an ITS, will not do." *Id.* at *27–28. That is particularly true here where the RPMs for large whales are actions that NMFS is already legally required to do under the MMPA. *See* Draft BiOp at 393–97; *see also, e.g.*, 16 U.S.C. §§ 1387(d)(1) (requiring NMFS to monitor incidental mortality and serious injury of marine mammals to, *inter alia*, "identify changes in fishing methods or technology that may increase or decrease incidental mortality or serious injury"), 1386 (requiring stock assessments for marine mammal species that include analysis of the impacts of commercial fisheries on the stock and other factors contributing to the decline). Moreover, the RPMs—consisting of further modeling and study—will not actually mitigate the impact of take of ESA-listed whales and therefore do not serve the purpose of an RPM. *See* 50 C.F.R. § 402.14(i) (RPMs must "**minimize** [the] impact" of incidental take (emphasis added)). Indeed, the amount or extent of sublethal (and implicit lethal) take that NMFS is proposing to authorize is the same level of both non-lethal and lethal take it estimates will occur via operation of the federal fisheries aftern implementation of the ALWTRP measures. In other words, the ITS arbitrarily authorizes a level of take co-extensive with the (unlawfully limited) agency action under review.

Second, NMFS's approach—purporting to authorize non-lethal take, but not lethal take, because lethal take is not yet authorized under the MMPA—is inconsistent with the law. The MMPA prohibits all take of marine mammals unless otherwise authorized. NMFS has not—and, especially for right whales, cannot—authorize non-lethal take under section 101(a)(5)(E).[98] And the MMPA prohibits not only take via death, but also actions that capture marine mammals and "any act of pursuit, torment, or annoyance" that has the potential to injure or disturb a marine mammal, including disruption of behavioral patterns "including migration, breathing, nursing, breeding, feeding" activities. 16 U.S.C. § 1362(13), (18). While NMFS can authorize take incidental to commercial fisheries via section 118 for species not listed under the ESA, the MMPA makes clear that when ESA-listed species are at issue, both sections 101(a)(5)(E) and 118 apply. *See id.* §§ 1371(a)(5)(E), 1387(a)(2). NMFS cannot authorize sublethal take of ESA-listed marine mammals simply by issuing amendments to the ALWTRP via section 118.

Third, NMFS's draft ITS obscures the tremendous number of sublethal takes it purports to authorize by specifying this take as an annual average percentage of the population over a five-year period, i.e., 11.04% per year. Based on the current estimated population, NMFS proposes to authorize sublethal take of **nearly 38** right whales per year (not including the 2.2 M/SI that are already baked into this estimate).

NMFS's approach is especially arbitrary considering that it proposes to authorize sublethal take of other ESA-listed whales as a specific (and much smaller) number—an average of only one sublethal take of fin and sperm whales and 1.89 sei whales per year. NMFS does not explain why it proposes to authorize take as a specific number for other whale species, but a percentage of the population for right whales.

And the percentage it does propose to authorize likely underestimates the extent of sublethal take from the fisheries given that NMFS has concluded nearly 100 right whales a year exhibit new scars indicating interactions with ropes, which is nearly 30% of the current population.[99] Indeed,

---

[98] Indeed, NMFS may not authorize any take whatsoever—whether lethal or non-lethal—of North Atlantic right whales, or any other ESA-listed large whale, by commercial fishing operations under section 101(a)(5)(E) unless it determines that lethal take (i.e., mortality and serious injury) will have a negligible impact on that species. 16 U.S.C. § 1371(a)(5)(E)(i)(I).

[99] *See, e.g.*, Email from Colleen Coogan, NMFS to Atlantic Large Whale Take Reduction Team, RE: Take reduction target approaches considered, Apr. 18, 2019.

NMFS admits that its proposed ITS does not include the 4.085% of the population that NMFS estimates is taken via sublethal entanglements in state fisheries. *See* Draft BiOp at 227. Nor does this estimate account for the revisions that will have to be made to the agency's assumptions on total annual average M/SI in U.S. commercial fisheries based on Pace et al. 2021.

Moreover, despite recognizing in both the Draft BiOp and elsewhere (1) that the sublethal take of female right whales has harmful impacts not only to individual whales but also to the population and its prospects for recovery, *see, e,g.*, Draft BiOp at 220; (2) that "even without accounting for injury, the drag from carrying rope and other gear for long periods of time can be energetically more expensive for a female than the migratory and developmental costs of pregnancy;"[100] and (3) that "[e]ven if disentangled, there are several injuries that can have costs lasting long after disentanglement," including "trauma wounds from rope cuts that may or may not eventually heal, and damage to baleen plates that can prevent efficient filter feeding for many years since these plates grow slowly;"[101] NMFS's ITS arbitrarily treats all sublethal takes as equal.

NMFS's approach for right whales also undermines the purpose of an ITS. An ITS must "set forth a 'trigger' that, when reached, results in an unacceptable level of incidental take, invalidating the safe harbor provision, and requiring the parties to re-initiate consultation." *Ariz. Cattle Growers' Ass'n v. U.S. Fish & Wildlife*, 273 F.3d 1229, 1249 (9th Cir. 2001); 50 C.F.R. § 402.16(a)(1). Setting a level of permissible sublethal take as a percentage of the overall population will make knowing when that level of take has been exceeded impossible, particularly where (a) NMFS's official population estimates for a year are not made official until several years later; and (b) given that the vast majority of entanglements that occur each year go undetected, there is no way to calculate how many new sublethal entanglements have occurred in any given year, let alone the average entanglements each year over a five-year period. Nor is there any way to adequately monitor such takes. And by explicitly excluding M/SI from the ITS, even though the assumption on entanglement percentages itself included both lethal and non-lethal, NMFS has avoided any chance of having to reinitiate consultation based on exceedance of the ITS via detected M/SI. *See* 50 C.F.R. § 402.16(a)(1).

Further, the percentage-based ITS for sublethal take of right whales ignores the basic notion that, as the population continues to decline, the impact of sublethal takes on an even smaller population will have an ever greater impact on the species' prospects for survival and recovery. *See, e.g.*, Draft BiOp at 95, 326, 327. Yet the ITS would allow more than 11% of the right whale population to be entangled each year for five years before reinitiating consultation, no matter how small it becomes.

<u>Fourth</u>, NMFS's suggestion in the ITS that it will amend the ITS to authorize lethal take of right whales under the ESA at some point after it authorizes such take under the MMPA is disingenuous. NMFS has never authorized take of right whales incidental to the operation of the fisheries under either the MMPA or the ESA. Indeed, NMFS has acknowledged that it cannot

---

[100] *See, e.g.*, Right Whale Recovery Tech Memo at 12.

[101] *Id.*

authorize lethal take of right whales by the lobster fishery because such deaths have more than a negligible impact on the species. *See, e.g.*, *Ctr. for Biological Diversity v. Ross*, 2020 U.S. Dist. LEXIS 62550, at *26. It is the essence of arbitrary agency action for NMFS to continue to authorize these fisheries that it acknowledges will kill and seriously injure right whales at unsustainable levels when it knows it cannot lawfully authorize such take because of the critically imperiled status of the right whale.

Finally, despite recognizing that the fishery could also take right whales and other whales via fishing vessel operations, *see, e.g.*, Draft BiOp at 146, the ITS fails to specify the amount or extent of this take or include measures to mitigate the impact of this take on the species.

XI. NMFS's Authorization and Management of the Fisheries Violates its Substantive Duties under Section 7(a)(2) of the ESA

NMFS is in violation of section 7(a)(2) of the ESA. Pursuant to section 7(a)(2), NMFS is required to "insure" that any of its actions or approvals are "not likely to jeopardize the continued existence of any endangered . . . species," including North Atlantic right whales. *See* 16 U.S.C. § 1536(a)(2). This substantive duty applies to NMFS's permitting, management, and authorization of fisheries in both state and federal waters under the ALWTRP and relevant fishery management plans.

An agency violates its substantive section 7(a)(2) duty by relying on an invalid biological opinion. *Wild Fish Conservancy v. Salazar*, 628 F.3d 513, 532 (9th Cir. 2010). Where the biological opinion is facially flawed, the action agency's reliance on it is arbitrary. *Ctr. for Biological Diversity v. BLM*, 698 F.3d 1101, 1127–28 (9th Cir. 2012); *Wild Fish Conservancy*, 628 F.3d at 532. "Where the opinion's flaws are '*legal* in nature' . . . '[d]iscerning them requires no technical or scientific expertise,' and the failure to do so may result in 'an action based on reasoning 'not in accordance with law' and . . . thus arbitrary and capricious.'" *Id.* (citations omitted).

As explained above, a federal court has already found that NMFS's existing biological opinion on the American lobster fishery is unlawful for failing to include an ITS, and further indicated that the biological opinion's jeopardy analysis may also have been unlawful for focusing solely on entanglements that lead to mortality and serious injury as defined by the MMPA, rather than the full effects of the action under the ESA. *Ctr. for Biological Diversity v. Ross*, 2020 U.S. Dist. LEXIS 62550, at *28–29. NMFS's biological opinions on other Atlantic fisheries suffer from similar flaws.[102] Yet NMFS continues to rely on these opinions in authorizing and managing the fisheries that are the subject of the Draft BiOp. This is unlawful. *See Ctr. for Biological Diversity v. Bernhardt*, 982 F.3d at 750 (holding that action agency's reliance on invalid no jeopardy biological opinions was arbitrary); *Mayo v. Jarvis*, 177 F. Supp. 3d 91, 146 (D.D.C. 2016) (same); *Ctr. for Biol. Diversity v. Nat'l Marine Fisheries Serv.*, 977 F. Supp. 2d

---

[102] *See, e.g.*, NMFS, Endangered Species Act Section 7 Consultation on the Continued Implementation of Management Measures for the Northeast Multispecies, Monkfish, Spiny Dogfish, Atlantic Bluefish, Northeast Skate Complex, Mackerel/Squid/Butterfish, and Summer Flounder/Scup/Black Sea Bass Fisheries [Consultation No. F/NER/2012/01956] GARFO-2012-00006, Dec. 16, 2013.

55, 90–91 (D.P.R. 2013) (holding NMFS's reliance on a biological opinion with an inadequate ITS "violated its substantive duty to ensure that the continued operation of the Fishery did not jeopardize" listed coral species).

Finalizing the Draft BiOp as written will not change this, as NMFS's Draft BiOp is invalid on its face for the reasons described above. Moreover, as also described above, new information reveals that NMFS's authorization and management of the fisheries is not only harming right whales, but actively driving the species toward extinction, which only underscores the arbitrariness of the agency's continued reliance on the facially invalid biological opinions.

XII. NMFS's Authorization and Management of the Fisheries Violates, and Will Continue to Violate, Section 9 of the ESA

NMFS is in violation of the ESA's prohibition on "taking" or causing others to take endangered species. The prohibition makes it unlawful for any person to "cause [an ESA violation] to be committed." 16 U.S.C. §§ 1538(a), (g). Courts have made clear that a "governmental third party pursuant to whose authority an actor directly exacts a taking . . . may be deemed to have violated the provisions of the ESA." *Strahan v. Coxe*, 127 F.3d 155, 163 (1st Cir. 1997).

The Draft BiOp admits that the fisheries will cause the take of endangered right whales (and other whales) via lethal and non-lethal entanglements. NMFS does not currently have a valid ITS for its authorization and management of any of the fisheries analyzed in the Draft BiOp. And its Draft BiOp does not propose a lawful ITS. By continuing to permit, authorize, and manage the fisheries, including through its implementation of management measures and the issuance of annual MMAP authorizations and fishing permits under the ALWTRP, MMPA and applicable fishery management plans, NMFS's actions have caused and will continue to cause the unpermitted take of endangered North Atlantic right whales (and other whales) in violation of section 9 of the ESA. In proposing to continue to authorize the fisheries without a valid ITS, NMFS is committing itself to continue its blatant violation of section 9 of the ESA.

XIII. NMFS Cannot Make Any Irreversible Commitment of Resources Before Consultation is Completed

Section 7(d) of the ESA provides that once a federal agency initiates consultation on an action under the ESA, the agency "shall not make any irreversible or irretrievable commitment of resources with respect to the agency action which has the effect of foreclosing the formulation or implementation of any reasonable and prudent alternative measures which would not violate subsection (a)(2) of this section." 16 U.S.C. § 1536(d). Section 7(d) prohibitions remain in effect throughout the consultation period and until the federal agency has satisfied its obligations under section 7(a)(2) that the action will not result in jeopardy to the species.

While NMFS previously issued a memorandum concluding that its continued authorization of the fisheries at issue in the Draft BiOp would not violate section 7(d) of the ESA, NMFS should reexamine that conclusion in light of the plethora of new information indicating the increasingly dire status of the right whale and the role U.S. fisheries play in not only impeding the right whale's recovery but its very survival. Indeed, NMFS predicated its finding on the fact the agency "retains the legal authority to restrict activities of fishery participants should new information require modification of current restrictions."[103] New information clearly indicates that NMFS must modify existing restrictions to save the right whale.

XIV. Conclusion

NMFS's Draft BiOp is riddled with legal inadequacies in what is the agency's apparent attempt to justify a pre-determined outcome—that continued operation of U.S. commercial fisheries will not jeopardize any listed species, including critically endangered right whales. Its approach is the essence of arbitrary agency decisionmaking and threatens to push right whales even closer to the brink of extinction. NMFS must substantially revise the Draft BiOp—and the draft ALWTRP regulation— to comply with its legal obligations under the ESA.

Sincerely,

/s/ *Kristen Monsell*
Kristen Monsell
Oceans Legal Director & Senior Attorney
Center for Biological Diversity
kmonsell@biologicaldiversity.org

/s/ *Erica Fuller*
Erica Fuller
Senior Attorney
Conservation Law Foundation
efuller@clf.org

/s/ *Jane Davenport*
Jane Davenport
Senior Attorney
Defenders of Wildlife
jdavenport@defenders.org

/s/ *Laura Smythe*
Laura Smythe
Staff Attorney
lsmythe@humanesociety.org
Sharon Young
Senior Strategist, Marine Issues
syoung@humanesociety.org
The Humane Society of the United States

---

[103] Memorandum for Michael Pentony, Assistant Regional Administrator for Sustainable Fisheries from Kimberly Damon-Randall, Assistant Regional Administrator for Protected Resources, Reinitiating Section 7 Consultation on the Batched Fisheries, American Lobster, and Atlantic Deep-Sea Red Crab Biological Opinions, Oct. 17, 2017.

<u>*/s/ Keisha Sedlacek*</u>
Keisha Sedlacek
Director of Regulatory Affairs
Humane Society Legislative Fund
ksedlacek@hslf.org

<u>/s/ *Francine Kershaw*</u>
Francine Kershaw, Ph.D.
Staff Scientist, Marine Mammal Protection & Oceans
Natural Resources Defense Council
fkershaw@nrdc.org

Attachment D

Received: 24 June 2020 | Accepted: 5 September 2020
DOI: 10.1111/mms.12753

ARTICLE

Marine Mammal Science

Body growth of North Atlantic right whales (*Eubalaena glacialis*) revisited

Sarah M. E. Fortune[1,2] | **Michael J. Moore**[3] | **Wayne L. Perryman**[4] | **Andrew W. Trites**[1]

[1]Marine Mammal Research Unit, Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, British Columbia, Canada

[2]Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, Manitoba, Canada

[3]Biology Department, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts

[4]Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, California

Correspondence
Sarah Fortune, Freshwater Institute, Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, Manitoba R3T 2N6, Canada.
Email: sarahmefortune@gmail.com

Abstract

Knowing size-at-age is important for determining food requirements and making inferences about the nutritional status of individuals and their populations. Accurate growth curves are also needed to quantify drug dosages to treat wounded or entangled animals. However, body sizes are often based on small numbers of measured animals that must be improved as new data become available. We updated an existing body growth model for North Atlantic right whales (NARWs) using new data from dead animals and from older individuals. Our models indicate that NARWs attain mean lengths and weights of 4.3 m and 1.0 mt at birth, and 13.1 m and 31.7 mt when sexually mature. Calves more than double their length and attain nearly three-quarters of their asymptotic adult size during their first year of life. Overall, our length estimates agreed well with previous estimates, but our mass-at-age values were considerably higher. These differences revealed that necropsy data used alone in allometric models underestimate mass due possibly to several of the stranded animals in the database having been chronically entangled and in poor body condition. Augmenting the database with healthier individuals, such as harvested North Pacific right whales, yielded mass predictions that reflect both healthy and unhealthy individuals.

KEYWORDS

body size, *Eubalaena glacialis*, growth models, length, mass, morphometry, photogrammetry

1 | INTRODUCTION

Body size is related to sexual maturity, longevity, reproductive strategies, metabolic needs, and abundance, and is arguably the most important trait of individual animals (Kenagy & Trombulak, 1986; Laws, 1956; Speakman, 2005; White, Ernest, Kerkhoff, & Enquist, 2007). Because body mass is largely linked to age at sexual maturity, fast growing species reach maturity sooner than slower growing species. Such is the case for cetacean species that are expected to attain sexual maturity after reaching ~85% of their maximum length (Laws, 1956). Rates of body growth thus influence reproductive output and population dynamics, while body mass affects metabolic rates, energy expenditure, and food requirements (Brodie, 1975). Overall, body size is important when it comes to several aspects of the biology, ecology, and management of species.

Growth curves for North Atlantic right whales (*Eubalaena glacialis*) have been derived from small numbers of opportunistic measurements of dead animals collected by different institutions and individuals over many years (Moore, Knowlton, Kraus, McLellan, & Bonde, 2004; Sharp et al., 2019). This database has evolved and grown with time as errors were corrected and new information became available. Given the importance of having accurate growth curves to determine food requirements and make inferences about the reproductive and nutritional status of populations, or to set drug dosages of sedatives and antibiotics to treat injured whales (Barratclough et al., 2014; Moore et al., 2010), it is important to periodically review the existing morphometric database and update the published growth curves as necessary.

The most recent growth curve for North Atlantic right whales was published in 2012 (Fortune et al., 2012) using measures of length and mass from necropsied animals (Moore et al., 2004), and photogrammetric measurements from live animals (Perryman & Lynn, 2002). Since then, new body size data were added to the database (including animals >22 years old, the upper limit for the previous growth curve), and some of the morphometric measurements included in the North Atlantic Right Whale Consortium Necropsy Database were removed when discovered to have had been estimated rather than measured (North Atlantic Right Whale Consortium, 2018). As a result of these shortcomings, the existing body growth curves for North Atlantic right whales need to be corrected and updated.

Our goal was to use recently acquired data to improve the existing growth models for right whales and generate more robust estimates of body size at age to allow better predications of food requirements to be made, as well as drug dosages to be determined. We also sought to better understand the rapid growth of nursing calves and decelerated growth of juveniles and adults.

2 | MATERIALS AND METHODS

2.1 | Length

We modeled the relationship between length and age for North Atlantic right whales using data obtained during necropsies (lengths were measured directly from dead animals) and from photogrammetry (lengths were obtained from photographs of live animals at-sea). Photogrammetric measurements (*n* = 133) were taken from 94 unique individuals in the Bay of Fundy between 2000 and 2002 as described by Fortune et al. (2012). Aerial images of individual right whales were collected from a Twin Otter aircraft equipped with a KA-76A United States military reconnaissance camera that was mounted over an 18-in. camera port located in the hull of the aircraft. The majority of the photogrammetric data were obtained using a fixed focal length 126-mm lens with Kodak Aerial Ektachrome film. The aircraft altitude and ground speed of the aircraft were used to determine the camera cycle rate, whereby adjacent frames overlapped by 60%–80%. The goal of the rapid cycle rate was to permit each whale to be photographed on 3–4 frames during a single photo pass. For each image taken, location (global positioning system) and altitude (radar altimeter) data were simultaneously recorded. Prior to each field season, the radar altimeter bias was determined by collecting a series of images of a floating target of known size and conducting a regression analysis. The altimeter bias was subsequently used to correct the altitude for each image used for photogrammetric measurements (Perryman & Lynn, 2002).

Body lengths were measured during necropsies of 29 known-age individuals between 1970 and 2017 and represented the straight-line distance from the snout to the fluke notch. The straight-line distance was determined by laying a measuring tape parallel to the animal on the ground and measuring the distance from the tip of the rostrum to the fluke notch. Measurement errors can be attributed to the many individuals who took these body length measurements, as well as the difficulty associated with placing the tape measure at the precise location that is perpendicular to the snout tip and fluke notch. Body lengths of necropsied individuals that were mechanically hauled onto the beach prior to measurement were corrected for potential stretching (~9% body length; George, Zeh, Suydam, & Clarkm, 2004).

Age classes of all measured animals were determined for individual whales by matching photographs of their unique callosity patterns (Kraus et al., 1986) using the North Atlantic Right Whale Consortium Identification Database (North Atlantic Right Whale Consortium, 2018). We also estimated the ages of individuals (in decimal years) based on when they stranded or were photogrammetrically measured, and their estimated median date of birth of January 5 (Fortune et al., 2012). Detailed descriptions of how ages were estimated, and how necropsies and aerial photogrammetry were conducted are contained in Fortune et al., (2012).

2.2 | Growth curves

We fit four standard growth functions to the length-at-age data, including the Putter (Equation 1; von Bertalanffy, 1938; Ricker, 1979), von Bertalanffy (Equation 2; von Bertalanffy, 1938; Ricker, 1979), Gompertz (Equation 3; Gompertz, 1825; Zach, Liner, Rigby, & Mayoh, 1984), and logistic equation (Equation 4; Ricker, 1979):

$$S_t = A\left(1 - e^{-k(t-t_0)}\right) \tag{1}$$

$$S_t = A\left(1 - e^{-k(t-t_0)}\right)^3 \tag{2}$$

$$S_t = Ae^{-ce^{-kt}} \tag{3}$$

$$S_t = \frac{A}{1 + e^{-k(t-t_0)}} \tag{4}$$

where S is length at age t for males and females, A is asymptotic size, t_0 is time at which size is theoretically zero, c is the constant of integration (Zach et al., 1984) and k is indicative of growth rate (Ricker, 1979).

We fit length-at-age models as per Fortune et al. (2012) in a 2-phased approach with nonlinear least squares regression. We fit standard growth functions to length-at-age data for individuals aged 0–1.65 years (*Phase 1*) and older animals aged 1.65–30.5 years (*Phase 2*). We used the statistical program R (nls package; R Development Core Team, 2016) for analysis. *Phase 1* represented rapid calf growth and *Phase 2* represented decelerated growth of juveniles and adults. The inflection point between models was determined based on the age where the difference between predicted lengths of *Phase 1* and *2* models was equal to zero. Model selection was made by observing the Akaike information criterion (AIC) and selecting the model with the lowest AIC and greatest weight. Since some photogrammetrically measured animals were seen in more than 1 year and were measured as many as three times, we created (i.e., bootstrapped) 10,000 data sets from the 162 measurements by randomly selecting duplicate length measurements to be removed. Resampling was done to avoid issues related to nonindependence of observations whereby one length-at-age measurement per individual per model simulation was selected randomly. Growth curves were fit to the bootstrapped samples and mean model parameters were extrapolated from the bootstrap replicates to define the "best model." Confidence intervals (95%) were subsequently calculated by ordering bootstrap replicates into the 2.5% and 97.5% quartiles.

We used a linear mixed-effects model and a repeated-measures analysis of variance (ANOVA) to test for sexual dimorphism through comparison of mean length-at-age measurements for adult (9–30 years) male and female right whales. This analysis accounted for violations of independence by including animal ID as a random factor as there were duplicate length measurements for photogrammetrically measured individuals.

2.3 | Mass

Mass-at-age was derived from the allometric relationship of length and mass determined from 13 dead whales (North Atlantic Right Whale Consortium, 2018; Moore et al., 2004; Sharp et al., 2019) as described by Fortune et al. (2012). We linearized Schultz's (1938) allometric model:

$$W = aL^b \tag{5}$$

to predict mass based from body length:

$$\log_{10}W = b\log_{10}L + \log_{10}a \tag{6}$$

where W is mass in kilograms, L is length in centimeters, a is a constant factor, and b is an exponential constant. We tested the significance of coefficients using a two-tailed Student's t-test (Zar, 1996). Model uncertainty was incorporated by bootstrapping the allometric model 10,000 times to generate a distribution of predicted masses for given lengths. We also compared the relationship derived for North Atlantic right whales to that derived for 16 North Pacific right whales (*Eubalaena japonica*) (Omura, Oshumi, Nemoto, Nasu, & Kasuya, 1969).

3 | RESULTS AND DISCUSSION

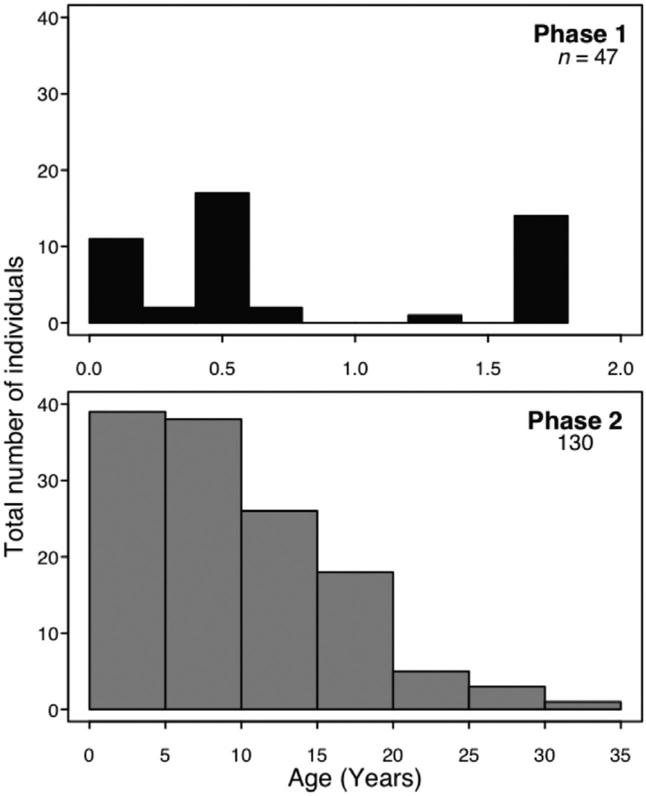
3.1 | Length

The 2-phased Gompertz model best described the growth of North Atlantic right whales (Figure 1, Table 1), although the von Bertalanffy and Putter models presented similar AIC scores and weights suggesting that right whale growth may be adequately described using several growth functions (Anderson, 2008). We nevertheless selected the model with the lowest AIC and greatest weight. Furthermore, we biologically justified using the Gompertz model over the von Bertalanffy model because the Gompertz equation accounted for somatic and reproductive development, while the von Bertalanffy model only accounted for somatic growth (Neuenhoff, Cowan, Whitehead, & Marshall, 2011).

To find a point of inflection where the multiphase growth curves met, we fit two Gompertz growth models to data for younger (0–1.65 years) and older (1.65–30.5 years) animals. Morphometric data were only available for one individual between 0.65 and 1.65 years (1.27 years). We found that the inflection point occurred at 0.79 years and that the average age of individuals used to fit the *Phase 1* was 0.78 ± 0.62 *SD* and 9.70 ± 6.68 *SD* years for *Phase 2* (Figure 1).

The Gompertz growth functions were fit in a two-phased approach whereby *Phase 1* included animals between 0 and 1.65 years and *Phase 2* included whales between 1.27 and 30.5 years and bootstrapping was used to account for model uncertainty. We found that the point of inflection (i.e., where the two-phased growth curves met) occurred at 0.79 years. Since we did not have morphometric data for animals >0.65 and ≤ 1.26 years (*Phase 1*)

FIGURE 1 Distribution of ages for the morphometric measurements used to generate multiphase length-at-age growth curves for North Atlantic right whales calves (*Phase 1* model fit to data spanning birth to 1.65 years) and juveniles and adults (*Phase 2* fit to data >1.28 years). To ensure both models intersected, some of the same measurements for young juveniles were used to fit both phases of the model. After finding the inflection point at 0.79 years, the models were truncated whereby *Phase 1* included animals between 0 and 0.79 years and *Phase 2* included whales between 0.80 and 30.5 years.



and > 0.79 and < 1.27 years (*Phase 2*) length-at-age predictions for these age ranges using the Gompertz equation should be interpreted with caution. Mean (± *SD*) Gompertz model parameters (from 10,000 bootstrap replicates) were: 1,067.19 ± 19.67 for *A*, 0.93 ± 0.08 for *c*, and – 3.11 ± 0.28 for *k* for *Phase 1*; and 1,362.75 ± 22.88 for *A*, 0.37 ± 0.03 for *c*, and – 0.18 ± 0.03 for *k* for *Phase 2*. The average age of individuals used to fit the *Phase 1* was 0.78 ± 0.62 *SD* and 9.70 ± 6.70 *SD* years for *Phase 2* (Figure 1).

The rapid growth of calves occurred between ages 0 and 0.79 years (*Phase 1*; Figure 2; 288.35 days), and the decelerated growth of older animals occurred from 0.80 to 30 years old (*Phase 2*; Figure 2). Calves were estimated to gain an average of 559 cm (± 43 *SD*) from birth to near weaning (0.79 years), representing 1.94 cm per day (± 0.15) if a constant growth rate is assumed.

Right whales attained 90% of their maximum body length (1,362 cm) at 8 years of age—which is about when females become sexually mature (assuming age at first parturition is 9 years and pregnancy lasts ~12 months; Hamilton, Knowlton, Marx, & Kraus, 1998). Sexual dimorphism appears to occur near sexual maturity based on the measured sizes of males and females between 8.0 and 8.9 years (females measured 1,309 cm ± 0.177 *SD*, *n* = 2, on average and males measured 1,197 cm ± 0.183 *SD*, *n* = 4).

Predicted asymptotic length (~95% of maximum length) occurred at 12 years, which follows findings from previous studies (Fortune et al., 2012). Thus, calves were estimated to more than double their length and to attain almost three-quarters of the asymptotic adult length at 1 year old (when weaning is assumed to occur).

Including sex as a fixed factor yielded a better linear mixed-effects model than a null model that did not distinguish between the body length of adult males and females (Log Likelihood ratio test LRT = 9.7, *p* = .002). Slopes (repeated-measures ANOVA, *F*(1,41) = 10.5, *p* = .002) and intercepts (repeated-measures ANOVA, *F* (1,41) = 22,356.3, *p* < .0001) of the model for adult males and females (≥9 years old) differed significantly from one

TABLE 1 Parameter estimates (A, k, c, t_0) (± *SE*) for the 2-phased growth models (Putter, von Bertalanffy, Gompertz, and logistic; Equations 1–4) for North Atlantic right whales (see "Materials and Methods" for model parameters description), where A is asymptotic size, k is indicative of growth rate, c is the constant of integration, and t_0 is time at which size is zero. Length measurements are in centimeters and age is in decimal years. AIC values are shown along with the difference in AIC values between fitted models, the likelihood of each model, and the weight of each model (i.e., the weight of evidence in favor of each model). The model with the greatest AIC weight was considered to be the "best" model.

Model	A	k	c	t_0	AIC values	AIC differences	Likelihoods	AIC weights
Phase 1 (0–0.79 years)								
Putter	1,079.037 ± 23.676	0.613 ± 0.025	—	2.336 ± 0.281	540.658	1.748	0.417	0.187
von Bertalanffy	1,071.000 ± 21.260	0.267 ± 0.015	—	2.824 ± 0.301	539.324	0.414	0.813	0.364
Gompertz	1,067.353 ± 20.479	0.923 ± 0.058	−3.075 ± 0.315	—	538.910	0.000	1.000	0.448
Logistic	1,039.574 ± 22.351	—	—	3.328 ± 0.424	551.5023	12.593	0.002	0.001
Phase 2 (0.80–30 years)								
Putter	1,365.000 ± 21.120	0.311 ± 0.017	—	0.149 ± 0.025	1,471.243	0.307	0.858	0.305
von Bertalanffy	1,362.000 ± 20.000	0.114 ± 0.007	—	0.160 ± 0.026	1,471.031	0.095	0.954	0.339
Gompertz	1,360.675 ± 19.501	0.361 ± 0.023	−0.166 ± 0.026	—	1,470.936	0.000	1.000	0.356
Logistic	1,285.664 ± 10.285	—	—	0.639 ± 0.046	1,540.582	69.646	0.000	0.000

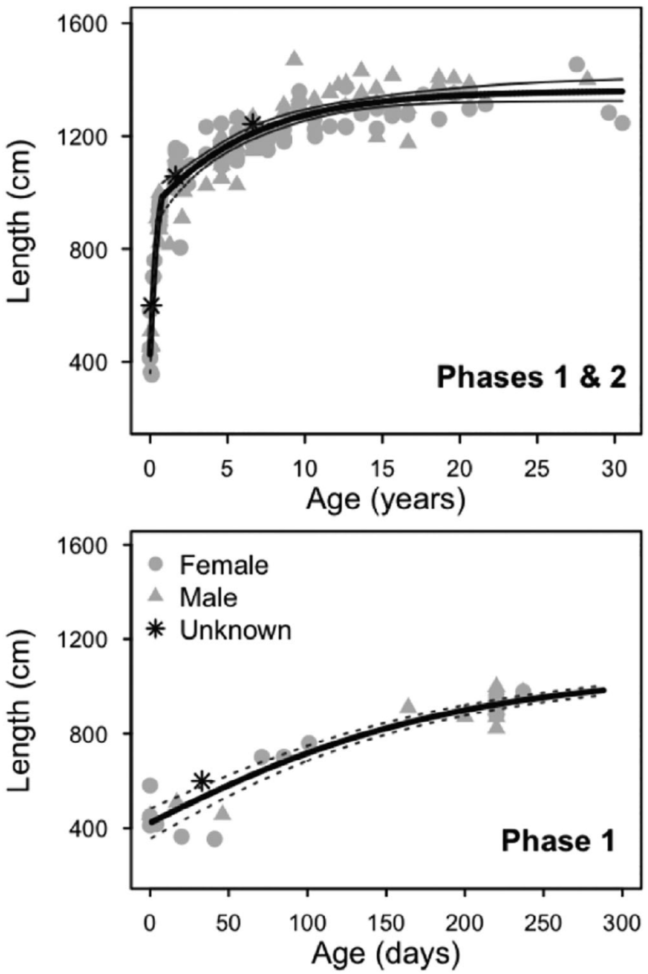


FIGURE 2 Mean 2-phase (*Phase 1* and *2*) and 1-phase Gompertz growth curves for North Atlantic right whales. The 95% confidence intervals (dashed lines) were derived from 10,000 bootstrap replicates. Length-at-age can be calculated using the equations provided in the upper graph with age expressed in years. *Phase 1* includes growth from birth to 0.79 years old, and *Phase 2* describes growth for right whales >0.79 years old. The multiphase Gompertz growth equations based on mean model parameters as determined by bootstrapping were *Phase 1* length = 1,067.35 * exp[−0.923 * exp (−3.08 * Age]) and *Phase 2* length = 1,360.68 * exp[−0.36 * exp (−0.16 * Age)].

another. This was consistent with sexual dimorphism, with adult females (1,345.7 cm ± 61.2 *SD*) being 4% larger on average than adult males (1,291.9 cm ± 56.1 *SD*) (Figure 3).

3.2 | Mass

In terms of body mass, our models show that North Atlantic right whales gain considerable mass during their first year of life, with calves growing an average of ~42 kg/day and weighing over 13 mt after 0.79 years (based on the mean birth mass of 1,022 ± 252 kg and mean inflection mass of 13,206 ± 747 kg; Table 2). Calves near the onset of independence (9.6 months) were 13 times heavier than their birth mass and had attained 47% of the mass of a sexually mature animal. However, this rate of increase in body mass dropped significantly between weaning (~1 year) and sexual maturity (9 years), i.e., ~4.9 kg/day. Mean body mass was an estimated 13.7 mt at weaning, and 28.2 mt when mature.

The mass-to-length relationship did not differ significantly between North Atlantic and North Pacific right whales (two-tailed t-test, $t(27) = 2.05$, $p > .05$), although the harvested North Pacific right whales were likely older and bigger animals compared to the North Atlantic right whales in the analyses (Figure 4, Table 3). We found that mass-at-age estimates differed considerably depending on which allometric model was used. For example, mass-at-

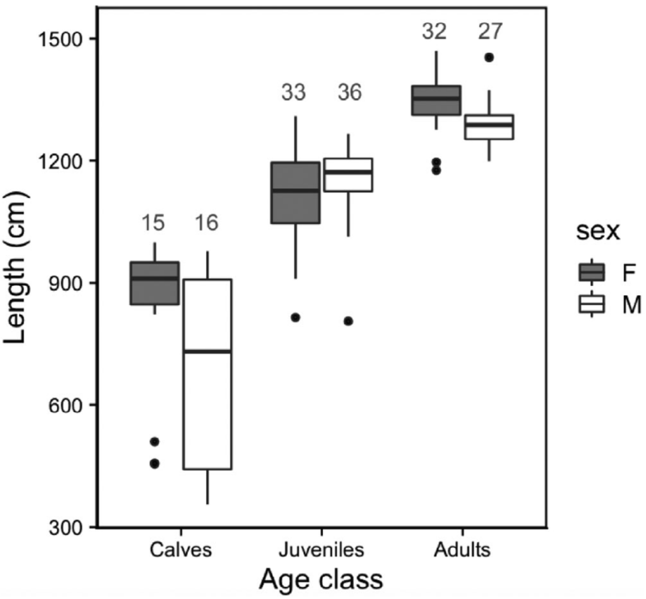


FIGURE 3 Body length (cm) for necropsied and photogrammetrically measured male and female North Atlantic right whales by age class (calves ≤1 year; juveniles >1 and < 9 years; adults ≥9 years). The horizontal black bar represents the medians, the interquartile range is represented by the box, the whiskers indicate nonextreme maximum and minimum values, and outliers are represented by black dots.

age estimates were lower when using an allometric model constructed for North Atlantic right whale necropsy data alone compared to the model that included North Pacific right whale whaling data (Figure 5). Additionally, we found that by increasing the sample size to include North Pacific right whales and adding larger and likely older animals to the data set, we reduced model uncertainty (i.e., smaller 95% confidence limits). Consequently, it appears that including North Pacific right whales results in body mass predictions that are more precise and better represent healthy individuals.

Comparing our new estimates with previous studies (Fortune et al., 2012) shows similar body lengths-at-age whereby updated lengths are 4.6% ± 9.47 *SD* lower than previous estimates on average. However, mass-at-age estimates differ considerably such that updated weights are 12.8% ± 6.03% *SD* heavier on average compared to our earlier predictions. This notable difference in predicted mean body mass is due to excluding masses that were estimated rather than weighed from the North Atlantic right whale necropsy database, the addition of new animals weighed since 2012 and the inclusion of North Pacific right whales that were presumably healthy at their time of death.

In the previous study (Fortune et al., 2012), a significant difference between allometric models for North Pacific and North Atlantic right whales led us to only use North Atlantic right whale weights to predict the age-specific weights of North Atlantic right whales. However, our new allometric model for North Atlantic right whales derived from additional morphometric data (and the removal of estimated weights from the database) did not differ significantly from the North Pacific allometric model. Further support for combining morphometric data from the two species of right whales comes from a recent photogrammetric study that found genetically related *Eubalaena* species share a similar morphology (Christiansen et al., 2020). We consequently combined both data sets into a single model that encompassed a much broader range of ages and sizes of right whales. This new model, built with a more inclusive data set of right whale body sizes and ages, yields estimates that better reflect body weights of healthy right whales.

A second notable difference between our previous and revised growth models for North Atlantic right whales is the placement of the inflection point between *Phase 1* and *Phase 2* growth. Our revised model indicates that it occurs earlier (0.79 years) than we previously estimated (1.05 years), i.e., at 9.6 months rather than at 13 months of age. These differences in length-at-age estimates reflect inclusion of the new data from older animals in our analysis.

TABLE 2 Predicted mean mass and length measurements (± *SD*) for North Atlantic right whales. Daily growth rates in length (cm/day) and mass (kg/day) were calculated using mean model predictions for length-at-age and mass-at-age. Mean allometric model coefficients for *Phase 1* growth were $a = -5.091821 \pm 0.2578327$ and $b = 3.077823 \pm 0.08325852$. Mean parameter estimates for *Phase 2* growth were $a = -5.096379 \pm 0.2592405$ and $b = 3.079408 \pm 0.08360103$.

Age (years)	Mass (kg)	Mass growth (kg/day)	Length (cm)	Length growth (cm/day)
0	1,022 ± 252	0.00	426 ± 33	0.00
0.25	4,553 ± 444	38.70	695 ± 17	2.95
0.5	9,220 ± 594	51.15	875 ± 11	1.97
0.75	12,771 ± 724	38.92	973 ± 10	1.07
0.79	13,206 ± 747	29.79	989 ± 27	1.10
1	13,737 ± 1,270	6.93	996 ± 26	0.25
2	16,026 ± 1,122	6.27	1,048 ± 18	0.14
3	18,236 ± 1,063	6.05	1,093 ± 14	0.12
4	20,319 ± 1,087	5.71	1,132 ± 12	0.11
5	22,244 ± 1,156	5.27	1,167 ± 11	0.10
6	23,994 ± 1,234	4.79	1,194 ± 11	0.08
7	25,564 ± 1,302	4.30	1,218 ± 11	0.07
8	26,959 ± 1,354	3.82	1,239 ± 11	0.05
9	28,187 ± 1,392	3.36	1,256 ± 10	0.05
10	29,262 ± 1,421	2.95	1,272 ± 10	0.04
11	30,197 ± 1,445	2.56	1,285 ± 9	0.04
12	31,007 ± 1,470	2.22	1,296 ± 9	0.03
13	31,707 ± 1,497	1.92	1,306 ± 9	0.03
14	32,310 ± 1,530	1.65	1,315 ± 9	0.02
15	32,829 ± 1,568	1.42	1,322 ± 9	0.02
16	33,274 ± 1,611	1.22	1,328 ± 10	0.02
17	33,656 ± 1,657	1.05	1,333 ± 10	0.01
18	33,983 ± 1,706	0.90	1,338 ± 11	0.01
19	34,263 ± 1,757	0.77	1,342 ± 12	0.01
20	34,504 ± 1,807	0.66	1,345 ± 13	0.01
21	34,709 ± 1,857	0.56	1,348 ± 14	0.01
22	34,885 ± 1,905	0.48	1,351 ± 15	0.01
23	35,036 ± 1,951	0.41	1,353 ± 15	0.01
24	35,166 ± 1,994	0.36	1,355 ± 16	0.01
25	35,277 ± 2,035	0.30	1,357 ± 17	0.01
26	35,372 ± 2,073	0.26	1,358 ± 17	0.00
27	35,453 ± 2,109	0.22	1,359 ± 18	0.00
28	35,523 ± 2,141	0.19	1,360 ± 19	0.00
29	35,584 ± 2,171	0.17	1,361 ± 19	0.00
30	35,635 ± 2,198	0.14	1,362 ± 20	0.00

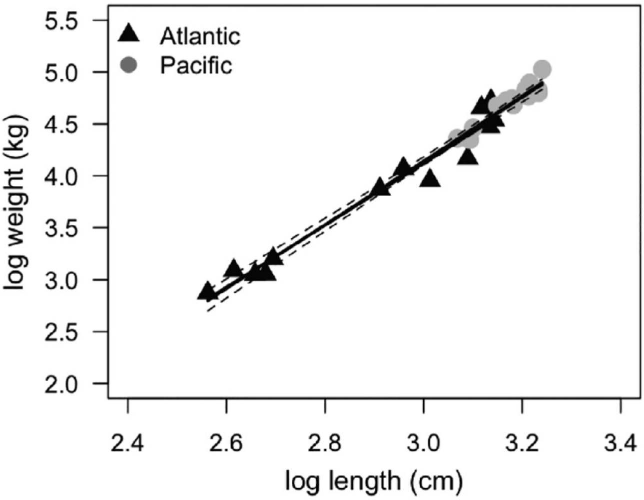


FIGURE 4 Mass-length relationships for North Atlantic (▲) and North Pacific (●) right whales (*Eubalaena glacialis* and *E. japonica*). A linear regression was fit to the log-transformed data for both species: $r^2 = 0.98$, $p < .001$. Fitted parameters for North Atlantic and North Pacific right whales ($a = 0.000008634158$, $b = 3.06$) were used to model mass-at-age.

3.3 | Biological implications of new growth curves

Our updated growth models indicate that right whales are considerably larger in mass than previously recognized, which means that previously estimated energy requirements have been underestimated for some age-classes on a mass-specific basis. More specifically, sexually mature right whales require more energy per unit body mass than previously thought because their estimated body mass exceeds the upper limits of previous estimates (Fortune et al., 2012). However, the predicted mass of calves and juveniles compare favorably to previous estimates and are within the reported uncertainty. For example, the predicted weights of sexually immature whales (0–8 years) were 8.67% (± 6.91 *SD*) heavier on average than previous estimates. Conversely, sexually mature animals (9–22 years) were 16.3% (± 0.73 *SD*) heavier on average.

Our body mass estimates are also higher than what others have predicted using three-dimensional volumetrics (Christiansen et al., 2019, 2020). For example, Christiansen et al. (2019, 2020) predicted that North Atlantic right whales weighed 940 kg at birth (8% lower than our mean model predictions, but within the 95% CIs). They also predicted that right whales weigh 7,830 kg when weaned, which is 15% lower than our model predictions and outside the 95% CIs (based on a body length of 8.8 m). They further predicted that right whales weigh 20,680 kg at sexual maturity (27% lower than our model predictions and outside the 95% CIs based on the assumption that right whales attain sexual maturity at 9 years of age). Reconciling these differences in predicted mass is challenging because live animals cannot be weighed to validate model predictions and dead animals often include few mature animals and many animals in poor health.

Informative comparisons can be made between model predictions and morphometric measurements obtained from necropsies. For example, our model predictions were just 3% heavier than the weight of a recently born calf (Case number 80; Table 3) that weighed 1,586 kg and measured 495 cm in body length. Another necropsied calf measuring 910 cm weighed 11,772 kg, which was 15% heavier than our mean model predictions (9,984.7 kg), but within the 95% confidence limits. Lastly, an animal approaching sexual maturity measuring 12.29 m and weighing 14,785 kg was considerably underweight compared to our model predictions (24,535 kg). However, this animal was entangled and considerably emaciated at the time of measurement.

Although it is unknown how much weight chronically entangled whales may lose, substantial decreases in blubber thickness have been documented (van der Hoop, Corkeron, & Moore, 2017). Lactating North Atlantic right whale mothers, for example, are believed to lose 25% of their total body weight during the lactation period (Christiansen et al., 2018). As such, the differences between predicted and observed weight values (40% difference in mass) may

TABLE 3 North Atlantic right whale necropsy and Pacific right whale whaling data used in allometric mass models. One animal (No. 27) was weighed without baleen, and others (No. 34, 44, and 49) were weighed in parts and had 6.8% added to their measured mass estimates to account for fluid loss. A fourth animal (No. 45) was likely underweight relative to its body length, and as was entangled in fishing gear, appeared thin to emaciated and was weighed without baleen. Similarly, animals 32 and 120 were also entangled at the time of death and were in poor nutritive condition. Animal No. 80 was also emaciated at the time of necropsy, likely due to the inability to obtain sufficient energy as a nursing calf. Note that the previous analysis (Moore et al., 2007) included body masses for Case No. 28, 29, and 40, which were estimated rather than measured. Furthermore, body masses of Case No. 34, 21, and 32 were corrected after verifying necropsy reports, and Case No. 106, 120, and 139 are new animals that were added to our analysis.

Species	Sex	Length (cm)	Weight (kg)	Case No.	Field ID/EgNo
Atlantic	M	412	1,225	21	MH89-424-Eg
Atlantic	F	1,360	29,700	27	EgNo 1223
Atlantic	M	1,030	9,035	32	EgNo 2366*
Atlantic	F	478	1,136	34	Eg_Jan_02_96 calf
Atlantic	F	455	1,130	42	RKB-1451
Atlantic	F	1,370	52,804	44	EgNo 1014
Atlantic	F	1,229	14,785	45	EgNo2030*
Atlantic	F	910	11,772	49	NY-2680-2001
Atlantic	M	365	749	73	EgNEFL0704
Atlantic	M	495	1,586	80	KLC 022 Eg**
Atlantic	F	1,390	34,600	106	EgNo 2320
Atlantic	F	1,310	45,359	120	MME-16-249Eg*
Atlantic	F	815	7,481	139	IFAW17-182Eg
Pacific	M	1,470	52,870	NA	NA
Pacific	M	1,510	55,250	NA	NA
Pacific	M	1,520	48,250	NA	NA
Pacific	M	1,610	67,770	NA	NA
Pacific	M	1,640	78,500	NA	NA
Pacific	M	1,700	65,760	NA	NA
Pacific	M	1,710	67,240	NA	NA
Pacific	M	1,240	22,250	NA	NA
Pacific	M	1,710	63,490	NA	NA
Pacific	F	1,170	22,870	NA	NA
Pacific	F	1,630	58,590	NA	NA
Pacific	F	1,660	63,130	NA	NA
Pacific	F	1,710	63,490	NA	NA
Pacific	F	1,740	106,500	NA	NA
Pacific	F	1,260	28,920	NA	NA
Pacific	M	1,410	47,560	NA	NA

Note: For reference purposes, animal FieldID/EgNo marked with one asterisk (*) denote animals that were entangled and underweight and animals with two asterisks (**) were not entangled but were underweight at the time of death presumably due to issues with energy acquisition while nursing.

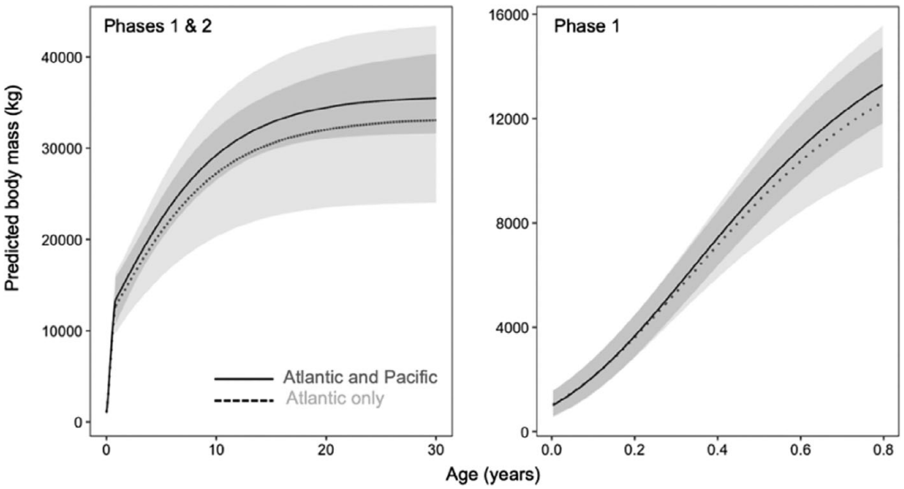


FIGURE 5 Predicted body mass (kg) at age (years) for North Atlantic right whales using the bootstrapped multiphase Gompertz length-at-age predictions (*n* = 10,000 replicates) and an allometric mass-at-length model that was constructed using (1) North Atlantic right whale necropsy (Atlantic only) data and (2) North Pacific right whale whaling data and North Atlantic right whale data (Atlantic and Pacific). We bootstrapped the model to generate 10,000 predictions of mass-at-age and sorted the predicted values into 95% quartiles by ordering the bootstrap replicates of mass-at-age into 2.5% and 97.5% quartiles. The light gray shaded region represents the 95% confidence limits for the Atlantic only model and the smaller, dark gray region reflects the confidence limits for the Atlantic and Pacific model.

be attributed to compromised body condition caused by lactation, reduced feeding efficiency, and increased energetic costs associated with being entangled (van der Hoop et al., 2017), and may provide insight into the extreme physiological consequences of chronic entanglement.

The comparatively low predicted body weights previously estimated for mature North Atlantic right whales were likely due to biases in the source data used to establish the earlier allometric relationship between body length and mass. Several of these data came from underweight North Atlantic right whales that were emaciated and in poor overall health due to entanglement in fishing gear (Sharp et al., 2019). Supplementing this database with lengths and weights of North Pacific right whales recorded during commercial whaling provided a more comprehensive set of measurements of healthy-sized individuals.

Bigger body sizes require more energy for growth and maintenance of mass. In our case, our revised growth model has little consequence for the energy needs of young animals (e.g., predicted mean mass gains were 33.9 kg/day for previous models and are 34.8 kg/day for the updated equations between 0 and 1 year). However, the considerably greater body mass of adult right whales suggests they have higher metabolic demands. It appears, for example, that sexually mature right whales (9 years) require 12.9% (or 82.53 MJ) greater food intake per day to meet their basal metabolic costs. Assuming the costs associated with swimming (or active metabolism) are twice maintenance costs, the energy needed to meet active and basal metabolism for a 9-year-old animal will be 25.8% higher in total than previously predicted. In contrast, the basal metabolisms of older individuals between 20 and 22 years are 12% higher than previously estimated (i.e., 760.13 MJ/day for a 22-year-old animal based on the new model using an average mass of 34,885 kg compared with 662.03 MJ/day using the previous model assuming a mean mass of 26,639 kg). Consequently, the new predictions of body mass result in elevated metabolic rates, lending further support to certain ages of right whales being more vulnerable to nutritional stress than others. This is particularly important for reproductively mature females, who may be able to withstand short periods of reduced feeding if they can replenish their blubber reserves during the postlactation period (Christiansen et al., 2018; Miller et al., 2011).

Improved estimates of body mass models contribute to the care and conservation of North Atlantic right whales. Ship strikes (Kite-Powell, Knowlton & Brown, 2007; Vanderlaan & Taggart, 2007) and fishing gear entanglements (Caswell, Fujiwara, & Brault, 1999; Clapham, Young, & Brownell, 1999; Hamilton & Kraus, 2019; Johnson et al., 2005) are the leading causes of mortality for this endangered species. Consequently, accurate estimates of right whale mass are needed to help mitigate anthropogenic mortality. As an example, an adult right whale 9 years old, weighing 23.4 tons, and not emaciated due to chronic entanglement (Barratclough et al., 2014) would require 2.34 kg (i.e., 0.1 mg/kg; van der Hoop et al., 2014) of anesthetic (butorphanol and midazolam) to facilitate disentanglement by reducing swimming speed and evasiveness (Noren, 2011). Conversely, we predict that a whale of the same age, that is 16.9% heavier (28,187 kg) than previously predicted, would require 2.82 kg of sedation. These revised mass estimates will enable more accurate drug dosages to be determined and administered to animals prior to disentanglement.

A limitation of our earlier growth equations was that veterinarians needed to extrapolate beyond the upper age-limits of the model (i.e., 22 years). However, the additional data used to derive the updated growth curves means that dosages can now be determined with greater confidence for older animals (between 22 and 30 years). Overall, our updated mass-at-age predictions will assist in determining the correct dosages of medication for right whales that need to be sedated or treated for infections caused by entanglement and ship strike wounds.

3.4 | Conclusions

Adding new body size data, correcting errors in some of the previous records, and using an improved allometric model to predict mass that includes North Pacific right whale measurements from whaling records has yielded better models of body growth for North Atlantic right whales. The new models show that right whales are on average larger than originally predicted and that the inflection point in their 2-phased growth occurs earlier in development than previously thought (i.e., at ~10 months compared with 13 months; Fortune et al., 2012). This suggests that calves experience a deceleration in growth prior to weaning (assuming whales wean after 12 months). The revised growth models show that right whale calves experience rapid growth between 0 and 9.6 months, and decelerated growth between 9.7 months and 9 years.

Our revised growth models have implications for the conservation and management of North Atlantic right whales. Most notably, they indicate that energetic requirements associated with basal and active metabolism are likely higher than previously believed—particularly for adult animals (9 years) and juveniles that are approaching sexual maturity. These are important findings because juveniles and lactating North Atlantic right whales have the highest predicted daily energy needs, and may experience periods of food shortage based on comparisons with prey ingestion (Fortune, Trites, Mayo, Rosen, & Hamilton, 2013). Consequently, the energy deficit incurred by these demographic groups may be greater than originally thought. They also indicate that higher dosages of sedatives and antibiotics than originally predicted should be used to treat wounded animals that are not emaciated due to chronic entanglement.

ACKNOWLEDGMENTS

North Atlantic right whale identification data used to age animals in decimal years were maintained by the New England Aquarium and provided by the North Atlantic Right Whale Consortium. We appreciate the contributions of the many organizations to this database. We are also grateful to the many people who have assisted with right whale necropsies and right whale aerial photogrammetry research over the years—and particularly thank S. Sharp, W. A. McLellan, R. A. Bonde, M. Lynn, and D. Potter. Aerial photogrammetry data were collected under Northeast Fisheries Science Center Permits 775-1600 and 917-1600 and postmortem procedures were done under National Oceanic and Atmospheric Administration (NOAA) Permit 932-1905-01-MA-009526. We appreciate the helpful edits provided by three anonymous reviewers and our editor, which improved this manuscript.

AUTHOR CONTRIBUTIONS

Sarah Fortune: Conceptualization; formal analysis; investigation; methodology; project administration; visualization; writing-original draft; writing-review and editing. **Michael Moore:** Data curation; funding acquisition; methodology; project administration; writing-review and editing. **Wayne Perryman:** Conceptualization; data curation; funding acquisition; methodology; writing-review and editing. **Andrew Trites:** Investigation; resources; supervision; writing-review and editing.

ORCID

Sarah M. E. Fortune https://orcid.org/0000-0001-6505-9378
Wayne L. Perryman https://orcid.org/0000-0003-2312-8552

REFERENCES

Anderson, D. R. (2008). *Model based inference in the life sciences: A primer on evidence*. New York, NY: Springer.

Barratclough, A., Jepson, P. D., Hamilton, P. K., Miller, C. A., Wilson, K., & Moore, M. J. (2014). How much does a swimming, underweight, entangled right whale (*Eubalaena glacialis*) weigh? Calculating the weight at sea, to facilitate accurate dosing of sedatives to enable disentanglement. *Marine Mammal Science*, *30*, 1589–1599.

Brodie, P. F. (1975). Cetacean energetics, an overview of intraspecific size variation. *Ecology*, *56*, 152–161.

Caswell, H., Fujiwara, M., & Brault, S. (1999). Declining survival probability threatens the North Atlantic right whale. *Proceedings of the National Academy of the Sciences of the United States of America*, *96*, 3308–3313.

Christiansen, F., Dawson, S., Durban, J., Fearnbach, H., Miller, C., Bejder, L., & Moore, M. (2020). Population comparison of right whale body condition reveals poor state of the North Atlantic right whale. *Marine Ecology Progress Series*, *640*, 1–16.

Christiansen, F., Sironi, M., Moore, M. J., Di Martino, M., Ricciardi, M., Warick, H. A., & Uhart, M. M. (2019). Estimating body mass of free-living whales using aerial photogrammetry and 3D volumetrics. *Methods in Ecology and Evolution*, *10*, 2034–2044.

Christiansen, F., Vivier, F., Charlton, C., Ward, R., Amerson, A., Burnell, S., & Bejder, L. (2018). Maternal body size and condition determine calf growth rates in southern right whales. *Marine Ecology Progress Series*, *592*, 267–282.

Clapham J, P., Young B., S., & Brownell, R. L., Jr. (1999). Baleen whales: Conservation issues and the status of the most endangered populations. *Mammal Review*, *29*, 35–60.

Fortune, S. M., Trites, A. W., Mayo, C. A., Rosen, D. A. S., & Hamilton, P. K. (2013). Energetic requirements of North Atlantic right whales and the implications for species recovery. *Marine Ecology Progress Series*, *478*, 253–272.

Fortune, S. M., Trites, A. W., Perryman, W. L., Moore, M. J., Pettis, H. M., & Lynn, M. S. (2012). Growth and rapid early development of North Atlantic right whales (*Eubalaena glacialis*). *Journal of Mammalogy*, *93*, 1342–1354.

George, J. C., Zeh, J., Suydam, R., & Clark, C. (2004). Abundance and population trend (1978–2001) of western Arctic bowhead whales surveyed near Barrow, Alaska. *Marine Mammal Science*, *20*, 755–773.

Gompertz, B. (1825). On the nature of the function expressive of the law of human mortality, and on the new mode of determining the value of life contingencies. *Philosophical Transactions of the Royal Society of London*, *115*, 513–583.

Hamilton, P. K., & Kraus, S. D. (2019). Frequent encounters with the seafloor increase right whales' risk of entanglement in fishing groundlines. *Endangered Species Research*, *39*, 235–246.

Hamilton, P. K., Knowlton, A. R., Marx, M. K., & Kraus, S. D. (1998). Age structure and longevity in North Atlantic right whales *Eubalaena glacialis* and their relation to reproduction. *Marine Ecology Progress Series*, *171*, 285–292.

Johnson, A., Salvador, G., Kenney, J., Robbins, J., Landry, S., & Clapham, P. (2005). Fishing gear involved in entanglements of right and humpback whales. *Marine Mammal Science*, *21*, 635–645.

Kenagy, G. J., & Trombulak, S. C. (1986). Size and function of mammalian testes in relation to body size. *Journal of Mammalogy*, *67*, 1–22.

Kite-Powell, H. L., Knowlton, A. R., & Brown, M. W. (2007). Modeling the effect of vessel speed on right whale ship strike risk. *Project Report for NOAA/NMFS Project NA04NMF472*.

Kraus, S. D., Moore, K. E., Price, C. A., Crone, M. J., Watkins, W. A., Winn, H. E., & Prescott, J. H. (1986). The use of photographs to identify individual North Atlantic right whales *Eubalaena glacialis*. *Report of the International Whaling Commission, Special Issue 10*, 145–151.

Laws, R. M. (1956). Growth and sexual maturity in aquatic mammals. *Nature*, *178*, 193–194.

Miller, C. A., Reeb, D., Best, P. B., Knowlton, A. R., Brown, M. W., & Moore, M. J. (2011). Blubber thickness in right whales *Eubalaena glacialis* and *Eubalaena australis* related with reproduction, life history status and prey abundance. *Marine Ecology Progress Series*, *438*, 267–283.

Moore, M. J., Knowlton, A. R., Kraus, S. D., McLellan, W. A., & Bonde, R. K. (2004). Morphometry, gross morphology and available histopathology in North Atlantic right whale (*Eubalaena glacialis*) mortalities (1970–2002). *Journal of Cetacean Research and Management*, *6*, 199–214.

Moore, M., Walsh, M., Bailey, J., Brunson, D., Gulland, F., Landry, S., & Rowles, T. (2010). Sedation at sea of entangled North Atlantic right whales (*Eubalaena glacialis*) to enhance disentanglement. *PLoS ONE*, *5*(3), e9597.

Neuenhoff, R. D., Cowan, D. F., Whitehead, H., & Marshall, C. D. (2011). Prenatal data impacts common bottlenose dolphin (*Tursiops truncatus*) growth parameters estimated by length-at-age curves. *Marine Mammal Science*, *27*, 195–216.

Noren, D. P. (2011). Estimated field metabolic rates and prey requirements of resident killer whales. *Marine Mammal Science*, *27*, 60–77.

North Atlantic Right Whale Consortium. (2018). *North Atlantic Right Whale Consortium identification database*. Boston, MA: New England Aquarium. https://www.narwc.org/.

Omura, H., Oshumi, S., Nemoto, T., Nasu, K., & Kasuya, T. (1969). Black right whales in the North Pacific. *Scientific Reports of the Whales Research Institute, Tokyo*, *21*, 1–78.

Perryman, W. L., & Lynn, M. S. (2002). Evaluating the nutritive condition and reproductive status of migrating gray whales (*Eschrichtius robustus*) based on analysis of photogrammetric data. *Journal of Cetacean Research and Management*, *4*, 155–164.

R Development Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Ricker, W. E. (1979). Growth rates and models. In W. S. Hoar, D. J. Randall, & J. R. Bret (Eds.), *Fish physiology: Bioenergetics and growth* (Vol. 8, pp. 677–743). Orlando, FL: Academic Press.

Schultz, L. P. (1938). Can the weight of whales and large fish be calculated? *Journal of Mammalogy*, *19*, 480–487.

Sharp, S. M., McLellan, W. A., Rotstein, D. S., Costidis, A. M., Barco, S. G., Durham, K., & Moore, M. J. (2019). Gross and histopathologic diagnoses from north atlantic right whale eubalaena glacialis mortalities between 2003 and 2018. *Diseases of Aquatic Organisms*, *135*, 1–31. https://doi.org/10.3354/dao03376

Speakman, J. R. (2005). Body size, energy metabolism and lifespan. *Journal of Experimental Biology*, *208*, 1717–1730.

van der Hoop, J., Corkeron, P., & Moore, M. (2017). Entanglement is a costly life-history stage in large whales. *Ecology and Evolution*, *7*, 92–106.

van der Hoop, J., Moore, M., Fahlman, A., Bocconcelli, A., George, C., Jackson, K., & Zoodsma, B. (2014). Behavioral impacts of disentanglement of a right whale under sedation and the energetic cost of entanglement. *Marine Mammal Science*, *30*, 282–307.

Vanderlaan, A. S. M., & Taggart, C. T. (2007). Vessel collisions with whales: The probability of lethal injury based on vessel speed. *Marine Mammal Science*, *23*, 144–156.

von Bertalanffy, L. (1938). A quantitative theory of organic growth (inquiries on growth laws. II). *Human Biology*, *10*, 181–213.

White, E. P., Ernest, S. K. M., Kerkhoff, A. J., & Enquist, B. J. (2007). Relationships between body size and abundance in ecology. *Trends in Ecology & Evolution*, *22*, 323–330.

Zach, R., Liner, Y., Rigby, G. L., & Mayoh, K. R. (1984). Growth curve analysis of birds: The Richards model and procedural problems. *Canadian Journal of Zoology*, *62*, 2429–2435.

Zar, J. H. (1996). *Biostatistical analysis* (3rd ed.). Upper Saddle River, NJ: Prentice-Hall.

How to cite this article: Fortune SME, Moore MJ, Perryman WL, Trites AW. Body growth of North Atlantic right whales (*Eubalaena glacialis*) revisited. *Mar Mam Sci*. 2020;1–15. https://doi.org/10.1111/mms.12753

Conservation Physiology

Volume 9 • 2021 10.1093/conphys/coaa133

SOCIETY FOR EXPERIMENTAL BIOLOGY

Research article

Stress and reproductive events detected in North Atlantic right whale blubber using a simplified hormone extraction protocol

Katherine M. Graham*, **Elizabeth A. Burgess and Rosalind M. Rolland**

Anderson Cabot Center for Ocean Life at the New England Aquarium, Central Wharf, Boston, MA 02110, USA

***Corresponding author:** Anderson Cabot Center for Ocean Life at the New England Aquarium, Central Wharf, Boston, MA 02110, USA.
Email: kgraham@neaq.org

As studies quantifying steroid hormones in marine mammal blubber progress, methodological refinements may improve the utility and consistency of blubber hormone measurements. This study advances blubber extraction methodologies by testing a simplified extraction protocol that reduces time and complexity compared to a protocol widely used in cetacean blubber studies. Using blubber samples archived from remote biopsy ($n = 21$ live whales) and necropsy collection ($n = 7$ dead whales) of North Atlantic right whales (NARW; *Eubalaena glacialis*) of known life history states, we performed analytical and biological validations to assess the feasibility of measuring reproductive (testosterone, progesterone) and glucocorticoid (cortisol) hormones in blubber via enzyme immunoassay following the simplified extraction. Analytical validations (parallelism, accuracy, extraction efficiency, repeatability) showed the simplified extraction produced similar results to the extended protocol, offering a more efficient and consistent technique. In live, apparently healthy whales, blubber testosterone concentrations (mean ± SE) were significantly higher in males (2.02 ± 0.36 ng/g) compared to females (0.81 ± 0.15 ng/g). Blubber progesterone was highest in a confirmed pregnant female (60.3 ng/g), which was 12-fold greater than the mean concentration of non-pregnant females (4.56 ± 0.88 ng/g). Blubber cortisol concentrations in whales that died from anthropogenic causes averaged 5.31 ± 2.28 ng/g, whereas most live, healthy whales had cortisol values below 1 ng/g. Among living whales, a whale actively entangled in fishing gear had the highest blubber cortisol measurement (3.51 ng/g), exhibiting levels similar to whales that died from acute entanglement (2.88 ± 0.42 ng/g). Overall, the highest blubber cortisol concentration (18.0 ng/g) was measured in a dead whale with a severe chronic entanglement, approximately 30-fold greater than mean blubber cortisol of apparently healthy whales (0.58 ± 0.11 ng/g). The methodological approach presented here provides a reference for researchers interested in an alternative, streamlined technique for hormone extraction of cetacean blubber and contributes to the diverse tool set for stress and reproductive assessments of endangered NARWs.

Key words: Anthropogenic impact, blubber hormones, entanglement, North Atlantic right whale, steroid hormone extraction, validation

Editor: Steven Cooke

Received 15 May 2020; Revised 16 October 2020; Editorial Decision 11 December 2020; Accepted 14 December 2020

Cite as: Graham KM, Burgess EA, Rolland RM (2021) Stress and reproductive events detected in North Atlantic right whale blubber using a simplified hormone extraction protocol. *Conserv Physiol* 9(1): coaa133; doi:10.1093/conphys/coaa133.

Introduction

Blubber has become a widely used sample matrix for reproductive and stress assessments of both odontocete (for examples see: Kellar *et al.*, 2006, Kellar *et al.*, 2009, Trego *et al.*, 2013, Kellar *et al.*, 2015, Trana *et al.*, 2016, Champagne *et al.*, 2018), and mysticete whales (e.g. Mansour *et al.*, 2002, Kellar *et al.*, 2013, Vu *et al.*, 2015, Mello *et al.*, 2017, Pallin *et al.*, 2018, Carone *et al.*, 2019, Atkinson *et al.*, 2020). For instance, pregnant females can be readily identified using blubber progesterone concentrations in several whale species (Mansour *et al.*, 2002, Kellar *et al.*, 2013, Pallin *et al.*, 2018, Inoue *et al.*, 2019, Atkinson *et al.*, 2020), and blubber cortisol measurements have shown promise for assessing human impacts (Kellar *et al.*, 2015) and environmental stressors (Trana *et al.*, 2016) on cetaceans. Blubber collected from free-swimming whales using remote biopsy methods or from dead whales during necropsy procedures can be used to explore physiological questions about specific individuals and populations (Hunt *et al.*, 2013, Rolland and Moore, 2018). Furthermore, the acquisition of blubber from numerous cetaceans has routinely occurred for other studies focusing on genetic or contaminant analysis (Noren and Mocklin, 2012, Booth *et al.*, 2020), with archived collections from previous efforts potentially available for hormone analysis (e.g. Trego *et al.*, 2013, Boggs *et al.*, 2019, Cates *et al.*, 2019).

Most blubber hormone studies have utilized immunoassays for quantification. In preparation for immunoassay, hormones are extracted from blubber tissue using an organic solvent. Nearly all published blubber hormone studies using immunoassays follow an extraction method outlined by Kellar *et al*. (2006, 2015), which was originally modified from Mansour *et al*. (2002). Although successful for tested species, this methodology is relatively complex, consisting of repeated solvent and supernatant transfers and requiring a variety of relatively hazardous chemicals (including diethyl ether, an extremely flammable chemical). Hormone extraction is the most labour-intensive component of sample analysis, and hence possibly the most error-prone part of the process because the margin of error increases with each additional step, which in turn could have consequences for data interpretation (Palme, 2005, Palme *et al.*, 2013). In the field of wildlife endocrinology, methodologies for extracting steroid hormones from many alternative sample matrices have been expanded and optimized over time (Wasser *et al.*, 2000, Palme, 2005, Hunt *et al.*, 2014, Burgess *et al.*, 2016, Hunt *et al.*, 2017, Richard *et al.*, 2017, Rolland *et al.*, 2019). Exploring simplification of complex extraction protocols, in tandem with validation testing of the procedure and resultant data, can help advance physiologic studies of wildlife populations (Palme *et al.*, 2013, Palme, 2019). Thus, it would be advantageous to develop a more streamlined hormone extraction protocol for cetacean blubber.

Endocrine studies using blubber tissue require careful biological validation and interpretation because blubber hormone measurements could be affected by sample collection (e.g. sampling depth, sample mass, specimen condition) and/or intrinsic factors (such as body condition or metabolism) (Kellar *et al.*, 2009, Kellar *et al.*, 2006, Kellar *et al.*, 2015, Trana *et al.*, 2015, Mello *et al.*, 2017, Pettis *et al.*, 2017). Many of the factors involved in the collection of blubber from cetaceans are inherently variable and not under the full control of researchers due to the logistics of remotely darting a free-swimming animal (e.g. the mass of blubber collected is influenced by the angle at which the dart strikes the whale) (Noren and Mocklin, 2012), or accessibility of carcasses (most whale caracasses beach in a state of advanced decomposition) (Mello *et al.*, 2017). Given these circumstances, evaluation of hormone measurements can be strengthened by studying well-known individuals and populations. As demonstrated in a number of studies, the critically endangered North Atlantic right whale (NARW; *Eubalaena glacialis*) is a model species that has provided physiological validation of hormone analyses in alternative matrices (e.g. faeces, baleen, respiratory vapor) (Rolland *et al.*, 2005, Hunt *et al.*, 2016, Burgess *et al.*, 2018). This large whale species has been consistently monitored since 1980, and the North Atlantic Right Whale Identification and Sightings Database (www.rwcatalog.neaq.org) holds comprehensive sighting and life history data for individually identifiable whales (Hamilton *et al.*, 2007). Additionally, long-term assessment of faecal hormones in right whales have yielded extensive data on the endocrine patterns expected for various reproductive states in this species (Rolland *et al.*, 2005, Hunt *et al.*, 2006, Burgess *et al.*, 2017, Rolland *et al.*, 2017). Because NARWs face increased anthropogenic and environmental pressures (fishing gear entanglements, vessel interactions, human-generated underwater noise, climate change and shifting prey distributions) and non-sustainable reproductive rates (Meyer-Gutbrod and Greene, 2017, Corkeron *et al.*, 2018, Sharp *et al.*, 2019), the availability of efficient and diverse tool sets to monitor stress and reproduction is critical to guiding management and recovery efforts (Harcourt *et al.*, 2019).

The objectives of this study were to analytically validate a simplified protocol for extracting steroid hormones from blubber tissue and then, utilizing this simplified extraction method, characterize reproductive and stress-related hormones in blubber of live and dead NARWs of known life history states. To this end, we (i) conducted immunoassay validations to determine the feasibility of measuring three steroid hormone types (testosterone, progesterone and cortisol) in blubber of NARWs; (ii) evaluated a simplified blubber hormone extraction method alongside a more complex extraction protocol that is widely used in cetacean blubber studies; (iii) compared hormone concentrations in matched blubber and faecal samples to preliminarily examine concordance of blubber hormone measurements relative to a well-studied sample matrix for NARWs; (iv) examined blubber hormone profiles in apparently healthy, free-swimming NARWs of known sex and reproductive states; and (v) investigated blubber cortisol concentrations in whales that died from anthropogenic causes of entanglement in fishing gear and vessel strikes versus living whales.

Materials and methods

Sample collection

A total of 28 blubber samples archived from remote biopsy or necropsy of individual NARWs were used in this study. All samples were collected under federal permits to the New England Aquarium (NEAq) and Canadian Whale Institute (National Marine Fisheries Service permits: 655-1652, 655-1652-01, 14 233 and 19 674; Canada's Department of Fisheries and Oceans permits under the Species at Risk Act) and the International Fund for Animal Welfare (National Marine Fisheries Service permits: 18786 and 18 786-02) and approved by NEAq's Institutional Animal Care and Use Committee. Blubber biopsy samples ($n = 21$) were collected from free-swimming NARWs in the Bay of Fundy, Canada, from July through September in 2006–2017. Biopsy sampling was conducted using an Excalibur crossbow with 150-pound draw weight fitted with a custom made, floating dart containing a stainless steel collection tip of 7 mm diameter by 3 cm length (Brown *et al*., 1991). The dart was aimed at the dorsal lateral region of the whale to remove a small plug of epidermis and underlying blubber (ranging in depth from 0.2 to 1.7 cm; mean 0.8 ± 0.43 cm). The biopsy sample was retrieved, and the epidermal layer was removed for genetic analysis (Frasier *et al*., 2006). The remaining dermis and hypodermis (referred to as blubber) was archived for hormone analysis.

Blubber tissue sections (∼10 x 10 x 10 cm) were dissected from dead whales ($n = 7$) during necropsies conducted in the months of April, May and August–October in 2016–2018 following standard necropsy procedures for NARWs (McLellan *et al*., 2004; Sharp *et al*., 2019). The state of carcass decomposition was graded based on Geraci and Lounsbury (2005; see Table 1). If present, faeces were collected from the rectum during necropsy. Matched blubber and faecal samples were available from three whales, enabling comparison of hormone concentrations across matrices. All samples were kept frozen at −20°C or − 80°C until hormone analysis.

Individual whales were photographed and identified based on unique patterns of cornified epithelium (i.e. callosities) and permanent scars using the North Atlantic Right Whale Identification Database (Kraus *et al*., 1986, Hamilton *et al*., 2007, Right Whale Consortium, 2019), as well as genetic profiling of epithelial DNA (Frasier *et al*., 2006, Frasier *et al*., 2013, Right Whale Consortium, 2019). Whales were categorized based on age and reproductive history (Table 1; Hamilton *et al*., 1998): calves (<1 year old, associated with their mother, likely nursing), juveniles (never calved and 1–8 y.o.), adults (year before first calving or ≥ 9 y.o.). Pregnancy was confirmed by identification of the female with a newborn calf in the year following sampling. Females sighted with a dependent calf at time of sampling were considered lactating. Adult females that were not pregnant or lactating were referred to as 'resting' (Rolland *et al*., 2005). Biopsied whales were free-swimming and considered apparently healthy at sampling, except for one juvenile female (Eg4510) that was entangled in snow crab fishing gear at the time of sample collection. This whale was observed with a buoy and line exiting the left side of the mouth, and line exiting the right side of the mouth which was being pulled downward below the surface by the heavy weight of the gear. The whale had extensive rope abrasions across wide regions of the body and active bleeding at the peduncle region. Based on these observations, the entanglement injury was classified as moderate (defined as extensive skin abrasions or cuts that extended into the blubber; Knowlton *et al*., 2015). These factors suggest that this whale had recently (within the last month) become entangled (Right Whale Consortium, 2019).

For necropsy cases, each dead whale was given a case number (Table 1). Two of the dead NARWs could not be assigned an individual identification due to decomposition of carcass; however, for both whales, sex was determined by visual observation or genetic analysis and age class (calf, juvenile or adult) was based on body length (Moore *et al*., 2004). Cause of death was attributed to acute entanglement (hours to days) in four cases, chronic entanglement (weeks to months) in one case and blunt force and/or propeller trauma from vessel strike in two cases (Table 1). Further details on pathology and cause of death of these whales are described in Sharp *et al*. (2019).

Hormone extraction

Blubber samples were trimmed of any remaining epidermal tissue using a clean scalpel blade. For all samples, 0.1 ± 0.05 g of blubber tissue was extracted. Sample masses of 0.1 g to 0.2 g have been widely used in blubber hormone studies; here, we chose to test protocols using the lower mass due to restricted amounts of tissue from biopsy collection. For biopsy samples less than 0.1 g, the entire blubber plug was extracted and only samples greater than 0.07 g were included in the study. For necropsy specimens, blubber was subsampled at a similar mass (0.1 g) and depth below the epidermis as biopsy samples to increase comparability between both sources of tissue collection.

Two different protocols for extracting hormones from blubber were tested: (1) an 'extended' protocol following methods described by Kellar *et al*. (2006, 2015), which was a modification of Mansour *et al*. (2002); and (2) a 'simplified' protocol adapted from a steroid tissue extraction protocol by immunoassay manufacturer, Arbor Assays (Ann Arbor, MI); see https://www.arborassays.com/assets/Tissue-Extraction-190402.pdf), with slight modifications to accommodate our laboratory equipment and reduce reagent volumes for a smaller sample mass.

Extended protocol: Full details are described in Kellar *et al*. (2015). In brief, this was a multi-step organic extraction

Table 1: Life history details of individual whales that were sampled for blubber in this study (total $n = 28$) using either remote biopsy (live whales) or necropsy procedures (dead whales).

Biopsy samples ($n = 21$)		
Age class and sex	*Number of individuals*	*Notes*
Adult females	5	pregnant, $n = 1$; lactating, $n = 3$; resting, $n = 1$
Juvenile females	4	active entanglement (moderate severity), $n = 1$
Adult males	7	
Juvenile males	5	
Necropsy samples ($n = 7$)		
Age class and sex	*Case number(#)*	*Cause of death*
Adult female	MME16–249 (3)	Chronic entanglement
Adult female	IFAW18–281 (4)	Acute entanglement
Juvenile female	IFAW17–182 (3)	Blunt force trauma, vessel strike
Juvenile male	IFAW17–320 (4)	Acute entanglement
Juvenile male	IFAW17–375 (4)	Acute entanglement
Juvenile male	IFAW18–244 (3)	Acute entanglement
Calf male	IFAW16–082 (3)	Propeller trauma, vessel strike

[#] The decomposition code (graded from 2–5) assigned to the carcass at time of necropsy, as described by Geraci and Lounsbury (2005). Code 3: decomposed, but with organs intact. Code 4: severe decomposition, organs not recognizable, but carcass intact. Cause of death is the underlying condition that started the chain of events leading to death; from Sharp *et al*. (2019).

consisting of homogenizing blubber (~0.1 g) in 1.0 ml of 100% ethanol (ACS reagent grade ≥ 99.5%; #459844, Sigma Aldrich) using an Omni Bead Ruptor 4 (catalogue #25–010, Omni International), followed by another wash step of 0.5 ml of ethanol. Resulting supernatants were collected, combined and evaporated and the residue resuspended in 2.0 ml of ethanol:acetone mix (4:1). The supernatant was transferred and evaporated before further extraction with 2.0 ml of diethyl ether. The supernatant was again collected and evaporated, then resuspended in 1.5 ml of acetonitrile (#271004, Sigma Aldrich) followed by the addition of 1.5 ml of hexane (#34859, Sigma Aldrich). The acetonitrile portion was separated, and an additional 1.5 ml of hexane added. The acetonitrile portion was again transferred, evaporated, and the final residue stored frozen at −20°C. Prior to immunoassay, sample extracts were resuspended in 0.5 ml of assay buffer (#X065, Arbor Assays) and vortexed thoroughly.

Simplified protocol: Blubber tissue (~0.1 g) was placed into homogenization tubes with grinding media (2.8 mm ceramic beads (catalogue #19–628) and one 6.5 mm ceramic bead (#19–682; Omni International)) and 1.0 ml of 100% ethanol. The sample was homogenized for six 45 s intervals using an Omni Bead Ruptor 4, similar to the extended protocol. The homogenate-ethanol mixture was transferred to a glass test tube (T1). The original homogenization tube with remaining grinding media was rinsed with 1.0 ml ethanol, vortexed and the supernatant was transferred to T1. Fluid in T1 was evaporated under airflow. Next, 2.0 ml of acetonitrile was added to the homogenate residue in T1, and the tube was vortexed (10 min) and then centrifuged (3500 rpm for 10 min at 4°C). The supernatant was transferred to a new tube (T2) followed by the addition of 4.0 ml of hexane, and the contents vortexed (5 min) then centrifuged to separate the acetonitrile and hexane layers. The acetonitrile layer was aspirated, transferred into a final tube (T3) and evaporated under airflow. Final dried extract residues were capped, sealed with parafilm and stored frozen (−20°C). Prior to immunoassay, sample extracts were resuspended in a mixture of 0.1 ml ethanol and 0.4 ml assay buffer (#X065, Arbor Assays) then vortexed thoroughly (2 min). The sample was allowed to rest at room temperature for 5 min before repeating the vortex and rest intervals twice more to solubilize the hormone.

Hormone analysis

Immunoreactive testosterone, progesterone and cortisol were quantified in blubber extracts using commercially available enzyme immunoassay systems (catalogue #ISWE001, ISWE003, ISWE002, respectively; Arbor Assays, Ann Arbor, MI), following the manufacturer's protocols. These bulk-reagent immunoassay kits were developed specifically for measuring hormones and their metabolites in alternative sample matrices from diverse wildlife species. All samples, standards and controls were assayed in duplicate, with the coefficient of variation (CV%) between all duplicates < 10%. Quality control samples of high (~30%) and low (~70%) binding were included on each plate, with resulting inter-assay CVs of 1.6% and 3.6% for testosterone ($n = 7$ assays); 6.2%

and 11.4% for progesterone ($n = 7$ assays); and 1.8% and 5.3% for cortisol ($n = 7$ assays). Final results were reported as nanograms of immunoreactive hormone and metabolites per gram of blubber tissue (ng/g), subsequently referred to simply as blubber testosterone, progesterone and cortisol. Antibody cross-reactivity, assay sensitivity and lower limit of detection values are available on the manufacturer's website: www.arborassays.com/products/.

Analytical validations

Blubber from dead whales was used to conduct analytical validations and evaluate both hormone extraction methodologies. These large sections of blubber tissue could be repeatedly subsampled and provided matched pairs of near-identical samples from the same localized region of blubber tissue enabling comparison of extraction techniques.

First, to ensure the selected immunoassays could reliably detect and measure the three hormones of interest in NARW blubber extracts, we conducted the following analytical validations: (i) parallelism; and (ii) accuracy. Parallelism was tested by serially diluting a pool of blubber extracts (from 1:1 (neat) to 1:256) and assessing the resulting dilution curve against the standard curve for differences in slope. Expected results should show no significant difference between the curves (F-test, $P > 0.05$), indicating the assay can reliably detect the hormone of interest (Grotjan and Keel, 1996). Assay accuracy was tested by spiking the standard curve with an equal volume of pooled sample extracts. When plotted, observed versus expected hormone values should be linear (ideal $r^2 > 0.95$) with a slope between 0.7–1.3 (ideal slope = 1.0), demonstrating that the sample matrix does not interfere with antibody binding (Ezan and Grassi, 2000, Grotjan and Keel, 1996).

Next, to evaluate the suitability of using a simplified extraction protocol as an alternative to the widely used extended extraction, we conducted experimental comparisons using both extractions protocols based on: (iii) extraction efficiency; (iv) within-extraction method variation; and (v) comparison of final hormone measurements. Extraction efficiency was tested using a separate set of 10 biopsy-sized blubber subsamples (~0.1 g each) for each individual hormone of interest. Six of these subsamples were placed into individual homogenization tubes and each tube was spiked with a known concentration of hormone at 40 ng in dH_2O, and then left overnight at 4°C to allow the hormone solution to soak into the blubber. The other four subsamples were each placed into homogenization tubes containing dH_2O without added hormone (non-spiked) and left overnight at 4°C. The following day, subsamples were assigned to either the simplified extraction or the extended protocol ($n = 3$ spiked and $n = 2$ non-spiked for the two protocols; $n = 10$ total for each hormone) before immunoassay. Extraction efficiency (%) was calculated as the mean concentration of hormone minus mean background (non-spiked samples), divided by the known amount of hormone added before extraction and multiplied by 100 (Palme, 2019). Within-extraction method variation tested the precision or repeatability of a hormone measurement across multiple extracts generated by each extraction protocol. For this test, blubber was dissected into 20 subsamples that were randomly assigned to extraction using either the simplified protocol ($n = 10$) or extended protocol ($n = 10$). Within-extraction method variation was quantified as the CV% between hormone measurements of 10 replicate extracts per protocol. Finally, we assessed the differences in absolute hormone concentration measured in paired subsamples taken from each of the seven dead whales. For each whale, four blubber subsamples were taken, which allowed for two subsamples to be assigned to each extraction protocol. The resultant extracts were assayed, and hormone concentrations were averaged for each extraction method, with the final measurements compared between the two methods.

To examine concordance of blubber hormone concentrations to faeces (a previously validated and well-studied sample matrix for measuring hormones in NARWs), we used matched blubber and faecal samples that were collected from three dead whales. Faecal samples were processed and analysed for faecal androgens, progestagens and glucocorticoids following methods described by Rolland *et al.* (2005) and Hunt *et al.* (2006). Blubber samples were extracted by the simplified extraction prior to measurement.

Blubber hormone concentrations of NARWs and biological validation

To characterize reproductive and glucocorticoid hormone concentrations in NARW blubber, testosterone, progesterone and cortisol were measured using the validated Arbor Assays immunoassay systems (see *Analytical validations*). Based on validation results, blubber samples from all whales ($n = 28$) were extracted using the simplified extraction protocol and resulting sample extracts were diluted 1:3 in assay buffer (#X065, Arbor Assays) prior to assay. Hormone data were compared across whales of different sexes, age classes, reproductive states and health statuses to evaluate whether blubber sample measurements reflect endocrine profiles expected for whales of known life history states.

Data analysis

Data from analytical validation tests of parallelism, accuracy, extraction efficiency and within-extraction method variation were compared between extraction protocols. A paired *t*-test was used to assess differences in measured hormone concentrations of blubber subsamples extracted following each protocol. Hormone values in matched blubber and faecal samples for three individuals, were graphically presented to observe congruence of trends between these alternative matrices. Descriptive statistics (mean ± SEM) were used to summarize the data set. Hormone concentration data were $\log_{10}$-transformed for the following analyses to meet assumptions of normality and homogeneity of variance, which were tested using Shapiro–Wilk test and Levene's test. Blubber hormone concentrations of live, apparently healthy whales ($n = 20$ out of 21 biopsy samples; one biopsy (from Eg4510) was excluded due to active entanglement) were examined using a univariate general linear model (GLM). A full factorial model was used to analyse the effect of sex, age class (i.e. juvenile or adult) and their interaction on hormone concentrations (dependent variable) of whale blubber samples, with the following equation: $y_i = \beta_0 + \beta_1$ sex$_i$ $+ \beta_2$ age class$_i$ $+ \beta_3$ sex × age class$_i$ $+ \epsilon_i$ where y is the response variable, β is the population slope and fixed effect parameters (including β_0 as the population intercept) and ϵ is a random error term associated with the ith observation. To avoid omission of any individual whale due to missing data fields in the GLM, we deliberately classed one female of uncertain age as 'adult'. This decision was grounded on available data that showed this female was older than 7 years of age (based on sighting records) and successfully calved 17 months after sampling—and therefore, this female was presumed to be nearing reproductive maturity when blubber sampling occurred.

To consider the possible effect of abiotic factors on measured hormone variables in the full set of blubber samples ($n = 28$; both live and dead whales), we used a multivariate GLM. Key attributes of sample storage time (i.e. number of years from sample collection until hormone analysis), mass of the analysed sample (measured in grams) and whale survival at time of sampling (i.e. live or dead whale, as associated with biopsy or necropsy sampling) were included as explanatory variables into the model designed to analyse all dependent variables (testosterone, progesterone and cortisol concentrations) simultaneously, with the following equation: z_{ik} = constant $+ c_1$ storage time$_i$ $+ c_2$ sample mass$_i$ $+ c_3$ whale surivival$_i$ where z is the combination of response variables (observation i for the linear combination k) and c is the coefficient measuring the relative contribution of each variable. Univariate between-subjects F-tests that indicated the effect of each factor on each dependent variable were also produced by the GLM framework. All statistical analyses were performed using SPSS (version 25) and significance level was set at 0.05 for all statistical tests.

Results

Analytical validations

For both extraction protocols, serially diluted blubber extracts demonstrated parallelism to the standard curve for testosterone, progesterone and cortisol immunoassays (all $P > 0.05$; Fig. 1 and Table 2). Blubber extracts derived using the simplified method demonstrated reasonable accuracy for all hormones tested and yielded similar results to the extended protocol (all slopes between 0.7 and 1.2, $r^2 > 0.99$; Fig. 1 and Table 2). Analytical validation results indicated that hormone metabolites extracted from NARW blubber by either protocol can be detected by the assay antibody across a range of concentrations (parallelism test) and that substances inherent to the extract matrices do not interfere with accurate hormone measurement (accuracy test).

Extraction efficiency ranged from 61–74% for the simplified protocol and 55–81% for the extended protocol (Table 2). Both protocols had similar overall recoveries across all hormones (mean 68% for both protocols). The simplified protocol resulted in higher recovery of progesterone (70% compared to 55%), but conversely, slightly higher recovery of testosterone was observed for the extended protocol (81% compared to 74%). For cortisol, relatively similar extraction efficiencies were found for both the simplified (61%) and extended extraction protocols (67%). Within-extraction method variability was lower for samples extracted by the simplified protocol (range 6.4–14.9%) compared to the extended method (19.1–35.2%), with the best result for the measurement of cortisol (6.4%) (Table 2).

Overall, hormone measurements from matched subsamples extracted using the two protocols were similar for all hormone types (testosterone: $t_{(6)} = -2.01$, $P = 0.09$; progesterone: $t_{(6)} = -1.69$, $P = 0.14$; cortisol: $t_{(6)} = 0.31$, $P = 0.98$). Generally, testosterone and progesterone concentrations were higher in extracts generated using the simplified extraction protocol (averaging 1.9 and 2.2 times higher, respectively) compared to the extended extraction protocol extracts (Fig. 2). At higher sample concentrations, there was greater variation in resulting hormone values between the simplified and extended protocols (Fig. 2).

Blubber hormone concentrations paralleled faecal hormone patterns for three whales with matched sample types, with hormone concentrations in blubber two or three orders of magnitude lower than faeces (Fig. 3). In both blubber and faeces, the highest concentrations of reproductive hormones (testosterone and progesterone) were observed in the adult female (MME16–249) compared to two juvenile whales. The highest blubber and faecal glucocorticoid concentrations were also measured in whale MME16–249 that died following a severe, chronic entanglement (Table 1; Sharp *et al*., 2019).

Blubber hormone concentrations of NARWs and biological validation

Testosterone, progesterone and cortisol were measurable in all NARW blubber samples following extraction with the simplified protocol. In live, apparently healthy right whales, blubber testosterone concentrations were significantly higher in males (2.02 ± 0.36 ng/g; $n = 12$) than females (0.81 ± 0.15; $n = 8$) ($F_{1,16} = 5.90$, $P = 0.03$). Mean blubber testosterone of adult males (2.54 ± 0.50 ng/g; $n = 7$) was approximately twice as high as juvenile males (1.28 ± 0.32 ng/g; $n = 5$) and over three times greater than adult females (0.74 ± 0.17 ng/g; $n = 5$) (Fig. 4); however, differences associated with age class did not achieve statistical significance ($F_{1,16} = 0.52$, $P = 0.48$; interaction term: $F_{1,16} = 3.7$, $P = 0.07$). Blubber progesterone levels were similar in females (11.80 ± 0.12 ng/g; $n = 8$) and

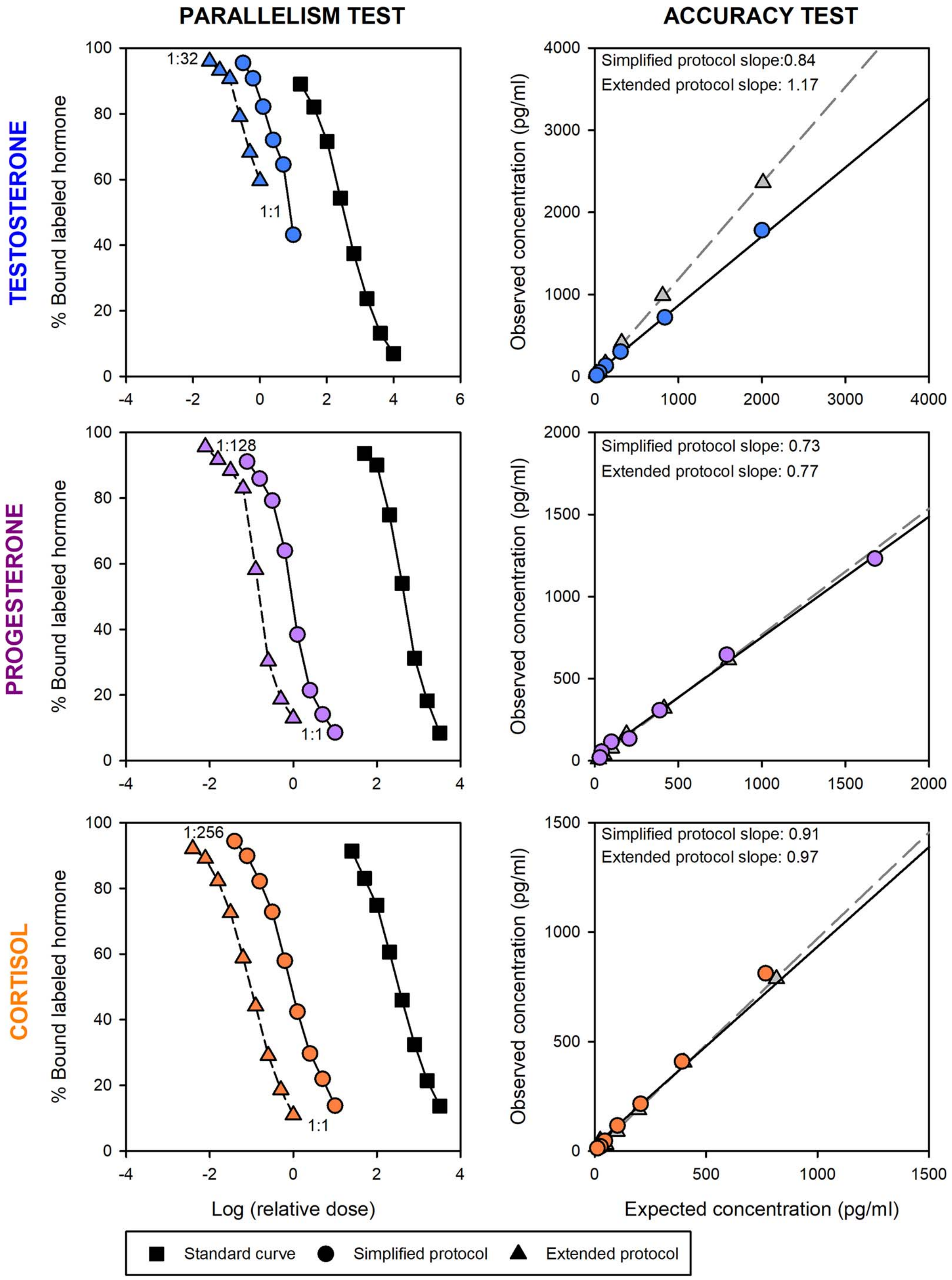


Figure 1: Validation test plots for testosterone (top row), progesterone (middle) and cortisol (bottom) of NARW blubber extracts using the simplified extraction protocol (circles: • with solid line) or extended extraction (triangles: ▲ with dashed line). Parallelism (left column) was observed between serially diluted sample curves (dilution range reported for each hormone) and standard curves (squares: ■) for both extraction methods across all hormones. [Note: In parallelism graphs, the relative dose (x-axis) of the sample serial dilution curves was displaced to avoid overlap]. Assay accuracy (right column) was demonstrated by the positive linear relationship of expected hormone concentration against observed concentration in spiked samples (simplified extraction protocol: circles •; extended extraction: triangles▲) and regression line slopes within the acceptable range of 0.7–1.3 (exact value reported on each graph).

Table 2: Analytical validation results (parallelism, accuracy, extraction efficiency and within-extraction method variation) for the simplified and extended extraction protocols.

	Parallelism (F-test$_{(df)}$; *P*-value)		Accuracy test (linear slope)	
Hormone	Simplified extraction	Extended extraction	Simplified extraction	Extended extraction
Testosterone	$F_{(1,9)} = 1.23$; $P = 0.30$	$F_{(1,8)} = 0.18$; $P = 0.68$	$y = 0.84x + 26.85$	$y = 1.17x + 15.35$
Progesterone	$F_{(1,10)} = 0.65$; $P = 0.44$	$F_{(1,9)} = 0.37$; $P = 0.56$	$y = 0.73x + 18.70$	y = 0.77x—0.43
Cortisol	$F_{(1,12)} = 0.08$; $P = 0.79$	$F_{(1,12)} = 0.09$; $P = 0.76$	$y = 0.91x + 24.88$	$y = 0.97x + 0.88$
	Extraction efficiency (% recovery)		Within-extraction method variation (mean %CV)	
Hormone	Simplified extraction	Extended extraction	Simplified extraction	Extended extraction
Testosterone	74%	81%	11.4%	21.6%
Progesterone	70%	55%	14.9%	35.2%
Cortisol	61%	67%	6.4%	19.1%

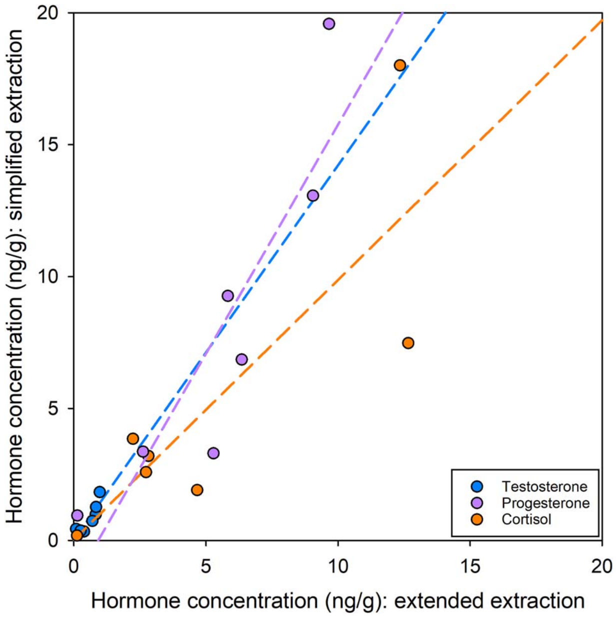


Figure 2: Comparison of hormone measurements (ng/g) in matched blubber subsamples extracted using the extended (x-axis) and simplified (y-axis) protocols. Coloured dotted lines represent the linear regression equation for each hormone type; testosterone (blue): $y = 1.42x + 0.02$; progesterone (purple): $y = 1.74x - 1.60$; cortisol (orange): $y = 0.98x + 0.03$.

males (4.70 ± 0.01 ng/g; $n = 12$) ($F_{1,16} = 0.74$, $P = 0.40$), as well as across age classes ($F_{1,16} = 0.11$, $P = 0.74$; interaction term: $F_{1,16} = 0.54$, $P = 0.47$). However, the highest blubber progesterone concentration (60.30 ng/g) was measured in a confirmed pregnant female (Fig. 4). This value was over 12-fold greater than mean blubber progesterone of non-pregnant females (4.56 ± 0.88 ng/g; $n = 7$).

For live, apparently healthy whales in this study, blubber cortisol concentrations were not significantly different between sexes ($F_{1,16} = 1.70$, $P = 0.21$), age classes ($F_{1,16} = 3.26$, $P = 0.09$), or reproductive groups (interaction term: $F_{1,16} = 0.97$, $P = 0.34$). However, adult males had blubber cortisol levels (0.94 ± 0.27 ng/g; $n = 7$) that averaged two times higher compared to juvenile males (0.37 ± 0.05 ng/g; $n = 5$), juvenile females (0.34 ± 0.07 ng/g; $n = 3$) and adult females (0.44 ± 0.10 ng/g; $n = 5$) (Fig. 4).

In the analysis examining abiotic factors, we found that storage time (Pillai's Trace = 0.24; $F_{3,22} = 2.33$, $P = 0.10$), sample mass (Pillai's Trace = 0.09; $F_{3,22} = 0.75$, $P = 0.53$) and whale survival (Pillai's Trace = 0.76; $F_{3,22} = 2.31$, $P = 0.10$) did not exhibit significant effects on measured hormone concentrations of blubber samples. Univariate tests also showed that storage time (7.7 ± 0.9 years; range: 0.4–12.6 years) and sample mass (0.10 ± 0.003 ng/g; range: 0.07–0.12 ng/g) did not significantly influence blubber testosterone, progesterone or cortisol measurements in this study (all $P > 0.05$). There was no effect of whale survival on reproductive hormone measurements, with similar blubber testosterone concentrations in live (1.48 ± 0.25 ng/g) and dead whales (0.85 ± 0.21 ng/g) ($F_{1,24} = 0.69$, $P = 0.42$), and similar levels of blubber progesterone in live (7.30 ± 2.70 ng/g) and dead whales (8.05 ± 2.47 ng/g) ($F_{1,24} = 2.89$, $P = 0.10$). However, there was a significant influence of whale survival on blubber cortisol concentrations ($F_{1,24} = 6.90$, $P = 0.02$).

Blubber cortisol concentrations of whales that died from anthropogenic causes were significantly greater (5.31 ± 2.28 ng/g; $n = 7$) than living whales (0.72 ± 0.18; $n = 21$), which typically had levels below 1 ng/g (Fig. 5). Notably, however, one live whale had an extreme cortisol concentration (identified as an outlier, Fig. 5) and this individual whale (Eg4510) was actively entangled in fishing line at the time of biopsy collection; whereas, all other live whales were free-swimming and considered apparently healthy. Whale Eg4510 had recently acquired an entanglement (classified as moderate in severity) and her blubber cortisol concentration (3.51 ng/g) was comparable to levels measured in whales that died from acute entanglement (2.88 ± 0.42 ng/g; $n = 4$). One dead whale

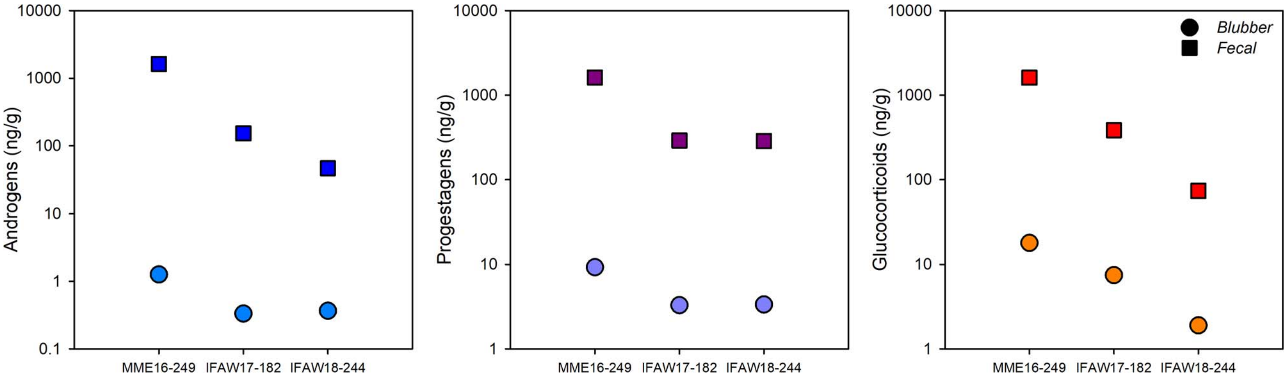


Figure 3: Matched blubber (circle) and faecal (square) hormone values (ng/g) collected from three whales during necropsy procedures. Patterns in blubber hormones showed similar trends to faecal hormones, albeit at concentrations two or three orders of magnitudes lower than in faeces. The y-axis is presented as a log scale.

that sustained a severe, chronic entanglement (MME16–249) had the highest blubber cortisol concentration (18.01 ng/g) measured in this study. Of the two whales that died from injuries related to vessel strikes, one whale (IFAW16–082) that suffered propeller-induced trauma had the lowest measured cortisol value in the study of 0.19 ng/g, whereas the other whale (IFAW17–182) that suffered blunt force trauma had a relatively high cortisol concentration (7.30 ng/g).

Discussion

This study presented a simplified protocol for extracting hormones from cetacean blubber and demonstrated the simplified extraction is a consistent and efficient alternative to a widely used extended protocol (Kellar *et al.*, 2006, 2015) for this essential sample preparation step. We performed and evaluated both extraction protocols (simplified and extended) to obtain comparable data on hormone measurement results for testosterone, progesterone and cortisol, providing a useful reference for future researchers. Moreover, data reported here are the first quantification of reproductive (testosterone and progesterone) and glucocorticoid (cortisol) hormones in NARW blubber tissue and revealed biologically meaningful hormone patterns can be measured in blubber, making it a valuable matrix for assessing reproductive and stress-related states in free-swimming whales, as well as for postmortem investigation.

Analytical validations

The simplified extraction protocol increased the efficiency and reproducibility of blubber hormone measurements and proved to be a reliable extraction technique for cetacean blubber studies. Using the simplified protocol, sample processing time was substantially reduced (>50%) and required fewer steps and hazardous chemicals (i.e. removal of highly volatile diethyl ether), making this simplified blubber hormone extraction technique potentially feasible for laboratories with limited resources (e.g. protective equipment, labour and supply costs). Most importantly, precision of hormone measurements was shown to improve when using the simplified extraction protocol, as all intra-sample CV values for the simplified protocol were near the standards recommended for wildlife endocrinology (i.e. <10%; Grotjan and Keel, 1996), with the best result for the measurement of cortisol (CV of 6.4%). Hormone extraction should be kept as simple as possible because additional steps increase the extent of variation, which could potentially impact accuracy of the final measurement (Burd, 2010, Palme, 2019). We posit that the higher variation measured between replicate samples extracted using the extended protocol may have resulted from inconsistent losses in hormones during repeated supernatant transfer steps. Kellar *et al.* (2006) also found high variation between identical samples when reporting on the use of the extended protocol for progesterone measurement (CV of 18%) but concluded that high variability inherent to this extraction methodology did not impede pregnancy determination. Nonetheless, it is preferable to minimize sources of intra-sample variability, particularly when detecting physiological changes at lower hormone concentration ranges (Millspaugh and Washburn, 2004, Watson *et al.*, 2013). The high variability associated with the extended extraction could be problematic, particularly for stress assessments that may be used in conservation management decisions, clinical diagnostics, or developing endocrine reference ranges for populations.

Extraction efficiency for the two protocols varied across hormone types, however this variation is expected given the range of wash steps and reagents with varying polarities used in each extraction protocol. Furthermore, extraction efficiency calculations that are based on adding exogenous parent steroids to the sample prior to extraction are often considered an artificial measure of true recovery (Palme *et al.*, 2013, Palme, 2019), particularly when hormone metabolites predominate in the tissue, as is the case for blubber (Boggs *et al.*, 2017, Atkinson *et al.*, 2020). Nonetheless, this approach

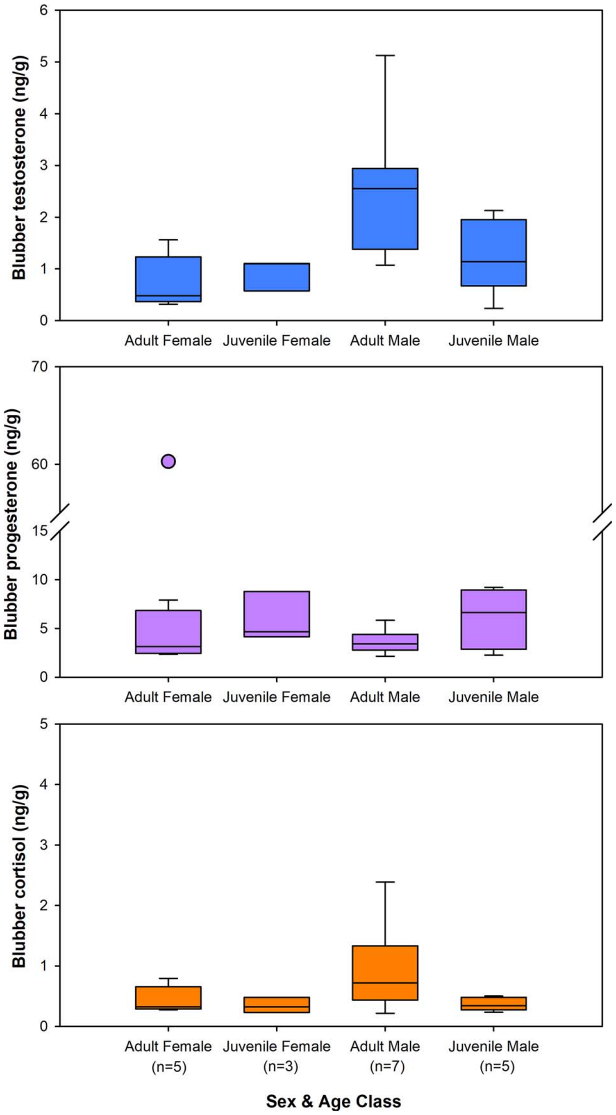


Figure 4: Blubber testosterone (top, blue), progesterone (middle, purple) and cortisol (bottom, orange) of live, apparently healthy NARWs across sexes and age classes. Boxplots encompass first and third quartiles, the line inside the box indicates the median value and whiskers represent the 10th and 90th percentiles. Note: In the progesterone graph, a break was inserted in the y-axis between 15 and 55 ng/g and the value for the pregnant female (denoted by a filled circle) was plotted separately due to its extremely high concentration.

does hold value in the present study for comparing between different extraction protocols. Refinement of the simplified extraction protocol, such as modifying the polarity and/or types of solvents used, may improve extraction efficiency and recovery further.

Successful analytical validation of commercial enzyme immunoassays tested in this study establishes these assays as suitable for measuring testosterone, progesterone, cortisol and associated metabolites in NARW blubber. Concentrations of hormones in NARW blubber were generally low, but comparable to levels measured in blubber of other large whale species (Clark *et al.*, 2016, Cates *et al.*, 2019, Atkinson *et al.*, 2020, Mingramm *et al.*, 2020). Studies using LC–MS/MS have established that cetacean blubber contains parent steroids (cortisol, progesterone and testosterone) as well as their metabolites, including cortisone, 17-hydroxyprogesterone, 11-deoxycorticosterone, 11-deoxycortisol and androstenedione (Boggs *et al.*, 2017, Galligan *et al.*, 2018, Boggs *et al.*, 2019, Dalle Luche *et al.*, 2019). Analysis of blue whale blubber showed progesterone was present in extracts (5%), although the majority of screened fractions (~67%) were found to be a more polar progesterone metabolite (Atkinson *et al.*, 2020). The use of broad-spectrum antibodies in this study permitted the quantification of blubber metabolite concentrations in all samples from NARWs. Future LC–MS/MS analysis of NARW blubber could be used to identify the predominant steroids and metabolites present in this tissue, enabling selection of more targeted immunoassay systems that may offer additional physiological insights from blubber; for example, identifying different stages of pregnancy based on shifts in the predominant steroids and metabolites (Legacki *et al.*, 2020).

Blubber hormone concentrations of NARWs and biological validation

Blubber testosterone, progesterone and cortisol in live, apparently healthy right whales followed expected physiologic patterns based on sex and reproductive state and were consistent with well-established faecal hormone patterns for the species (Burgess *et al.*, 2017, Hunt *et al.*, 2006, Rolland *et al.*, 2005, Rolland *et al.*, 2017). Adult male NARWs had higher testosterone and cortisol (and/or metabolites) in blubber compared to non-pregnant females and immature animals, presumably related to reproductive activity in males (Rolland *et al.*, 2005, Hunt *et al.*, 2006, Rolland *et al.*, 2017). A confirmed pregnant female was distinguished from non-pregnant animals by extremely high blubber progesterone concentrations (12-fold increase). Such physiological changes associated with pregnancy have also been measured in NARW faeces (Rolland *et al.*, 2005) and in the blubber of other large whale species (Kellar *et al.*, 2013, Clark *et al.*, 2016, Pallin *et al.*, 2018, Goertz *et al.*, 2019, Atkinson *et al.*, 2020). Most adult females in our biopsy sample set were lactating, with only one non-pregnant female considered to be in a resting state. Increasing sample sizes for reproductive females will better delineate the range of progesterone concentrations associated with reproductive cycling and pregnancy in blubber tissue.

Matched faeces and blubber collected from three individuals provided evidence that hormone patterns were similarly reflected in both matrices, though at different quantitative scales. This finding is consistent with bowhead

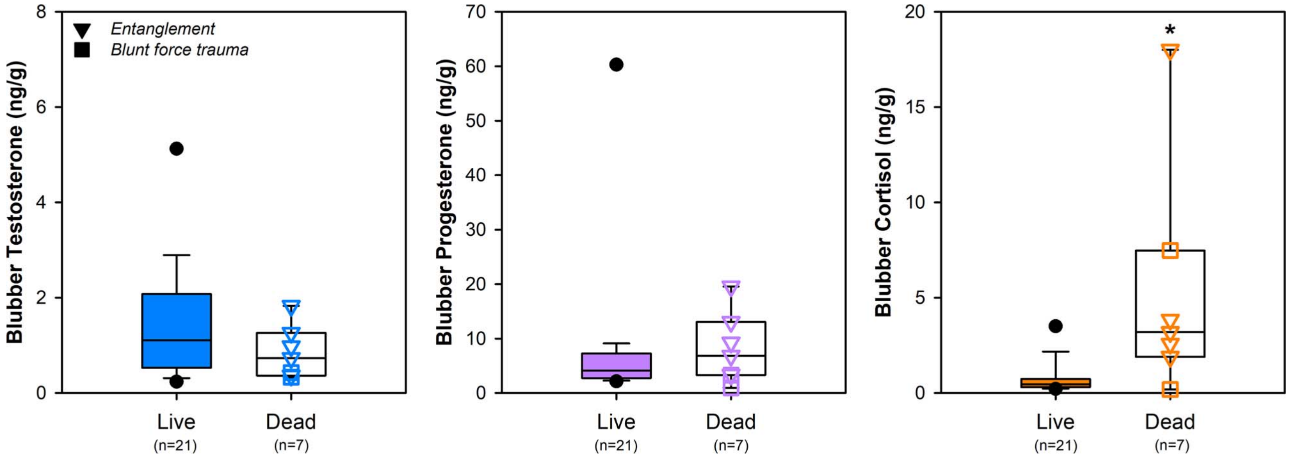


Figure 5: Blubber hormone concentrations for live whales (biopsy samples, $n = 21$) compared to necropsy samples from whales that died from anthropogenic causes ($n = 7$). For live whales, outliers beyond the 5th and 95th percentile are plotted with a circle. For dead whales, individual hormone values are plotted over the boxplot, with whales that died as a result of trauma from entanglement denoted by triangles (▼; $n = 5$) or vessel strike by squares (■; $n = 2$). Asterisk (∗) indicates a significant difference between the live and dead whales at $P < 0.05$.

whale progesterone concentrations that showed concordance among blubber, urine and serum samples (Kellar *et al.*, 2013). Since blood sampling and standard endocrine validations are not possible for most large whales, our preliminary data on matched alternative matrices lends further validity to the use of blubber hormone techniques for physiological assessment. Additionally, blubber hormone measurements may be useful to examine seasonality in free-swimming NARWs, a topic which remains understudied since faecal samples are often not obtainable during annual periods of fasting.

Abiotic factors (including storage time, sample mass and whale survival at time of sampling) should be considered when comparing different sources of tissue and these factors did not appear to hamper interpretation of hormone results in this study. We noted similarities between living and dead whales for both reproductive hormones (testosterone and progesterone), suggesting that carcasses in this study were still viable for hormone measurement. Furthermore, there was a wide variation in cortisol levels among dead whales (spanning the lowest and highest cortisol measurements in this study), suggesting these patterns were not due to tissue decomposition, and instead meaningfully reflect the time course of mortality or injury (similar to NARW faecal glucocorticoid patterns reported in Rolland *et al.*, 2017).

Cortisol data suggest that adrenal activation due to stressful anthropogenic impacts was captured in blubber tissue and the mode by which an animal died (entanglement in fishing gear or vessel strike) was the primary driver of postmortem cortisol levels. Increased blubber cortisol concentrations have been reported in other cetaceans following stressful events, including beach stranding of short-beaked common dolphins (Kellar *et al.*, 2015) and humpback whales (Mingramm *et al.*, 2020), and entrapment of beluga whales in sea ice (Trana *et al.*, 2016). The whale with the highest blubber cortisol measured in this study (MME16–249) died from a severe, chronic entanglement in fishing line that occluded the rostrum and was cinched at the flippers, restricting the ability of the mouth to open for feeding (Sharp *et al.*, 2019) leading to a prolonged decline in health and likely heightened adrenal activation. By contrast, the lowest measure of cortisol came from a whale (IFAW16–082) that died from propeller-induced trauma involving a deep laceration into the abdominal cavity, vertebral shearing and skull fractures (Sharp *et al.*, 2019). The trauma suffered by this individual likely led to a rapid death, with limited time for activating a stress response and/or uptake of hormone into blubber tissue, such that cortisol levels in the blubber of this whale reflected a prior physiological state of an otherwise apparently healthy individual preceding vessel strike. The other whale that sustained blunt force trauma from a vessel strike (IFAW17–182) had somewhat elevated cortisol levels but showed evidence of other pathologies that may have heightened adrenal activity in this individual prior to death (Sharp *et al.*, 2019). All four dead whales that were classified as acute entanglement cases showed intermediate cortisol levels, with evidence that two of these whales drowned (potentially an acute death) as a result of their entrapment in fishing gear (Sharp *et al.*, 2019). Blubber levels are likely a function of total cortisol production, with a lag time before accumulating in this peripheral tissue (possibly on the order of weeks to months for large whales, based on progesterone signal dynamics in pregnant bowhead whales (Kellar *et al.*, 2013)). Ultimately, using blubber glucocorticoid measurements for stress assessment in large whales may be most applicable for assessing threats sustained over longer period (weeks to months) rather than shorter term impacts (hours to days).

Conclusions

This study presents a useful and practical contribution towards advancing blubber hormone assessments for marine mammal populations by developing and validating a reliable, simplified hormone extraction protocol and then applying it to evaluate blubber hormone concentrations in well-studied NARWs. Optimization of blubber hormone measurements has the potential to expand the reach and reliability of this approach, benefitting researchers and management agencies studying vulnerable marine mammal populations. Using a small mass of blubber, we were able to measure and compare three different hormone types for reproductive and stress assessment of a large whale. Many blubber studies using immunoassays have focused on measuring a single hormone. However, the capacity to examine a suite of hormones is valuable for interpreting physiologic patterns, particularly because factors such as reproductive state can influence other hormone measures (e.g. adrenal hormones) (Hunt *et al*., 2006, Sheriff *et al*., 2011). Additional hormone types, such as thyroid hormones and aldosterone could also be explored in marine mammal blubber, as these data may be beneficial for more detailed physiological assessment. The hormone values reported here are important for establishing reference ranges of physiological information to which we can compare in future studies, especially given the increasing impact of human activities on the ocean (Maxwell *et al*., 2013, Fleishman *et al*., 2016) and animal welfare concerns (Moore and van der Hoop, 2012, Rolland *et al*., 2017, Papastavrou *et al*., 2017). Physiologic profiles measured in blubber are valuable for assessing the lethal and sublethal effects of major anthropogenic threats, including entanglements in fishing gear and vessel strikes, on NARWs as well as other vulnerable marine mammal populations.

Funding

This work was supported by Fisheries and Oceans Canada: Ocean Ecology Section (contract # F5211–180767).

Acknowledgements

The authors greatly appreciate the consistent and dedicated survey and biopsy sampling efforts of the New England Aquarium Right Whale Team and the Canadian Whale Institute, in particular Dr. Moira Brown, without whom this work would not have been possible. Thank you to Misty Niemeyer and team at the International Fund for Animal Welfare for providing the necropsy blubber samples used in this study, and to the necropsy teams who conducted sampling. The authors are grateful to the North Atlantic Right Whale Consortium data contributors for use of identification, sightings and necropsy reports that helped inform this study. Gratitude to Philip Hamilton, Kelsey Howe, Heather Pettis and Monica Zani for assistance with whale identification and life history data. We would also like to thank Dr. Hilary Moors-Murphy and Dr. Andrew Wright for facilitating project funding.

References

Atkinson S, Gendron D, Branch TA, Mashburn KL, Melica V, Enriquez-Paredes LE, Brownell RL Jr (2020) Pregnancy rate and biomarker validations from the blubber of eastern North Pacific blue whales. *Mar Mamm Sci* 36: 6–28.

Boggs AS, Ragland JM, Zolman ES, Schock TB, Morey JS, Galligan TM, Dalle Luche G, Balmer BC, Wells RS, Kucklick JR (2019) Remote blubber sampling paired with liquid chromatography tandem mass spectrometry for steroidal endocrinology in free-ranging bottlenose dolphins (*Tursiops truncatus*). *Gen Comp Endocrinol* 281: 164–172.

Boggs AS, Schock TB, Schwacke LH, Galligan TM, Morey JS, McFee WE, Kucklick JR (2017) Rapid and reliable steroid hormone profiling in *Tursiops truncatus* blubber using liquid chromatography tandem mass spectrometry (LC-MS/MS). *Anal Bioanal Chem* 409: 5019–5029.

Booth CG, Sinclair RR, Harwood J (2020) Methods for monitoring for the population consequences of disturbance in marine mammals: a review. *Front Mar Sci* 7: 115. doi: 10.3389/fmars.2020.00115.

Brown MW, Kraus SD, Gaskin DE (1991) Reaction of North Atlantic right whales (*Eubalaena glacialis*) to skin biopsy sampling for genetic and pollutant analysis. In GP Donovan, ed, *Report of the International Whaling Commission: Special Issue Volume 13*. International Whaling Commission, Cambridge, p. 9.

Burd EM (2010) Validation of laboratory-developed molecular assays for infectious diseases. *Clin Microbiol Rev* 23: 550–576.

Burgess EA, Hunt KE, Kraus SD, Rolland RM (2016) Get the most out of blow hormones: validation of sampling materials, field storage and extraction techniques for whale respiratory vapour samples. *Conserv Physiol* 4: cow24. doi: 10.1093/conphys/cow024.

Burgess EA, Hunt KE, Kraus SD, Rolland RM (2017) Adrenal responses of large whales: integrating fecal aldosterone as a complementary biomarker to glucocorticoids. *Gen Comp Endocrinol* 252: 103–110.

Burgess EA, Hunt KE, Kraus SD, Rolland RM (2018) Quantifying hormones in exhaled breath for physiological assessment of large whales at sea. *Sci Rep* 8: 10031. doi: 10.1038/s41598-018-28200.

Carone E, Pardo MA, Atkinson S, Mashburn K, Pérez-Puig H, Enríquez-Paredes L, Gendron D (2019) Sex steroid hormones and behavior reveal seasonal reproduction in a resident fin whale population. *Conserv Physiol* 7: coz059. doi: 10.1093/conphys/coz059.

Cates KA, Atkinson S, Gabriele CM, Pack AA, Straley JM, Yin S (2019) Testosterone trends within and across seasons in male humpback whales (*Megaptera novaeangliae*) from Hawaii and Alaska. *Gen Comp Endocrinol* 279: 164–173.

Champagne CD, Kellar NM, Trego ML, Brendan D, Rudy B, Wasser SK, Booth RK, Crocker DE, Houser DS (2018) Comprehensive endocrine response to acute stress in the bottlenose dolphin from serum, blubber, and feces. *Gen Comp Endocrinol* 266: 178–193.

Clark CT, Fleming AH, Calambokidis J, Kellar NM, Allen CD, Catelani KN, Robbins M, Beaulieu NE, Steel D, Harvey JT (2016) Heavy with child? Pregnancy status and stable isotope ratios as determined from biopsies of humpback whales. *Conserv Physiol* 4: cow050. doi: 10.1093/conphys/cow050.

Corkeron P, Hamilton P, Bannister J, Best P, Charlton C, Groch KR, Findlay K, Rowntree V, Vermeulen E, Pace RM (2018) The recovery of North Atlantic right whales, *Eubalaena glacialis*, has been constrained by human-caused mortality. *R Soc Open Sci* 5: 180892. doi: 10.1098/rsos.180892.

Dalle Luche G, Bengtson Nash S, Kucklick JR, Mingramm FM, Boggs AS (2019) Liquid chromatography tandem mass spectrometry for the quantification of steroid hormone profiles in blubber from stranded humpback whales (Megaptera novaeangliae). *Conserv Physiol* 7: coz030. doi: 10.1093/conphys/coz030.

Ezan E, Grassi J (2000) Optimization. In J Gosling, ed, *Immunoassays: A Practical Approach*. Oxford University Press, Oxford, pp. 187–210.

Fleishman E *et al.* (2016) Monitoring population-level responses to marine mammals to human activities. *Mar Mamm Sci* 32: 1004–1021.

Frasier T, Gillett R, Hamilton P, Brown M, Kraus S, White B (2013) Postcopulatory selection for dissimilar gametes maintains heterozygosity in the endangered North Atlantic right whale. *Ecol Evol* 3: 3483–3494.

Frasier TR, Rastogi T, Brown MW, Hamilton PK, Kraus SD, White BN (2006) Characterization of tetranucleotide microsatellite loci and development and validation of multiplex reactions for the study of right whale species (genus *Eubalaena*). *Mol Ecol Notes* 6: 1025–1029.

Galligan TM, Schwacke LH, Houser DS, Wells RS, Rowles T, Boggs ASP (2018) Characterization of circulating steroid hormone profiles in the bottlenose dolphin (*Tursiops truncatus*) by liquid chromatography–tandem mass spectrometry (LC–MS/MS). *Gen Comp Endocrinol* 263: 80–91.

Geraci JR, Lounsbury VJ (2005) *Marine Mammals Ashore: A Field Guide for Strandings*. National Aquarium in Baltimore, Baltimore, pp. 176–178.

Goertz CE, Burek-Huntington K, Royer K, Quakenbush L, Clauss T, Hobbs R, Kellar NM (2019) Comparing progesterone in blubber and serum to assess pregnancy in wild beluga whales (Delphinapterus leucas). *Conserv Physiol* 7: coz071. doi: 10.1093/conphys/coz071.

Grotjan HE, Keel BA (1996) Data interpretation and quality control. In EP Diamandis, TK Christopoulos, eds, *Immunoassay*. Academic Press, San Diego, pp. 51–95.

Hamilton PK, Knowlton AR, Marx MK (2007) Right whales tell their own stories: The photo-identification catalog. In SD Kraus, RM Rolland, eds, *The Urban Whale: North Atlantic Right Whales at the Crossroads*. Harvard University Press, Cambridge, pp. 73–102.

Hamilton PK, Knowlton AR, Marx MK, Kraus SD (1998) Age structure and longevity in North Atlantic right whales *Eubalaena glacialis* and their relation to reproduction. *Mar Ecol Prog Ser* 171: 285–292.

Harcourt R, van der Hoop J, Kraus S, Carroll EL (2019) Future directions in Eubalaena spp.: comparative research to inform conservation. *Front Mar Sci* 5: 530. doi: 10.3389/fmars.2018.00530.

Hunt KE, Lysiak NS, Moore MJ, Rolland RM (2016) Longitudinal progesterone profiles in baleen from female North Atlantic right whales (Eubalaena glacialis) match known calving history. *Conserv Physiol* 4: cow014. doi: 10.1093/conphys/cow014.

Hunt KE, Lysiak NS, Robbins J, Moore MJ, Seton RE, Torres L, Buck CL (2017) Multiple steroid and thyroid hormones detected in baleen from eight whale species. *Conserv Physiol* 5: cox061. doi: 10.1093/conphys/cox061.

Hunt KE *et al.* (2013) Overcoming the challenges of studying conservation physiology in large whales: a review of available methods. *Conserv Physiol* 1: cot006. doi: 10.1093/conphys/cot006.

Hunt KE, Rolland RM, Kraus SD, Wasser SK (2006) Analysis of fecal glucocorticoids in the North Atlantic right whale (*Eubalaena glacialis*). *Gen Comp Endocrinol* 148: 260–272.

Hunt KE, Stimmelmayr R, George C, Hanns C, Suydam R, Brower H Jr, Rolland RM (2014) Baleen hormones: a novel tool for retrospective assessment of stress and reproduction in bowhead whales (Balaena mysticetus). *Conserv Physiol* 2: cou030. doi: 10.1093/conphys/cou030.

Inoue S, Yasunaga G, Pastene LA (2019) Comparison of progesterone concentrations in blubber and plasma among female antarctic minke whales of known reproductive status. *Fish Sci* 85: 971–977.

Kellar NM, Catelani KN, Robbins MN, Trego ML, Allen CD, Danil K, Chivers SJ (2015) Blubber cortisol: a potential tool for assessing stress response in free-ranging dolphins without effects due to sampling. *PLoS One* 10: e0115257. doi: 10.1371/journal.pone.0115257.

Kellar NM, Keliher J, Trego ML, Catelani KN, Hanns C, George JC, Rosa C (2013) Variation of bowhead whale progesterone concentrations across demographic groups and sample matrices. *Endanger Species Res* 22: 61–72.

Kellar NM, Trego ML, Marks CI, Chivers SJ, Danil K, Archer FI (2009) Blubber testosterone: a potential marker of male reproductive status in short-beaked common dolphins. *Mar Mamm Sci* 25: 507–522.

Kellar NM, Trego ML, Marks CI, Dizon AE (2006) Determining pregnancy from blubber in three species of delphinids. *Mar Mamm Sci* 22: 1–16.

Knowlton AR, Robbins J, Landry S, McKenna HA, Kraus SD, Werner TB (2015) Effects of fishing rope strength on the severity of large whale entanglements. *Conserv Biol* 30: 318–328.

Kraus SD, Moore KE, Price CA, Crone MJ, Watkins WA, Winns HE, Prescott JH (1986) The use of photographs to identify individual North Atlantic right whales (*Eubalaena glacialis*). In RL Brownell Jr, PB Best, JH Prescott, eds, *Report of the International Whaling Commision: Special Issue Volume 10*. International Whaling Commission, Cambridge, p. 7.

Legacki EL, Robeck TR, Steinman KJ, Conley AJ (2020) Comparative analysis of steroids in cyclic and pregnant killer whales, beluga whales and bottlenose dolphins by liquid chromatography tandem mass spectrometry. *Gen Comp Endocrinol* 285: 113273. doi: 10.1016/j.ygcen.2019.113273.

Mansour AAH, Mkay DW, Lien J, Orr JC, Banoub JH, Ølen N, Stenson G (2002) Determination of pregnancy status from blubber samples in minke whales (*Balaenoptera acutorostrata*). *Mar Mamm Sci* 18: 112–120.

Maxwell SM *et al.* (2013) Cumulative human impacts on marine predators. *Nat Commun* 4: 2688. doi: 10.1038/ncomms3688.

McLellan WA, Rommel SA, Moore MJ, Pabst DA (2004) Right whale necropsy protocol. In *U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Office of Protected Resources*. Silver Spring.

Mello D, Colosio A, Marcondes M, Viau P, Oliveira C (2017) Feasibility of using humpback whale blubber to measure sex hormones. *J Exp Mar Biol Ecol* 486: 32–41.

Meyer-Gutbrod EL, Greene CH (2017) Uncertain recovery of the North Atlantic right whale in a changing ocean. *Global Change Biol.* 24: 455–464.

Millspaugh JJ, Washburn BE (2004) Use of fecal glucocorticoid metabolite measures in conservation biology research: considerations for application and interpretation. *Gen Comp Endocrinol* 138: 189–199.

Mingramm F, Keeley T, Whitworth D, Dunlop R (2020) Blubber cortisol levels in humpback whales (*Megaptera novaeangliae*): a measure of physiological stress without effects from sampling. *Gen Comp Endocrinol* 117: 104606. doi: 10.1016/j.ygcen.2020.113436.

Moore MJ, Knowlton AR, Kraus SD, McLellan WA, Bonde RK (2004) Morphometry, gross morphology and available histopathology in North Atlantic right whale (*Eubalaena glacialis*) mortalities (1970-2002). *J Cetacean Res Manage* 6: 199–214.

Moore MJ, van der Hoop JM (2012) The painful side of trap and fixed net fisheries: chronic entanglement of large whales. *J Mar Sci* 2012: 230653. doi: 10.1155/2012/230653.

Noren DP, Mocklin JA (2012) Review of cetacean biopsy techniques: factors contributing to successful sample collection and physiological and behavioral impacts. *Mar Mamm Sci* 28: 154–199.

Pallin L, Robbins J, Kellar N, Bérubé M, Friedlaender A (2018) Validation of a blubber-based endocrine pregnancy test for humpback whales. *Conserv Physiol* 6: coy031. doi: 10.1093/conphys/coy031.

Palme R (2005) Measuring fecal steroids: guidelines for practical application. *Ann N Y Acad Sci* 1046: 75–80.

Palme R (2019) Non-invasive measurement of glucocorticoids: advances and problems. *Physiol Behav* 199: 229–243.

Palme R, Touma C, Arias N, Dominchin MF, Lepschy M (2013) Steroid extraction: get the best out of faecal samples. *Wien Tierarztl Monatsschr* 100: 238–246.

Papastavrou V, Leaper R, Lavigne D (2017) Why management decisions involving marine mammals should include animal welfare. *Mar Policy* 17: 19–24.

Pettis HM, Rolland RM, Hamilton PK, Knowlton AR, Burgess EA, Kraus SD (2017) Body condition changes arising from natural factors and fishing gear entanglements in North Atlantic right whales *Eubalaena glacialis*. *Endanger Species Res* 32: 237–249.

Richard JT, Robeck TR, Osborn SD, Naples L, McDermott A, LaForge R, Romano TA, Sartini BL (2017) Testosterone and progesterone concentrations in blow samples are biologically relevant in belugas (*Delphinapterus leucas*). *Gen Comp Endocrinol* 246: 183–193.

Right Whale Consortium (2019) North Atlantic Right Whale Consortium Identification, Sightings, and Genetics Databases. In *Anderson Cabot Center for Ocean Life at the New England Aquarium*, Boston.

Rolland RM, Graham KM, Stimmelmayr R, Suydam RS, George JC (2019) Chronic stress from fishing gear entanglement is recorded in baleen from a bowhead whale (*Balaena mysticetus*). *Mar Mamm Sci* 35: 1625–1642.

Rolland RM, Hunt KE, Kraus SD, Wasser SK (2005) Assessing reproductive status of right whales (*Eubalaena glacialis*) using fecal hormone metabolites. *Gen Comp Endocrinol* 142: 308–317.

Rolland RM, McLellan WA, Moore MJ, Harms CA, Burgess EA, Hunt KE (2017) Fecal glucocorticoids and anthropogenic injury and mortality in North Atlantic right whales (*Eubalaena glacialis*). *Endanger Species Resear* 34: 417–429.

Rolland RM, Moore MJ (2018) Health Assessment of Large Whales. In FMD Gulland, LA Dieruf, KL Whitman, eds, *CRC Handbook of Marine Mammal Medicine*, EdEd 3. CRC Press, Boca Raton, pp. 835–848.

Sharp SM *et al.* (2019) Gross and histopathologic diagnoses from North Atlantic right whale *Eubalaena glacialis* mortalities between 2003 and 2018. *Dis Aquat Org* 135: 1–31.

Sheriff MJ, Dantzer B, Delehanty B, Palme R, Boonstra R (2011) Measuring stress in wildlife: techniques for quantifying glucocorticoids. *Oecologia* 166: 869–887.

Trana MR, Roth JD, Tomy GT, Anderson WG, Ferguson SH (2015) Influence of sample degradation and tissue depth on blubber cortisol in beluga whales. *J Exp Mar Biol Ecol* 462: 8–13.

Trana MR, Roth JD, Tomy GT, Anderson WG, Ferguson SH (2016) Increased blubber cortisol in ice-entrapped beluga whales (*Delphinapterus leucas*). *Polar Biol* 39: 1563–1569.

Trego ML, Kellar NM, Danil K (2013) Validation of blubber progesterone concentrations for pregnancy determination in three dolphin species and a porpoise. *PLoS One* 8: e69709. doi: 10.1371/journal.pone.0069709.

Vu ET, Clark C, Catelani K, Kellar NM, Calambokidis J (2015) Seasonal blubber testosterone concentrations of male humpback whales (*Megaptera novaeangliae*). *Mar Mamm Sci* 31: 1258–1264.

Wasser SK, Hunt KE, Brown JL, Cooper K, Crockett CM, Bechert U, Millspaugh JJ, Larson S, Monfort SL (2000) A generalized fecal glucocorticoid assay for use in a diverse array of non-domestic mammalian and avian species. *Gen Comp Endocrinol* 120: 260–275.

Watson R, Munro C, Edwards KL, Norton V, Brown JL, Walker SL (2013) Development of a versatile enzyme immunoassay for non-invasive assessment of glucocorticoid metabolites in a diversity of taxonomic species. *Gen Comp Endocrinol* 186: 16–24.

Vol. 143: 205–226, 2021
https://doi.org/10.3354/dao03578

DISEASES OF AQUATIC ORGANISMS
Dis Aquat Org

FEATURE ARTICLE

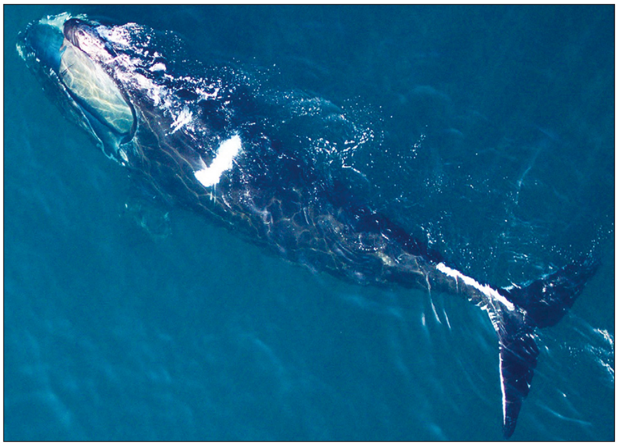
REVIEW

Assessing North Atlantic right whale health: threats, and development of tools critical for conservation of the species

Michael J. Moore[1,*], Teresa K. Rowles, Deborah A. Fauquier, Jason D. Baker, Ingrid Biedron, John W. Durban, Philip K. Hamilton, Allison G. Henry, Amy R. Knowlton, William A. McLellan, Carolyn A. Miller[1], Richard M. Pace III, Heather M. Pettis, Stephen Raverty, Rosalind M. Rolland, Robert S. Schick, Sarah M. Sharp, Cynthia R. Smith, Len Thomas, Julie M. van der Hoop[1], Michael H. Ziccardi

[1]**Woods Hole Oceanographic Institution, Woods Hole MA 02543, USA**
Co-authors' addresses given in a supplement; **www.int-res.com/articles/suppl/d143p205_supp.pdf**

ABSTRACT: Whaling has decimated North Atlantic right whales *Eubalaena glacialis* (NARW) since the 11th century and southern right whales *E. australis* (SRW) since the 19th century. Today, NARWs are Critically Endangered and decreasing, whereas SRWs are recovering. We review NARW health assessment literature, NARW Consortium databases, and efforts and limitations to monitor individual and species health, survival, and fecundity. Photographs are used to track individual movement and external signs of health such as evidence of vessel and entanglement trauma. Post-mortem examinations establish cause of death and determine organ pathology. Photogrammetry is used to assess growth rates and body condition. Samples of blow, skin, blubber, baleen and feces quantify hormones that provide information on stress, reproduction, and nutrition, identify microbiome changes, and assess evidence of infection. We also discuss models of the population consequences of multiple stressors, including the connection between human activities (e.g. entanglement) and health. Lethal and sublethal vessel and entanglement trauma have been identified as major threats to the species. There is a clear and immediate need for expanding trauma reduction measures. Beyond these major concerns, further study is needed to evaluate the impact of other stressors, such as pathogens, microbiome changes, and algal and industrial toxins, on NARW reproductive success and health. Current and new health assessment tools should be developed and used to monitor the effectiveness of management measures and will help determine whether they are sufficient for a substantive species recovery.



North Atlantic right whale (Catalog #3530 'Ruffian'), showing healed scarring from an entanglement 8 yr earlier.

Photo: J. Durban & Holly Fearnbach

KEY WORDS: Right whale · Health · Trauma · Reproduction · Stressor · Cumulative effects

---

*Corresponding author: mmoore@whoi.edu

Publisher: Inter-Research · www.int-res.com

1. INTRODUCTION

The North Atlantic right whale (NARW) *Eubalaena glacialis* species is Critically Endangered and declining. Past and current conservation measures have failed to maintain a recovery trajectory for the species. Therefore, better understanding of the current status of NARW health, and tools to evaluate health, are critical to reverse the decline and restart the recovery of this species. The challenges of studying large whales and their health include, but are not limited to, the following factors: distance-, weather- and season-dependent logistics; locating them; collecting and analyzing the data; and determining the causes of observed morbidity and mortality. A recent review of the right whale genus *Eubalaena* spp. (Harcourt et al. 2019) summarized the extensive relevant literature in the context of future directions for comparative research among the 3 extant species to inform conservation. Topics included variable recovery from historic whaling, linking individuals to population level response, adapting to shifting resources, emergent diseases and vulnerability under stress, and cumulative effects. Our review summarizes data, publications and past workshops, related to the health of NARWs as discussed at a workshop in Silver Spring, MD, USA, in June 2019 (Fauquier et al. 2020). Previous workshops are summarized in that report (Brownell et al. 1986, Best et al. 2001, Reeves et al. 2001, O'Hara et al. 2003, Rowles et al. 2006, International Whaling Commission 2010, Thomas et al. 2013, Sironi et al. 2018, Sisson & Long 2018). Additionally, we periodically refer to unpublished analyses of data by authors of this review to provide as current a perspective as possible. Most of those data are available from the NARW Consortium (NARWC) database collection (www.narwc.org/narwc-databases.html).

Implications and recommendations from the 2020 workshop, and consequent discussions, are then presented in the context of (1) furthering our overall understanding of NARW health, and (2) the use of health assessment tools to gauge the efficacy of measures designed to enhance the recovery of the NARW species. For a recent bibliography on this topic see https://repository.library.noaa.gov/view/noaa/20221.

For the purpose of this review, we define wildlife health following Stephen (2014, p. 427)

> Health is the result of interacting biologic, social, and environmental determinants that combine to affect the animal's or population's capacity to cope with change. Health cannot be measured solely by what is absent, but rather by characteristics of the animals and their ecosystem that affect their vulnerability and resilience. Wildlife health is not a biologic state but rather a dynamic social construct based on human expectations and knowledge.

Following centuries of whaling, with the last documented event in 1967 (Maul & Sergeant 1977), the NARW species underwent a very slow recovery (~2.8% yr^{-1}) until 2010 (Fig. 1). Since then, abundance has declined by 20%, so that as of 2020 there are about 356 animals remaining (Pace et al. 2017, NOAA 2020, Pettis et al. 2020). In 2020, the IUCN changed the species listing from Endangered to Critically Endangered (Cooke 2020), the only large whale species in the world to warrant this designation. The North Pacific right whale *E. japonica* is listed by the IUCN as Endangered, with the Northeast Pacific subpopulation as Critically Endangered. In contrast, most southern right whale (SRW) *E. australis* populations have recovered remarkably from historic whaling, despite a major setback from Russian whaling in the 1960s (Yablokov 1994, Corkeron et al. 2018). The species is listed as of Least Concern by the IUCN, although in some habitats SRW sightings have plateaued in recent years (Jackson et al. 2020, Stamation et al. 2020).

Right whales are individually identified using photographs of cornified skin patterns, called callosities, on their heads (Payne et al. 1983, Kraus et al. 1986, Kraus 1990). The North Atlantic Right Whale Catalog (http://rwcatalog.neaq.org) contains all known photographed sightings of NARWs from 1935 to the present (Hamilton et al. 2007). The Catalog is used to monitor their distribution, associations, survival, reproduction, movement, and health. There is an intensive photo-identification survey effort conducted annually in many NARW habitats resulting in an average of 75% of this species being photo-documented each year (Pettis et al. 2020). The Catalog is the hub of the NARWC database collection (www.narwc.org/narwc-databases.html).

A recent broad-scale NARW distribution shift began in 2010 or 2011 (Record et al. 2019). Sightings decreased drastically on the calving ground off the southeastern USA and in 3 northern feeding habitats (Davies et al. 2019, Gowan et al. 2019): Great South Channel (southeast of Cape Cod, MA, USA), Bay of Fundy, and Roseway Basin south of Nova Scotia (Canada). As much as 50% of this species had been seen in each of these habitats in some years prior to 2010 (Fauquier et al. 2020). Recently, annual counts have decreased to only about 100 individuals on average in the Great South Channel and 35 or fewer in the other 3 habitats (except in 2014 in the Bay of

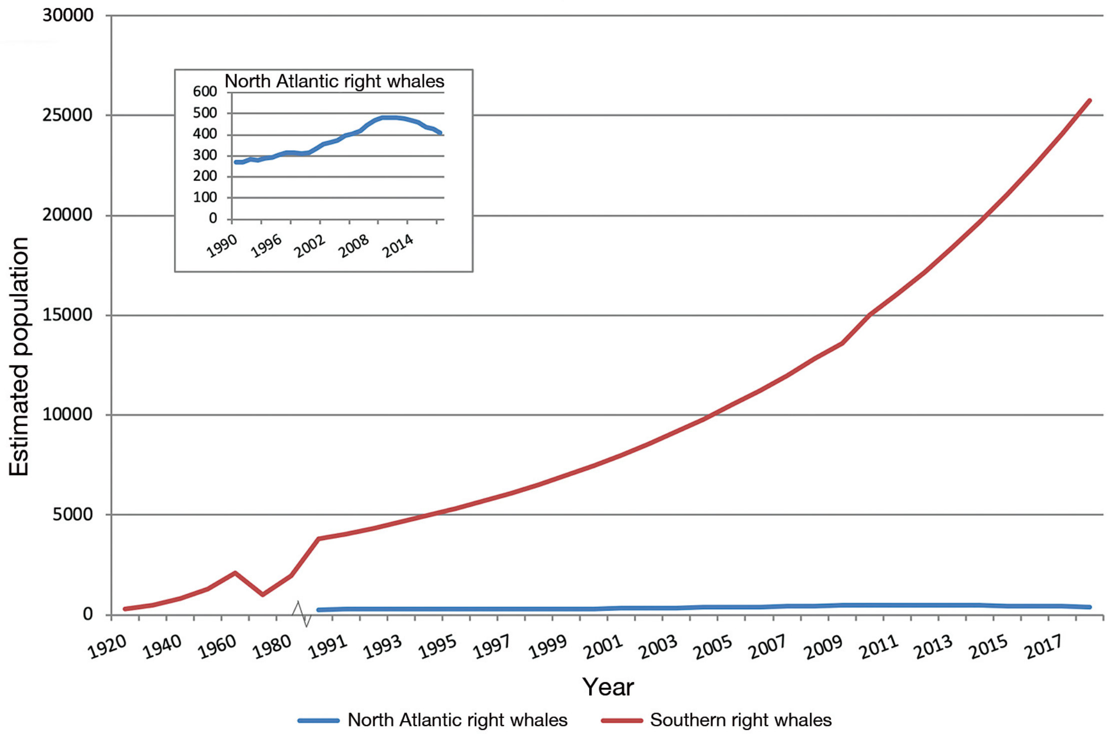


Fig. 1. Population trends in the North Atlantic and southern right whale species (estimates for North Atlantic species prior to 1990 are unavailable; southern estimates prior to 1990 on decadal scale). Illegal whaling caused a downturn in the southern species in the 1960s. Figure modified from Moore & Myers (2019); used by permission. Data from International Whaling Commission (2013), Pace et al. (2017), Pettis et al. (2020)

Fundy, when over 100 whales were present for a very short time). At the same time, sightings increased in one well-studied habitat, Cape Cod Bay, MA, USA, and in 2 lesser historically known feeding habitats: one south of Nantucket, MA, USA, and one in the Gulf of St. Lawrence, Canada. Since 2010, over 250 whales have been seen annually in the first region, and 100 to 150 have been seen annually in each of the latter two. In addition to sightings, passive acoustic data show an increased occurrence of NARW calls off the mid-Atlantic, herein described as north of Cape Hatteras to south of Cape Cod, and some calls along the edge of the continental shelf (Davis et al. 2017).

These distribution shifts have impacted the collection of sightings and photos and the data derived from those observations. The average percent of whales photographed and identified annually dropped from 81% during the 8 yr before the shift (2003 to 2010) to 68% during the 8 yr after the shift (2011 to 2018) (Pettis et al. 2020). This smaller percentage of the species being observed annually impacts the precision and potential accuracy of abundance estimates. The decrease in shipboard photographs, which had been primarily collected from historical high-residency areas (e.g. the Bay of Fundy and off the southeastern USA in the 2000s) affects the ability to assess body condition and scarring from shipboard images. Finally, mothers are being seen with their calves less frequently on the northern feeding grounds, making it harder to photo-identify those calves because their callosities are generally not well developed until the latter half of their birth year, and at the very least, this has delayed our ability to catalog those calves. These impacts on the photo-identification data collection have downstream effects (e.g. the potential underestimate in abundance and calf survival) that should be considered when analyzing the data and assessing monitoring power especially when comparing pre-2010 to post-2011 derived products (Fauquier et al. 2020).

In summary, cataloging the location and identification of individual NARWs, year by year, has been the cornerstone of our developing understanding of the health of individuals, their movements, and the species as a whole. Therefore, we need to regain adequate cataloging of the species, especially in light of the recent habitat shifts, by increasing photo identification effort in the mid-Atlantic, southern New England, and the Gulf of St Lawrence among other currently important habitat areas. In addition, we need to be better prepared for future shifts of distribution and rapidly shifting efforts to maintain adequate photo-identification of the population.

2. RESULTS

2.1. North Atlantic right whale trauma

2.1.1. North Atlantic right whale mortality

There has been little comparison of mortality patterns between SRW and NARW. Such comparisons as there are should be expanded. In Peninsula Valdés, Argentina (a well-studied SRW calving ground with low historical calf mortality) between 2003 and 2018, 20% (738/4403) of calves (mostly neonates) died (Fig. 2) (Sironi et al. 2018). Current theories as to the cause(s) include predation from kelp gull attacks (Sironi et al. 2018). There have been reports of SRW vessel strikes and entanglements (Van Waerebeek et al. 2007, Kemper et al. 2008, Zappes et al. 2013). However, these events have not precluded the species from a substantial post-whaling recovery (Fig. 1). In contrast, for NARW, human-induced trauma has been a major factor in the failure of that species to recover. Their perinatal mortalities are from natural causes, but older calves can be vessel struck, while juveniles and adults die acutely after asphyxiation in heavy fishing gear, or after severe vessel trauma, or chronically after a debilitating entanglement, or initially sublethal vessel trauma. From early Basque whaling through commercial whaling, by the 1930s NARW numbers had been reduced to possibly less than a hundred (Reeves et al. 2007). Incidental mortalities caused by commercial fishing operations and vessel strikes in the past 50 yr have kept the species numbers severely reduced, albeit with a slow recovery until 2010, but with a subsequent decline though 2020 as described above (Pettis et al. 2020). In the late 2010s, clustered mortality events occurred in the Gulf of St. Lawrence with 12 deaths in 2017 and 9 in 2019—the majority due to human activities (Daoust et al. 2018, Sharp et al. 2019, Bourque et al. 2020). This, along with mortalities in the USA, resulted in its National Marine Fisheries Service (NMFS, part of the National Oceanic and Atmospheric Administration [NOAA]) declaring an Unusual Mortality Event (www.fisheries.noaa.gov/national/marine-life-distress/2017-2020-north-atlantic-right-whale-unusual-mortality-event), a stranding that is unexpected, involves a significant die-off of any marine mammal population, and demands immediate response (16 USC § 1421h(6); see https://www.fisheries.noaa.gov/national/marine-mammal-protection/marine-mammal-protection-act).

A review of 54 NARW mortalities from 1970–2002 (Moore et al. 2004), an average of 1.7 (54/32) mortalities per year, found anthropogenic trauma in 77% (14/18) of juveniles and adults that were completely necropsied. Of these, the cause of death (COD) was determined to be vessel strike in 71% (10/14) while 29% (4/14) died of entanglement. The COD for the remaining 4 juveniles and adults could not be determined. More recently, Sharp et al. (2019) undertook a thorough review of 70 deaths between 2003 and 2018, an average of 4.7 (70/15) mortalities per year, in which 80% (56/70) of carcasses were examined externally and 63% (44/70) were necropsied. Where COD was determined, 88% (38/43) were anthropogenic in origin. The relative threat of entanglement in commercial fishing gear increased from the previous estimate, accounting for 58% (22/38) of the anthropogenic deaths, while vessel strike accounted for 42% (16/38) of these cases. Females accounted for 66% (19/29) of known-sex adult deaths. In both studies (Moore et al. 2004, Sharp et al. 2019), juvenile and adult mortalities of NARWs from known causes were all due to anthropogenic trauma. In the 1980s through the 2000s, deaths were overwhelmingly due to vessel strikes as animals transited either south to the calving grounds or back north to feeding grounds. During this time, necropsy teams documented 3 pregnant NARWs

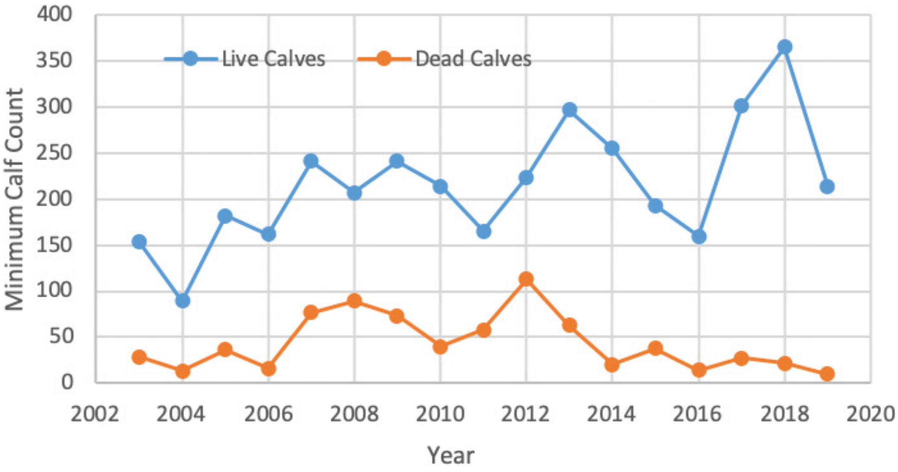


Fig. 2. Minimum counts of live and dead southern right whale calves in Peninsula Valdés, Argentina, 2001–2019. Data: Sironi et al. (2018), M. Sironi, V. Rowntree and M. Uhart pers. comm.

with evidence of vessel strikes in the mid-Atlantic and southeast USA, which motivated the development of coast-wide seasonal management areas (SMAs), where most vessels >65 ft (~20 m) are required to slow to 10 knots or less at certain times of the year (when NARWs are expected to be present) as a conservation strategy (Silber et al. 2014).

Diagnostic necropsies provide critical data, for maintaining an up-to-date understanding of how anthropogenic trauma on the species is changing in time and space. Without these data, the necessary ongoing optimization and evaluation of mitigation measures cannot occur.

2.1.2. Visual health and injury assessments

Assessment of live animals in the context of their catalogued individual identity gives a unique, sequential perspective on the status and trend of each animal and aids in identifying sublethal impacts that may affect reproductive success and therefore be targets for mitigation. The visual health assessment (VHA) method (Pettis et al. 2004, Rolland et al. 2016) allows for non-invasive assessments of NARW health using photographs taken from boats and aircraft. Data on body condition, skin condition (lesions and skin sloughing), rake marks (shallow striations in the skin) forward of the blowholes, and cyamids (whale lice) around the blowholes can be linked to the NARW Catalog (http://rwcatalog.neaq.org), allowing one to examine associations between health, individual life-history, and post-mortem information (www.narwc.org/narwc-databases.html). Analyses of these data have established connections between health, reproduction, and anthropogenic impacts (Pettis et al. 2004, Rolland et al. 2016). Two health conditions, emaciated body condition and swath skin lesions, have emerged as prognostic indicators of poor NARW survival (Pettis et al. 2004, Hamilton & Marx 2005). The incidence of these conditions has varied over time, with the highest incidence of both documented in 2011–2016 (Pettis 2019). Other types of skin lesions are regularly observed on NARW, though the etiology, and their impact on survival and reproduction are unknown (Pettis et al. 2004, Hamilton & Marx 2005, Rolland et al. 2016). Beginning in 2009, far more whales have been scored as thin, at least once annually, than the number scored with poor skin condition (Pettis et al. 2004). The VHA method has been valuable in retrospective analysis for evaluating sub-lethal anthropogenic injury impact on health, informing annual injury determinations and estimates of human impact on this species, and predicting survival (Pettis et al. 2004, Schick et al. 2013). Additionally, VHAs show promise in helping to estimate the time of death when whales are not sighted post injury (H. M. Pettis unpubl. data).

The VHA method has also enabled a broad, long-term assessment of the nature and impact of sublethal trauma on the species. Qualitatively, its applicability to the entire photo-ID catalog has made it a vital resource, given its sample size, and it should continue to be promulgated to adequately monitor the extent and variation in sub-lethal trauma impacts on the species. Quantitively it has been linked to demographic outcomes (Schick et al. 2016).

2.1.3. NOAA fisheries serious injury assessments

In the USA, NMFS is responsible for management of NARWs under the Endangered Species Act and Marine Mammal Protection Act (MMPA). As mandated by the MMPA, it estimates the number of human-caused mortalities and serious injuries of NARWs. Predicting the likely outcome for animals with substantive injuries is important to estimate the overall mortality incidence. Furthermore, recent modeling (Pace et al. 2021) has shown that only 38% of total mortality was detected during 1990–2017: this cryptic mortality factor is driven at least in part by NARW lost to follow up because they are emaciated and sink due to being negatively buoyant (Moore et al. 2020). Others will likely float offshore until they decompose, without ever being observed, or at least not reported. The extent of the crypsis was modeled by comparing the number of carcasses documented to the number of animals that disappeared from the photo-ID catalog through time. A formal method to assess the status of chronically traumatized individual NARWs, linked with an ongoing estimate of cryptic mortality, is critical to understanding their prognosis and overall mortality incidence.

NMFS serious injury (SI) assessments estimate annual rates of human-caused mortality and SI for all marine mammal stocks occurring within USA waters (NOAA 2012, 2020). NMFS Northeast Fisheries Science Center (NEFSC) has made SI determinations for western North Atlantic large whale stocks since 1999 using all available relevant injury event information including sighting history, necropsy reports, and health assessments when available. NEFSC used its own criteria to assess large whale injuries until 2012, when USA National SI criteria guidelines were established (NOAA 2012). NEFSC criteria used prior to 2012 did not count events for which there were insufficient data to make a lethal take determination against potential biological removal (PBR). A take is defined by the MMPA as 'to harass, hunt, capture, or kill, or attempt to harass, hunt, capture, or kill any marine mammal' (16 USC § 1362 (16)). PBR is defined by the MMPA as the maximum number of animals, not including natural mortalities, that may be removed from a marine mammal stock while allowing that stock to reach or maintain its optimum sustainable population. The National criteria now address such data-poor events by providing prorated values that count against PBR. A retrospective application of the National criteria to all NARW injury events from 2000 to present resulted in only 0.8% (14/184) events between 2000 and 2011 being changed from a 0 to a prorated value, which illustrates that injury determinations of this stock have been relatively consistent across the years despite evolving SI criteria (Fig. 3) and is likely due to the data-rich nature of NARW injury events. As seen in Fig. 3, and further supported by others (Knowlton et al. 2016), the rate of entanglement related SI and mortality has been increasing in the last decade, whereas that of vessel strike has decreased. The entanglement rate alone has remained above PBR throughout the timeline (i.e. since 2000). If it were not for disentanglement efforts, the situation would be even worse, as in some circumstances, disentanglement teams are able to avert SIs. However, the practice of not counting such cases towards PBR does devalue such data as an index of entanglement risk.

The SI determination process is the primary tool used by NMFS to include an estimate of the annual human-caused mortality and serious injury in annual stock assessment in the USA. It provides an annual update on the nature and extent of the different sources of lethal trauma to the species. A major limitation is the lag time from when data are available to when they are incorporated into a publicly available annual report. Given the current high incidence of serious injuries and mortalities, a closer to real-time analysis, and reporting, would facilitate equally prompt trauma mitigation enhancement.

2.1.4. Frequency, and effects, of vessel strikes and entanglement on North Atlantic right whale reproduction

During times of decadal prey declines, calving output is lower (Hlista et al. 2009, Meyer-Gutbrod et al. 2015). Additionally, quantifying the sublethal incidences of vessel and rope trauma on NARW reproductive success, in the context of their unfolding demographic and migratory history, is a critical aspect of understanding these sources of trauma. As part of the recent workshop, we updated earlier studies of vessel and rope trauma.

2.1.4.1. Vessel strikes. We examined NARW Catalog photographs of live individuals for evidence of external trauma from vessel strikes (propeller cuts or gashes) and necropsy reports for cause of death information. External sharp trauma wounds on both live and dead whales resulting from vessel strike were categorized as superficial, shallow, or deep, while blunt trauma cases were only determined from necropsy reports (Fig. 4). With the implementation of a USA ship-speed rule in 2008, there appeared to be some reduction in lethal vessel strikes for NARWs when comparing known vessel-struck carcass detections in or within 45 nmiles (74 km) of an active SMA pre- and post-rule, whereas for humpback whales *Megaptera novaeangliae* mortalities were

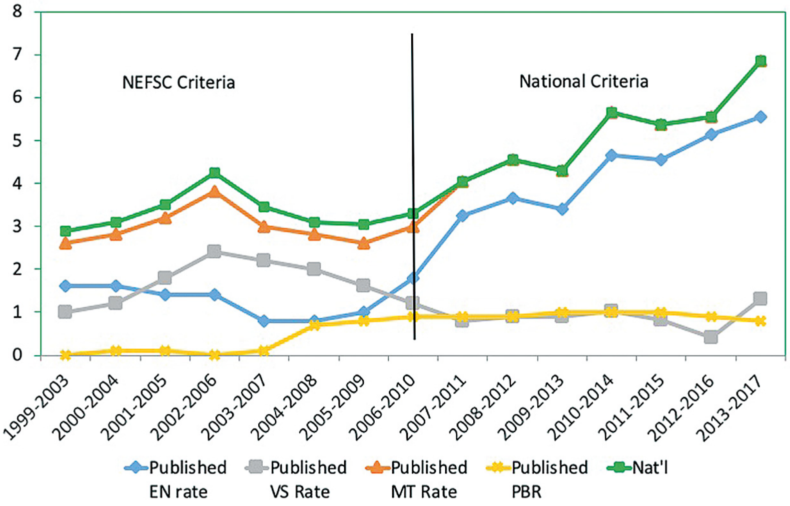


Fig. 3. Rolling 5 yr average of (USA and Canada) North Atlantic right whales (NARW) entanglement (EN), vessel strike (VS), total mortality (MT), and serious injury (SI, excluding 27 cases prevented by disentanglement), and potential biological removal (PBR). Northeast Fisheries Science Center (NEFSC) criteria were applied up to 2010. National (Nat'l) SI criteria were applied after 2010, and retroactively to earlier years, showing the minor difference between the 2 criteria

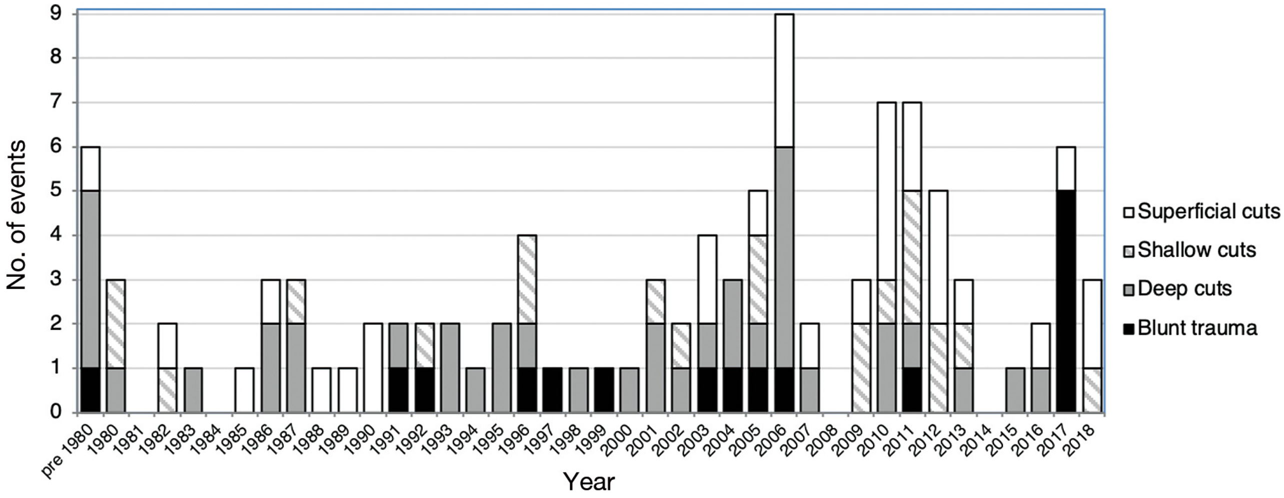


Fig. 4. Incidence of blunt trauma, and 3 degrees of severity of propeller cuts observed in 101 North Atlantic right whales. Of animals with cuts, 8 were found dead and 66 alive, but 7 of the latter were later presumed dead as a result. The 16 blunt trauma cases were all dead. Thus, a total of 29 were known or presumed dead from vessel strike (A. Knowlton et al. unpubl. data.)

reduced both inside and outside the areas (Laist et al. 2014) (Table 1). Meanwhile, van der Hoop et al. (2014) found no detectable reduction in vessel strike mortalities of all large whale species in the actual SMAs along the eastern USA, suggesting that the existing SMAs may not be large enough to provide adequate protection. Furthermore, in recent years right whales have ventured further into Canadian waters, with a shift into the Gulf of St. Lawrence, where no protection measures were in place until after at least one-third of the 12 mortalities in the region were reported as vessel strike in 2017 (Fig. 3; Daoust et al. 2018, Sharp et al. 2019). Two others of the 12 were acute entanglements, and 6 could not be diagnosed.

A recent assessment of fate by propeller wound category revealed that superficial and shallow cuts did not affect 3 yr survival, but deep cuts were lethal in the majority of cases (A. R. Knowlton & A. M. Costidis unpubl. data). A detailed, quantitative assessment of propeller cuts, carried out for 39 cases, showed that vessels >65 ft (~20 m) were involved in most of the deep cut cases, although there were 2 cases involving vessels in the 40–65 ft (12–20 m) length range that resulted in deep cuts and subsequent fatality (A. R. Knowlton & A. M. Costidis unpubl. data).

2.1.4.2. Entanglements. For entanglements, a total of 1538 interactions have been documented between 1980 and 2017 involving 86.1% (642/746) of the species; 8% (51/642) of these cases involved attached gear (Knowlton et al. 2012, A. R. Knowlton unpubl. data). Some whales have evidence of as many as 8 entanglement interactions over the course of a lifetime. Incidents of moderate and severe entanglements have become more prevalent in the last decade (Knowlton et al. 2016). These are known to cause health impacts and reduced survival, especially in reproductive females (Fauquier et al. 2020). The complexity of attached gear has also been assessed, and the majority of entanglements since the mid-1990s has been deemed high-risk, i.e. likely to be lethal without intervention, possibly because of increasing rope strengths, resulting from manufacturing changes (Knowlton et al. 2016). Based on these results, Knowlton et al. (2016) suggested maximum rope strengths of 1700 lb (~773 kg) for consideration in fixed fishing gear throughout the NARW range in order to allow more whales to break free from entanglements.

2.1.4.3. Impacts of human activities on reproductive females. An assessment of all reproductive females (i.e. females that have had a calf) since 1980 found that 42% (76/180) have either been found

Table 1. Vessel-struck North Atlantic right/ humpback whale deaths inside or within 45 nmiles (74 km) of seasonal management areas (SMA) versus those beyond 45 nmiles, before and after the SMA implementation on December 8, 2008 (Laist et al. 2014)

	Inside or <45 nmiles of SMA boundary		Beyond 45 nmiles of SMA boundary	
	Right	Humpback	Right	Humpback
1990 to Dec 8 2008	13	12	2	14
Dec 9 2008 to Dec 8 2013	0	2	2	4

dead or have disappeared, with at least one-third of those losses due to vessel strikes and entanglements. The effect of entanglement injury severity on fecundity indicates a cessation in calving for a period of time after a severe injury (van der Hoop et al. 2017a, A. R. Knowlton unpubl. data).

Both vessel strikes and entanglement continue to impact right whale reproductive success. Thus, to enable species recovery, reduction in mortalities have to be accompanied by substantial reduction of sub-lethal trauma as well.

2.1.5. Trends in growth and body condition from photogrammetry

Orthogonal aerial photogrammetry with accurate altitude data (Durban et al. 2016) can provide precise measurement of large whale length and width, enabling analysis of energy transfer during suckling (Christiansen et al. 2018). High-resolution drone images also provide information on skin condition, whale lice burdens, and the severity/incidence of entanglement wounds, notably coupled with quantitative photogrammetry measurements from the same whales.

Comparison between SRWs in Argentina, New Zealand, and Australia to NARWs in the North Atlantic revealed NARW juveniles, adults, and lactating females to be in generally poorer body condition and to be attaining shorter adult lengths than SRW (Fig. 5; Christiansen et al. 2020). Aerial photogrammetry studies to assess trends in growth and body condition of NARWs in Cape Cod Bay, MA, in March and April 2016–2020 (J. W. Durban unpubl. data) are being compared with aerial images collected by NOAA's Southwest Fisheries Science Center (SWFSC) during August 2000–2002 using manned aircraft flying over the Bay of Fundy. For both datasets, matching whales to the NARW Catalog enables body length, and width profiles, to be linked to whale age, sex, and life histories, and assessment of changes in an individual whale's condition over time. Ongoing analysis of the NARW time series (J. W. Durban unpubl. data) revealed some whales are growing more slowly in recent years compared to those growing during the 2000–2002 sampling, as inferred from reduced length at age relationships in the more recent surveys. Whales also appeared to be in poorer body condition in recent spring surveys compared to previous sampling, although the previous study took place in summer, so that change may be due to seasonal change in body condition of this capital breeder. Ongoing longitudinal monitoring during consistent spring sampling in Cape Cod Bay is being used to assess this.

2.1.6. Energetic cost of entanglement

NARW recovery is dependent on sustained reproductive success, which requires adequate body condition. Normal energy costs include metabolism, migration, foraging, and pregnancy; additional exogenous stress adds to those costs. Chronically entangled NARWs may carry fishing gear for months to years, and often show signs of considerable loss in energy reserves over that time period, as evidenced by emaciation. Drag measured from gear that was removed from entangled NARWs (van der Hoop et al. 2013, 2016) was combined with other measured parameters, allowing estimation of drag on new entanglement cases at the time of their observation (van der Hoop et al. 2017a). Drag measurements enabled estimation of the energetic cost of entanglement using biomechanics and physical models, and blubber thickness and body condition measurements (van der Hoop et al. 2017b). Impacts of entanglements persist even after disentanglement due to time needed for recovery (van der Hoop et al. 2017a). For the cases evaluated in these studies, the median energetic recovery is 1.3–3 mo (max. 16 mo).

The role of sub-lethal entanglement drag in reducing NARW health and fecundity should be a major consideration in comparing the efficacy of potential mitigation measures. Thus, while 1700 lb (~773 kg) breaking strength rope may reduce mortality and sever injury, it will continue to be a source of morbidity. Ultimately, removal of rope from the water column will better enable species recovery.

2.1.7. Acoustic trauma

Parks et al. (2007) showed that right whales call at a higher frequency, and at a lower rate, in higher noise conditions, perhaps as a response to increased background noise. This may increase communication range under such conditions (Tennessen & Parks 2016). The resultant health impacts of acoustic stressors are unclear (Rolland et al. 2012). Better understanding of the effects of background shipping and offshore wind energy production noise and episodic noise associated with seismic survey and windfarm installation are critical in terms of focused mitigation.

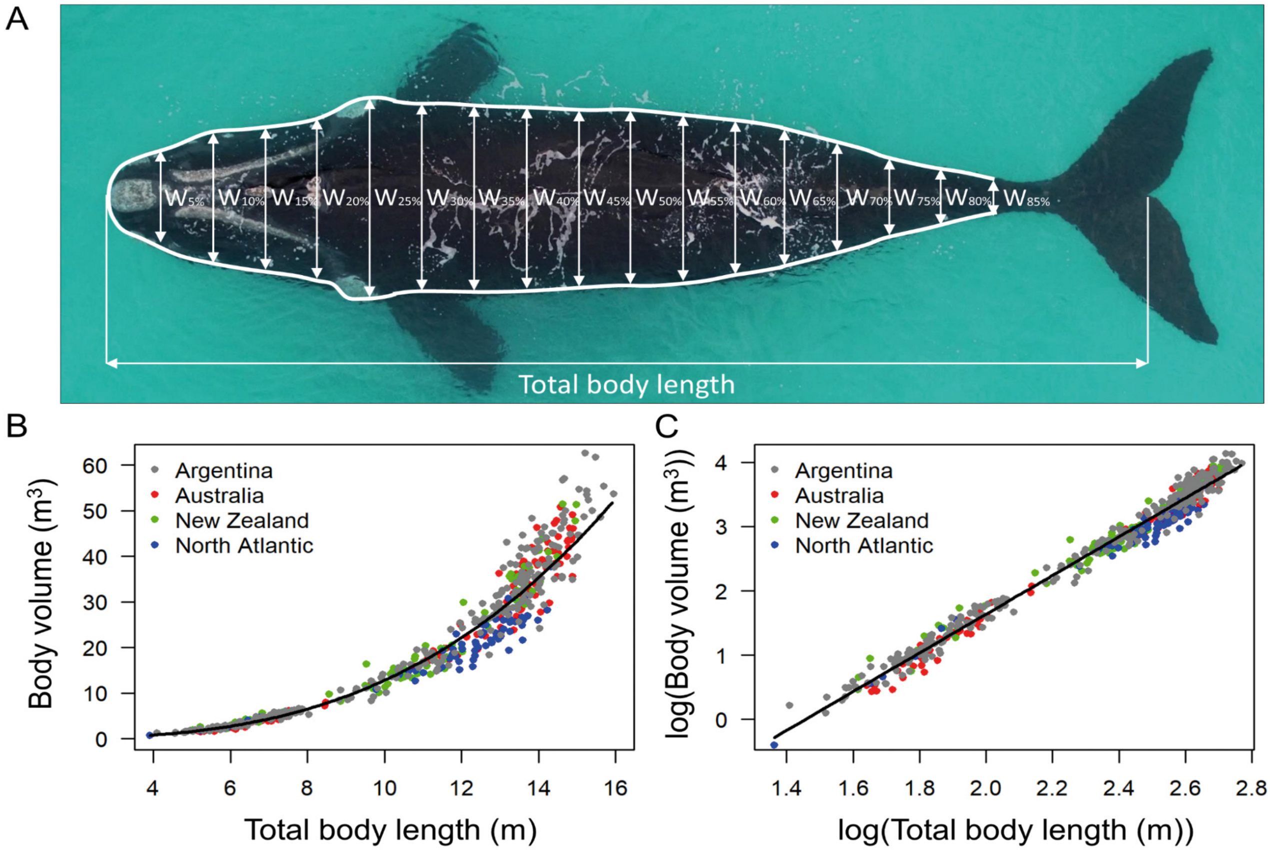


Fig. 5 . Body condition compared between southern right whales in New Zealand, Australia and Argentina, and North Atlantic right whales. Solid line represents the back-transformed fitted values of the linear model (reproduced from Christiansen et al. 2020; used by permission)

2.2. Reproduction in North Atlantic right whales

2.2.1. Reproductive success

NARW had one-third the calving success of SRW between 1992 and 2016 (Corkeron et al. 2018). Nutrition is a major determinant of reproductive success. In a study of SRW calving success in southern Brazil, significant correlations were found with krill densities, Oceanic Niño Index, and Antarctic sea ice area (Seyboth et al. 2016). Similarly, calving success in Argentina was tied to global climate signals (Leaper et al. 2006). A comparison of blubber thickness in SRW and NARW suggested that marked fluctuations in North Atlantic right whale reproduction have a nutritional component (Miller et al. 2011). However, right whale feeding success is dependent on fine-scale plankton densities that do, or do not, elicit feeding (Pershing et al. 2009). Hypotheses concerning NARW migration and foraging strategies have recently been reviewed (Kenney et al. 2020). Plourde et al. (2019) describe foraging areas for NARW in Canadian waters in the context of climate change and the documented shift in NARW distribution. However, the remoteness of most SRW feeding habitats makes access challenging; thus, direct comparisons between foraging SRW and NARW in terms of the nutritional basis for calving success have not yet been undertaken.

Between 2011 and 2018 an average of 12 NARW calves were born per year (including none born in 2018), compared to 1 of 23 per year during the previous 8 yr (Pettis et al. 2020). The calving index (annual percentage of reproductive females presumed alive and available to calve that was observed to produce a calf) averaged 47% from 2003 to 2010 but has dropped to an average of 17% since 2010.

In 2019, there were 92 known reproductively active females that had been seen alive in the previous 6 yr. In addition, there were another 36 females age 10 to 19 that had not yet been observed with a calf, and 30 immature females, suggesting the pool of future reproductive recruits is low. However, those calves born after 2010 that have not yet been cataloged are not included in this analysis, so the future female pool may be slightly larger (www.narwc.org/narwc-databases.html).

The inter-birth interval, which averaged 3.9 yr 2003–2010, increased to an average of 5.8 yr from 2011–2018, with a peak of 10.2 yr in 2017 (Pettis et al. 2020). The mean age of first parturition (Knowlton et al. 1994, Hamilton et al. 1998) for all known-age females is 10.2 yr (n = 76, range 5 to 23, SD 3.3). This analysis does not account for potential missed first calving events. The tail of the distribution includes 2 records over 19 yr of age: a first calving at 21 and 23 yr, both of which could be the result of missed calving events. However, the mean age of first parturition will likely increase in the future, as half of the known age females between 10 and 19 yr old have not yet been observed with a calf. The combination of the changes in inter-birth interval and age to first reproduction suggests that both parous and nulliparous females are experiencing delays in calving. It remains unknown how many of the current nulliparous 10 to 19 yr old females are biologically able to get pregnant and successfully reproduce. The timing of these calving delays corresponds with the recent distribution shifts described earlier, and those shifts may correlate with changing environmental conditions. Potential explanations for this reproductive cessation or delay are explored under other sections of this review, such as 2.2.2.

The low reproductive rate of NARWs is likely the result of several factors. Forty-nine females calved only once, and 53% (26/49) disappeared from the sighting record within 2 yr of that calving and very likely did not survive long enough to reproduce again. The remaining 47% (23/49) were seen 3 or more years after their first calving and thus were theoretically available to calve again. Ten percent (6/60) of females over 19 yr old have never calved. Given the age of first parturition presented above, it is unlikely these females will ever calve successfully. That percentage increases to 33.8% (46/136) if the 10 to 19 yr old nulliparous females are included, but these females may just be delaying calving and thus will likely enter the reproductive pool in the future. Another concern is evidence of low calf survival in some females. One female has been able to reproduce, but her calf survival is consistently low. She has had 6 calves, but the last 4 have not survived; at least 2 of them because they were apparently not successfully nursed (www.narwc.org/narwc-databases.html).

Other factors affecting reproductive success include changes in investment in offspring, differences in reproduction in relation to feeding habitats, and changes in NARW social interactions. Hamilton & Cooper (2010) showed that 71% (12/17) of all calves born in 2001 stayed with their mothers into the second year. They compared the fitness (age at first breeding and calving rate) of the 2001-born female calves that stayed with their mothers into the second year with those that did not and found no clear difference. In the late 1990s, some females that had a profile of being seen less frequently, which may indicate they fed in unknown habitats, continued to calve when other females stopped. All of the females that calved between 1998 and 2000 fit this profile. For the recent calving downturn, while 60% of the females in 2017 fit this profile, all of them had prolonged calving intervals equivalent to those of other females that calved during this time suggesting that, although they were calving, they were faring no better than the other females. Investigating these females that may feed elsewhere is hampered by the lack of a consistent or rigorous way to define and categorize them. Finally, the percent of sightings involved in surface-active groups appears to mirror the number of calves born (www.narwc.org/narwc-databases.html). This preliminary result could be explored by habitat to see whether the occurrence of these groups, some of which are related to mating, can be correlated with species-wide health. Reversing the trend of failed reproduction, by reducing sub-lethal trauma stands alongside reducing mortality as the 2 critical goals for enabling NARW species recovery.

2.2.2. Reproductive and stress hormones

Endocrine studies involving NARWs started in 1999 with the validation of immunoassays to measure steroid reproductive and stress hormone metabolites in fecal samples. Currently, immunoassays for a panel of 6 hormone classes including estrogen, progesterone, androgens, glucocorticoids, aldosterone, and thyroid hormones have been validated (Rolland et al. 2005, Hunt et al. 2006, Burgess et al. 2017, R. M. Rolland unpubl. data) for multiple biological matrices including the following: feces, blubber, blow (exhaled breath), and baleen (Rolland & Moore 2018). The temporal signature of hormones differs between these matrices from real-time or near-real-time (serum, blow), to days or months (feces and blubber), to years (baleen). Hormone measures from feces, and blubber integrate circulating levels of hormones over these different temporal scales and are especially valuable for assessment of chronic stress.

Over 400 fecal samples collected from 1999–2019 have been assayed for the 6 hormone classes mentioned above. Approximately one-third of the samples have been linked to identified NARWs with known life-history data. Results show that concentrations of fecal estrogens, progesterone, and androgens are reliable predictors of sex, pregnancy, and lactation in females and sexual maturity in males (Rolland et al. 2005). Three cases of pregnancy loss or undetected perinatal or young calf death have been inferred using highly elevated fecal progesterone metabolites and sighting records on the calving ground during the following winter, without a calf (R. M. Rolland unpubl. data). Levels of adrenal stress hormone metabolites vary with reproductive status, sex, and physiological state, and reflect relative adrenal cortical activity (Rolland et al. 2017). Comparison of fecal glucocorticoids (FGCs) in healthy NARWs, to those killed acutely (vessel strike), suffering long-term entanglement, or prolonged live stranding (chronic), found extreme elevations of FGCs in cases of severe, chronic illness or injury (Rolland et al. 2017). FGCs have been used to link shipping noise exposure in NARWs to elevated FGCs indicating chronic stress (Rolland et al. 2012). Fecal aldosterone levels provide an additional measure of adrenal cortical activation (Burgess et al. 2017). Fecal thyroid hormones are a biomarker of nutritional status in NARWs, as thyroid gland hormone concentrations decrease during seasonal nutritional deficits and increases during periods of energy abundance (R. M. Rolland unpubl. data).

Studies of chemical profiles in NARW baleen have shown a valuable timeline of data ranging from very recent levels at the gum line, to up to 8 yr prior at the tip (Hunt et al. 2016). In fact, baleen progesterone profiles from 2 NARWs showed elevations 2 orders of magnitude higher than baseline in time points corresponding to known pregnancies. Baleen from a chronically entangled NARW was analyzed for steroid and thyroid hormones and stable isotopes and showed an 8 yr profile of foraging and migration behavior, stress response, and reproduction, with a 23 mo progesterone peak correlating to a single known calving event and elevated triiodothyronine (T3) and thyroxine (T4), suggesting that the entanglement event began 3 mo before it was first sighted entangled (Lysiak et al. 2018). Reproductive and stress hormone studies can usefully continue to investigate the parameters impacting pregnancy and recruitment.

2.3. Biotoxins and parasites

A 6 yr (2001–2006) analysis of fecal samples collected in the Bay of Fundy showed that some NARWs were exposed to at least 2 classes of algal biotoxins: paralytic shellfish poisoning toxins (PSP), primarily saxitoxins and amnesiac shellfish poisoning, and domoic acid (DA) (Doucette et al. 2012). In this study, 73% (96/132) of samples tested positive for PSP toxins and 25% (31/126) tested positive for DA. Both biotoxins were also detected in a small number of fecal samples collected in Cape Cod Bay, the Great South Channel and Roseway Basin. The results of this study suggest that NARWs are exposed to both algal biotoxins on an approximately annual basis in multiple habitats for periods of up to 6 mo (April through September). There were similar exposure rates for females and males (PSP: ~70–80%; DA: ~25–30%). Both pregnant and lactating females were exposed to both biotoxins, suggesting the potential for maternal toxin transfer and possible effects on fetal and suckling animals. Additionally, 22% of the fecal samples tested for PSP and DA showed concurrent exposure to both neurotoxins, leading to questions of interactive effects (Doucette et al. 2012). While exposure to these biotoxins was not significantly linked with observed health effects in NARWs (and their sensitivity to these toxins remains unknown), there is a potential for indirect effects (e.g. increased susceptibility to anthropogenic risks: Doucette et al. 2012 discuss possible effects of PSP on whales: neurotoxic effects impacting organ function, diving reflex and effects of DA on reproduction — based on California sea lion research) that will likely never be measurable. These data provide baseline levels of these 2 biotoxins for comparison to exposure levels in the future. A study of the possible role of biotoxins in the calf mortality event in Peninsula Valdés, Argentina, found a relationship between *Pseudo-nitzschia* spp. densities (but not *Alexandrium tamarense*) and calf deaths (Wilson et al. 2016).

A 5 yr study (2002–2006) assessed the prevalence of *Giardia* and *Cryptosporidium* spp. using analysis of fecal samples (Hughes-Hanks et al. 2005, Rolland et al. 2007, R. M. Rolland unpubl. data). Fecal samples were examined for the presence of cysts/oocysts using an immunofluorescent assay procedure. The overall annual prevalence of *Giardia* was 68% (78/115) (range = 38–77%), *Cryptosporidium* oocysts were detected in 14% (16/115) of samples (range = 7–38%), and all *Cryptosporidium* positive samples were co-infected with *Giardia*. Molecular characterization and phylogenetic analysis of the NARW isolates were unsuccessful, so species and genotypes remain unknown. While the effects of these organisms on NARWs are generally unknown, co-infection with both *Giardia* and *Cryptosporidium* was found to be associated with a decline in body condition using a visual assessment method (R. M. Rolland unpubl. data).

Thus, SRW and NARW are clearly exposed to a variety of biotoxins and parasites, but their role in health determination remain unclear. Comparative biotoxin studies between SRW and NARW could be of value.

2.4. Modeling

2.4.1. Survival assessments and trends with emphasis on reproductive females

Mathematical modeling can be used to link the intermittent spatially referenced observations of individual NARWs and their visual health measurements to estimates of their movement between regions, underlying health, and survival. Such a model, based on a hierarchical Bayesian state-space modeling framework, was constructed using monthly time steps and 9 geographic regions and fitted to over 30 yr of sightings data (Schick et al. 2013, Rolland et al. 2016, Schick et al. 2016). An investigation found negative health impacts in NARWs entangled in gear. Individual's health declined between the date seen without injuries and the first date of entanglement detection, and the overall average health continued to decline for those whales with attached gear. Results were further parsed by entanglement severity and category, by presence/absence of gear, by sex, and, for females, by reproductive class (A. R. Knowlton unpubl. data). These declines in health were greater among whales categorized as having severe entanglements, both with and without gear present. The average health score during entangled periods was poorer for reproductively active females, with declines in health translating to lower reproductive output. Survival analysis as a function of sex and entanglement severity showed that severe injuries resulted in steep declines in individual survival, with the decline in survival being greater for females than for males.

The above model was built and fit to data (as well as incorporating expert opinion) pre-2011, before the documented shift in distribution; the model is currently being altered to account for the changing movement patterns and VHA data. The spatial portion of the model needs to be updated to accurately depict recent movement patterns into previously understudied regions, as well as to account for the changing VHA data collection platforms. The sightings model from (Schick et al. 2013) is (1) individual specific, but not time varying, and (2) indexed to survey effort in different regions. This component of the model needs to be updated in order to better account for recent changes in effort, and distribution.

2.4.2. Population models and assessment tool

A NARW population evaluation tool is under development, with objectives that include prospective estimates of extinction risk and other demographic characterizations over various time scales. The model will consist of a baseline scenario projection and a quantitative threat assessment to examine the effects of modifying projected threat influences on demographic processes (i.e. scenarios modified from baseline). Although the lethal impacts of threats are relatively straightforward to include in a population viability model, the non-lethal influence of entanglement wounding, vessel-collision wounding, anthropogenic noise, changes in prey distribution and quality, and contaminants on body condition, growth, reproduction and survival are more difficult to parameterize. Model projections that include influences of all threats are required, even while the functional relationships between threat and health outcomes are not well-known. The more these relationships can be bounded by expert opinion, the less uncertainty will be transferred into population projections.

Modeling survival and population assessment are important activities to inform managers of NARW status and trends. Further understanding of the interactions of multiple stressors and their impacts on mortality and morbidity will enhance ongoing management.

2.5. Emerging tools

2.5.1. Baleen whale microbiomes as potential indicators of health

In humans, microbiotas (assemblages of microorganisms) are linked to many aspects of health, such as body condition, digestion and nutrition, immune function, inflammation, and behavior (Ley 2010, Cho & Blaser 2012, Ezenwa et al. 2012, McFall-Ngai et al. 2013). Although microbiotas of marine mammals are not as well studied as those of humans, there is evidence of highly diverse skin, respiratory, gut and oral microbiomes that vary with host phylogeny, diet, habitat, and health (Apprill et al. 2014, 2020, Nelson et al. 2015, Sanders et al. 2015, Bik et al. 2016). Little is known about the microbiotas of right whales, but results from studies on the skin, blow, and gut microbiotas of other baleen whale species support a framework for using the microbiotas of these sample types to monitor baleen whale health, including that of right whales.

Blow and skin microbiotas of humpback whales from different geographical locations have been investigated by a few studies using high-throughput sequencing of the V4 region of the small subunit ribosomal RNA (16S rRNA) gene. In one study evaluating blow collected from seemingly healthy humpback whales (Apprill et al. 2017), 25 bacteria were found to be common to all samples — one of the most extensive core microbiotas found in any mammal to date. Similar results and sequences were also recovered in blow collected from southern hemisphere humpback whales (Pirotta et al. 2017). Apprill et al. (2017) also detected numerous genus-level relatives of mammalian pathogenic bacteria. Because the whales appeared healthy, these pathogen relatives likely were not acting as pathogens at the time, but such screening methods could be used to quickly identify samples that need to be examined for pathogens with finer resolution methods. Similar to the trends for core bacteria in the blow samples, 2 skin-associated bacterial taxa were common to seemingly healthy humpback whales from different oceans (Apprill et al. 2014, Bierlich et al. 2018), where abundances appeared to be affected by environmental conditions (Bierlich et al. 2018). Additionally, altered skin microbiotas were observed in a handful of humpback whales with compromised health (stranded, entangled) (Apprill et al. 2011, 2014). Taken together, these results suggest that screening for changes to the signatures of the skin and blow microbiotas, i.e. the presence of non-typical microbes, potential pathogens, and changes to the diversity of the overall microbiotas and/or the composition and abundance of core bacteria, could be used to monitor health of baleen whales (Apprill et al. 2011, 2014, 2017), including right whales.

To date, samples of blow (n = 120) have been collected from NARW and SRW (Argentina, and Auckland Islands, New Zealand) (C. A. Miller et al. unpubl. data). The microbiotas from these blow samples will be explored in the context of body condition measurements, life history traits, and other indices of health. They will also be screened at the genus level for relatives of pathogens and likely will be sequenced deeper to examine the function of the microbes, viruses, and genes involved in virulence. Given the conspicuous differences in body condition between NARW and SRW (Miller et al. 2011, Christiansen et al. 2020), the comparison of the blow-associated microbiotas between these populations has the potential to reveal information about right whale health, in addition to their different habitats and diets.

The gut microbiotas of mammals play an important role in digestion, nutrition, and health. Right whales depend on a diet rich in the high-energy lipids for achieving and sustaining the body fat reserves necessary for reproduction and survival, but little is known about how they digest these lipids because fresh samples of gut contents from right whales are rare. Native Alaskans harvest bowhead *Balaena mysticetus* whales for subsistence, and in the past, have generously allowed limited access to harvested whales for scientific purposes. Bowhead whales are a close taxonomic relative of right whales and consume prey rich in the same high-energy lipids. Hence, studies of lipid digestion and microbiotas in bowhead whales could provide important information for understanding right whale nutrition. In harvested bowhead whales, lipid digestion and microbial communities were mapped along the gastrointestinal tract (GI, forestomach through colon) by characterizing the lipid compositions (lipidomes) using HPLC-MS/MS and the microbiotas using high-throughput sequencing of the V4 region of the 16S rRNA gene (Miller et al. 2020). The lipidomes and microbiotas were tightly correlated as their compositions changed throughout the GI tract, with lipidomes and microbiotas being variable in the small intestine (the area of lipid digestion in mammals). The results suggested that wax esters, the primary prey lipids that are also prominent in right whale prey, were digested in the mid to distal small intestine and that specific bacteria appeared to play a role in their digestion. Despite differences in analytical methods, the bowhead whale gut microbiotas consisted of bacteria from many of the same phyla as Sanders et al. (2015) found in fecal samples from 7 right whales, but direct comparisons of lower level taxonomy are needed. However, because of the similarity in the diets and GI tract anatomy of right and bowhead whales and because they are phylogenetically closely related, these data from (Miller et al. 2020) may provide a model for right whale gut microbiome and lipid digestion, thereby potentially adding to the understanding of right whale nutrition, body condition and overall health.

Additionally, recent analysis of how host phylogeny and life history stage modify the gut microbiome in dwarf *Kogia sima* and pygmy *Kogia breviceps* sperm whales (Erwin et al. 2017, Denison et al. 2020) may also have relevance to study of right whale health.

Overall, skin, blow and gut-associated microbiomes show potential for usefulness in monitoring health of baleen whales — especially blow, which can be collected non-invasively. Paired gut microbiome and lipidome studies have the potential to provide insights into nutrition and body condition and may be useful for evaluating the mechanisms involved in balaenid whale nutrition. Many laboratories are now implementing portable sequencing techniques that could be used to rapidly screen for, and identify, altered microbiomes in field settings (Hu et al. 2018, 2019). This technology has the potential to provide diagnostic-type details about how baleen whale microbiomes change due to animal health and environmental or ecosystem-related alterations.

2.5.2. Small cetacean health assessments

Recent advances in small cetacean health assessments are important to review when considering new approaches for evaluating NARW health. In particular, the *Deepwater Horizon* (DWH) oil spill provided a major opportunity to develop a new synthesis of wild dolphin health assessment tools to better understand the response to a major stressor (Fauquier et al. 2020). These tools allowed for the diagnosis of reproductive failure, lung injury, impaired stress response, and poor body condition in common bottlenose dolphins *Tursiops truncatus* in the aftermath of the DWH disaster (Schwacke et al. 2014, Lane et al. 2015, Kellar et al. 2017, Smith et al. 2017). Although many of the tools utilized in small cetacean exams would need to be substantially modified for large whales, their potential application to NARW health assessment should be considered (Schwacke et al. 2014, NOAA 2015, Venn-Watson et al. 2015, Smith et al. 2017, Fauquier et al. 2020).

2.5.3. Predicting *Tursiops* survival and reproduction from health assessment data

An expert system developed for predicting survival and reproduction in dolphins based on health assessments could inform approaches for linking current NARW health measures to demography and suggest efficacious future measurements (L. Thomas pers. obs.). The 'Veterinary Expert System for Outcome Prediction' (VESOP) model in dolphins uses statistical models linking measurements of wild bottlenose dolphin health made during hands-on sampling of inshore dolphins with 2-yr-ahead survival and successful reproduction for pregnant females observed by follow-up surveys. Data from 8 populations were included. The numerous measurements of blood and other parameters taken during health assessments have been organized into panels of organ status or specified disease condition to identify abnormal cases for each panel using previously established reference ranges. One future component of the project is to assess how the models and methods developed may be applied to other species for which such comprehensive hands-on health assessments are not available. In particular, if a remote blood sampling device could be developed for large whales, this approach would substantially enhance our understanding of right whale health.

3. DISCUSSION

3.1. NARW health threats

Understanding NARW health has resulted from decades of research throughout the primary range of this species from Florida to Canada. The sharing and analysis of photographs, samples, and data from both live NARWs and carcasses, has been undertaken by a growing, evolving and integrated community of conservation biologists, modelers, and veterinarians. There is a collaborative ethic, in large part driven by the NARWC being focused on recovery of this endangered species. There is a strong level of collaboration between the USA and Canada at the federal, research and non-governmental organizational levels.

There is a substantial body of information that points to a major impact of lethal and sub-lethal anthropogenic trauma and stressors. However, establishing clear cause and effect linkages can be challenging, especially for the sublethal impacts given that multi-factorial processes are involved.

The key identified species-level concerns are low fecundity resulting in extended inter-birth intervals for some females, and others never calving at all, and poor survival (especially females) from high mortality and chronic morbidity. Together, these are the symptoms of the species downward trajectory. These species-level findings are in stark contrast to the high fecundity and good survival of SRWs. Although SRWs were similarly harvested down to a few hundred animals, in the post-whaling era, the relative lack of anthropogenic threats has allowed the SRW to rebound dramatically. Critical for NARWs is that they are exposed to substantially greater human activity than SRW, given that 90 % of the human species lives north of the equator (W. Rankin, The World's Population in 2000, by Latitude; www.radicalcartography.net/index.html?histpop). This is the fundamental basis for far greater risk of anthropogenic trauma to NARWs.

The primary known stressors for NARWs include food quantity and quality, entanglement, vessel strike, and noise. Climate change-driven distribution shifts of food, followed by the change in distribution of NARWs (Record et al. 2019) have complicated efforts to monitor and manage NARW health by decreasing the ability to document individuals on an annual basis. This requires management measures that are flexible and effective in the face of changing distributions and the uncertainty predicted by climate change. Of these stressors, vessel trauma and entanglement are potentially the most tractable to reduce, in terms of beneficial management actions. Vessel noise is also a serious concern. Fig. 6 summarizes stressors and tools that are important for NARW health studies.

This review identified that the primary tools for assessing individual health include visual health indicators, body condition (an integrated energetic index), presence of vessel strike and entanglement wounds and scars, and detection of biota (biotoxins, parasites, and most recently, microbiome status). Stress hormones sampled from blow, blubber and feces provide excellent shorter-term indicators of stress. The above tools are primarily collected using boat-based methods. Baleen samples collected at necropsy have provided data on health and nutrition over up to the last 8 yr of an animal's life.

Given the precarious status of the species, the primary roles of existing and potential new health assessment tools are (1) evaluation of the efficacy of management changes designed to enhance species recovery; (2) expansion of our understanding of NARW health and reproductive success; and (3) increased perspective of the relative significance and trends of anthropogenic versus food limitation/other impacts on population health. Central to these goals are models designed to recognize important stressors, responses to them, and to management changes. Table 2 summarizes the available tools for NARW health assessment in the context of each major stressor and their use in assessment of their health and efficacy of mitigation efforts. New and recent tools (Section 2.5 above) may include adaptions for NARW assessments based on those used in the evaluation of the impacts of the DWH spill on small odontocetes (e.g. photo identification, diagnostic pathology and modeling), further development of microbiome studies, possible systems to collect blood samples from large whales at sea, and infra-red thermography from vessels and manned or unmanned aircraft. In

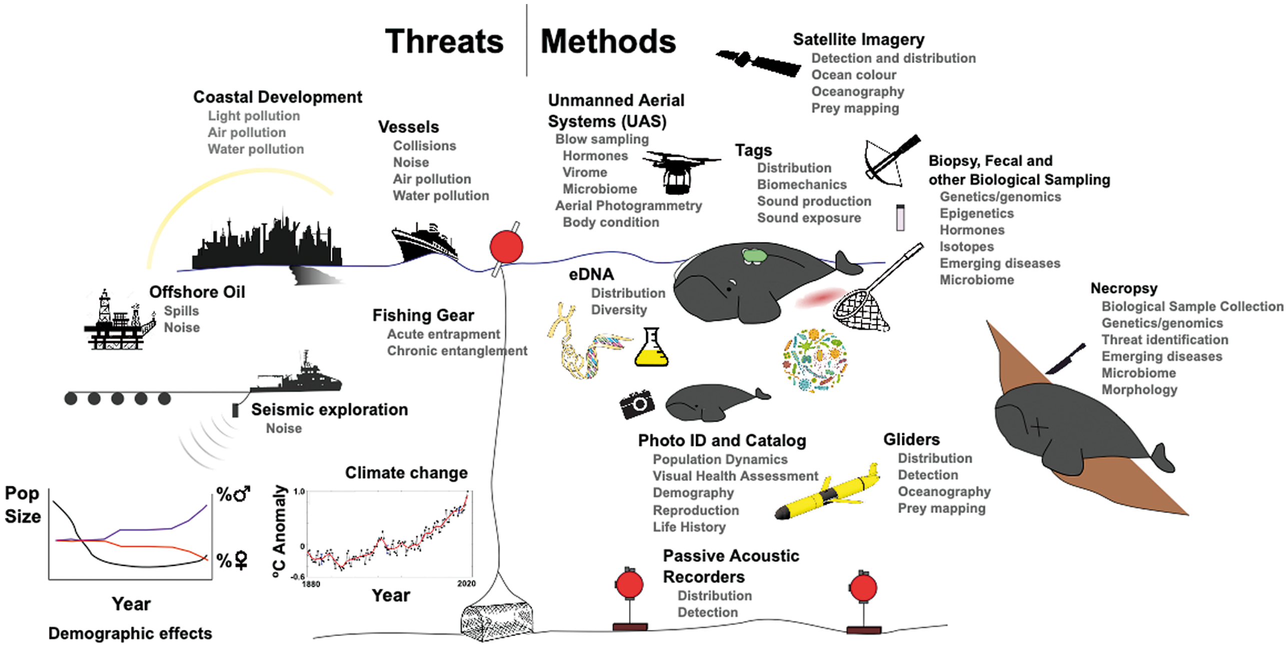


Fig. 6. Summary of the threats facing North Atlantic right whales, and current and potential health assessment methods. Fig. 3 modified from Harcourt et al (2019), with permission from the artist, Julie van der Hoop

light of the above review, we recommend implementing the following critical measures. Recommendations from the review are collated in Table 3.

Table 2. Application of health assessment tools. COD: cause of death; VHA: visual health assessment; PCOD: population consequences of disturbance

Stressor	How to measure occurrence	How to assess health impacts	How to assess efficacy of mitigation
Vessel strikes	Visual surveillance of living whales	VHA, photogrammetry, microbiome, hormones	High capture rate of living species; reduction in observed external injuries; improved VHA health scores; improved calving rates
	Cryptic mortality	Model to calculate estimate of takes	Reduction in estimate of annual takes
	Carcass detection and diagnosis	Necropsy	Reduction in carcass detections and COD of vessel strike
Entanglements	Visual surveillance of living whales	VHA, photogrammetry, microbiome, hormones	High capture rate of living species; reduction in observed external injuries
	Scarring analyses	PCOD; frequency of injury severity levels	Reduction in whales with attached gear; reduction in moderate and severe injuries
	Cryptic mortality.	Model to calculate estimate of takes	Reduction in estimate of annual takes
	Carcass detection and diagnosis	Necropsy	Reduction in carcass detections and COD of entanglement
Food limitation	Visual surveillance of living whales	VHA, Photogrammetry	Not manageable in relevant timescale
Ocean noise	Passive acoustic monitoring	Stress hormones	Change in ambient and episodic noise
	Sampling of live whales		
Harmful biota & pollution	Sampling of live or dead whales or prey species	Sample collection: food, blow, feces, blubber	Change in levels of observed effects: immune function, microbiome change, disease

3.2. Population

(1) Increased shipboard surveys in the recently recognized important NARW habitats are needed to improve our ability to track changes in species status, health, and entanglement or vessel strike wounding/scarring, as well as to collect biological samples.

(2) Survey efforts need to be flexible to detect future habitat shifts, and survey areas need to be updated. Satellite detection techniques should be employed in this regard as they mature (Bamford et al. 2020) to find new aggregations as possible.

(3) Increased aerial and vessel photographic capture of a larger portion of the species annually is necessary to track individual health and overall species health, as well as allow for continued modeling of vital rates.

(4) Further comparisons between SRW and NARW populations and individuals would potentially add understanding for the failure of the NARW recovery post-whaling.

3.3. Individual

(1) Consistent long-term collection of well-calibrated photogrammetric data are needed to provide essential perspectives on changing body condition and growth rates.

(2) Further investigations are needed to detect pregnancy, pregnancy loss, and perinatal loss in the reproductively viable female population. This will inform why fecundity rates are low, and to develop potential remediation actions. Specifically, further investigation is needed to identify the causes for the observed nulliparous females that are old enough to be sexually mature but have not calved.

(3) Increased effort to collect appropriate samples (e.g. biopsy, feces, blow) from adult females without a calf present are needed to allow assessment of pregnancy, pregnancy loss, and resting status through hormonal testing. Exploration into the stage of gestation during which pregnancy loss occurs could potentially be captured through this investigation and be instrumental in the identification of potential stressors that are inducing pregnancy loss.

Table 3. Summary of information needs and management actions

Section	Information needs
1	Increase the proportion of North Atlantic right whales (NARW) sighted annually, by expanding effort in current high use habitats such as mid-Atlantic, southern New England, and the Gulf of St Lawrence
2.1	Further compare the demographics of Southern right whales and NARW
2.1.1	Diagnostic beach necropsies, and assessment of carcasses at sea as practical
2.1.2	Current Visual Health Assessment of the entire photograph catalog of NARW to qualitatively assess the status and trends of NARW health
2.1.3	Method to categorize chronically traumatized whales to better prognosticate
2.1.4.1	Quantify live animal vessel strike trauma
2.1.4.2	Quantify live animal entanglement trauma
2.1.5	Quantitative assessment of body length and condition changes through time
2.1.6	Establish energetic models involving prey, rope drag, and other sub-lethal trauma to better understand reproductive failure
2.1.7	Acute and chronic effects of background and episodic noise trauma
2.2.1	Assessment of relationship of sub-lethal trauma to reproductive success
2.2.1	SRW vs. NARW foraging dynamics
2.2.1	Surface active group prevalence vs. calving rate by habitat
2.2.2	Endocrine basis of pregnancy and recruitment success, and stress response
2.3	Comparison of biotoxin exposure and effects in SRW and NARW
2.3	*Giardia* and *Cryptosporidium* vs. decline in body condition, including genotyping and tracking origin of infections
2.4	Survival, demographic and multiple stressor models
2.5.1	Microbiomes in the context of health and disease
2.5.3	Develop a large whale blood sampling tool
Section	**Management actions for conservation merit**
2.1.1	Use diagnostic necropsy data to evaluate effectiveness of NARW trauma mitigation strategies
2.1.4.1	Substantially reduce large vessel propeller trauma
2.1.4.2	Consider maximum rope strength of 1700 lb (~773 kg) throughout NARW range
2.1.4.3	Minimize sub-lethal vessel and entanglement trauma
2.1.6	Removal of rope from the water column to reduce trauma and energy loss in sub-lethal entanglements
2.1.7	Reduce background and episodic noise
2.2.1	Minimize sub-lethal and lethal trauma to enable NARW recovery

(4) Analysis of fecal, blow, and biopsy samples for microbiome and other biota are needed to enhance our understanding of overall health in this species.

(5) Greater capacity to retrieve and examine floating carcasses from substantial offshore distances to enhance evaluation of mitigation efforts.

3.4. Modeling

(1) An assessment of the interaction of multiple stressors in each major habitat is needed to enable more spatially precise management measures and to improve modeling efforts to determine how broad scale management measures may influence health and reproduction (Fig. 7).

(2) Population consequence of multiple stressor (PCOMS) and other models are needed to test the conservation and species recovery benefit of undertaking specific health assessment options.

3.5. Management

(1) Shifting mortality locations indicate the need for effective broad-scale management measures that allow healthy female NARWs to forage, conceive, deliver, and wean calves.

(2) Management needs are summarized in Table 3.

4. CONCLUSIONS

In contrast to SRW, the NARW species has failed to maintain a positive trajectory towards recovery from the impacts of historic whaling. The reasons for this are complex but center on the far greater pressure from human activities in the northern versus southern hemispheres.

The major known anthropogenic sources of lethal and sublethal NARW trauma are from collisions with vessels and fishing gear entanglement. These have

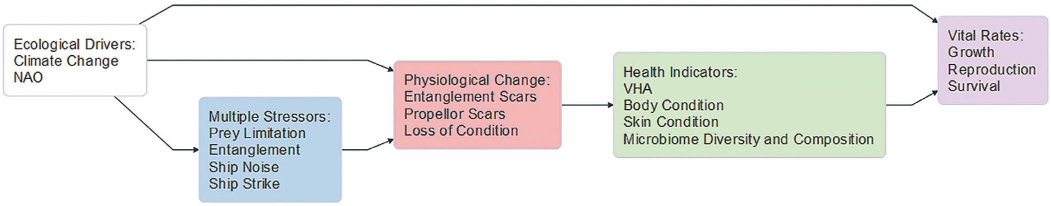


Fig. 7. Population consequence of multiple stressors conceptual model for North Atlantic right whales that links multiple stressors (blue box) to changes in physiology, trauma and condition (red box) that are detected from retrospective and drone-based studies (green box). All of these, as well as background environmental signals of climate change and the North Atlantic Oscillation (NAO), link to changes in growth (measured by drone photogrammetry), reproduction and survival (purple box). VHA: visual health assessment

increased in recent decades. Vessels have got larger and faster, increasing the lethality and frequency of collisions. Fishing gear strength has increased, with resultant increased morbidity and mortality from entanglement.

The already poor fecundity and survival of NARWs has devolved into a recent decline. The species peaked at 500 individuals in 2010. The best estimate for 2019 is approximately 360 animals.

Climate-driven changes in NARW habitat features (biological, physical, chemical) resulting in changes in migration and foraging patterns that have correlated with a further reduction in already poor reproductive success. Extreme recent warming of the Gulf of Maine, a major feeding habitat, has led to an increase in the use of the Gulf of St Lawrence, when ice free.

The interaction of sub-lethal stressors such as decreased energy intake and entanglement trauma must be better quantified in order to identify critical management strategies to enhance NARW body condition and reproductive success. While foraging success is the most critical determinant of health, little can be done to enhance it, whereas anthropogenic trauma is also a major factor and is avoidable, given adequate and effective management changes.

Tools critical to assessing the efficacy of measures to mitigate failed recovery include visual surveys, photo-ID catalog-based species analyses, annual scarring assessments, visual and photogrammetric health assessments, and necropsies. These efforts are ongoing but need to be continually optimized as environmental changes drive shifts in NARW distribution and behavior.

Investigation of individual health, analyzing blow, blubber, fecal, and other samples in addition to conducting complete necropsy examinations is critical to better understanding the health, reproductive status, and disease states of the NARW population. While we understand the fundamental role of trauma in NARW status, a more nuanced understanding of other aspects of their health would be hugely valuable.

Modeling is critical to our understanding of the status and trends of NARW health, and in particular for understanding the interactions of multiple stressors on both individuals and the species as a whole. Given the fragmented and changing nature of routine sighting and health assessment opportunities, models are critical to translate available data into best estimates of NARW status and trends.

Acknowledgements. This review summarizes material presented and discussed at a workshop on North Atlantic Right Whale Health Assessment, June 24–26, 2019, Silver Spring MD, USA (Fauquier et al. 2020). We thank all the participants of the workshop for their contributions. NA14OAR4320158 funded the drafting of this manuscript. We sincerely thank 3 anonymous reviewers for their constructive comments. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the authors and do not necessarily reflect the views of NOAA.

LITERATURE CITED

Apprill A, Mooney TA, Lyman E, Stimpert AK, Rappé MS (2011) Humpback whales harbour a combination of specific and variable skin bacteria. Environ Microbiol Rep 3: 223–232

Apprill A, Robbins J, Eren AM, Pack AA and others (2014) Humpback whale populations share a core skin bacterial community: Towards a health index for marine mammals? PLOS ONE 9:e90785

Apprill A, Miller C, Moore M, Durban J, Fearnbach H, Barrett-Lennard L (2017) Extensive core microbiome in drone-captured whale blow supports a framework for health monitoring. mSystems 2:e00119-e17

Apprill A, Miller CA, Van Cise AM, U'Ren JM, Leslie MS, Weber L and others (2020) Marine mammal skin microbiotas are influenced by host phylogeny. R Soc Open Sci 7:192046

Bamford CCG, Kelly N, Dalla Rosa L, Cade DE and others (2020) A comparison of baleen whale density estimates derived from overlapping satellite imagery and a shipborne survey. Sci Rep 10:12985

Best PB, Bannister JL, Brownell RL, Donovan GP (eds) (2001) Right whales: worldwide status. J Cetacean Res Manag Spec Issue 2:1–309

Bierlich KC, Miller C, DeForce E, Friedlaender AS, Johnston DW, Apprill A (2018) Temporal and regional variability in the skin microbiome of humpback whales along the Western Antarctic Peninsula. Appl Environ Microbiol 84: e02574-17

Bik EM, Costello EK, Switzer AD, Callahan BJ and others (2016) Marine mammals harbor unique microbiotas shaped by and yet distinct from the sea. Nat Commun 7: 10516

Bourque L, Wimmer T, Lair S, Jones M, Daoust PY (2020) Incident report: North Atlantic right whale mortality event in eastern Canada, 2019. Collaborative report produced by: Canadian Wildlife Health Cooperative and Marine Animal Response Society. http://cwhc-rcsf.ca/docs/2019%20NARW%20incident%20report_June%202020.pdf

Brownell R, Best P, Prescott J (1986) Right whales: past and present status. Rep Int Whal Comm Spec Issue 10: 1–289

Burgess EA, Hunt KE, Kraus SD, Rolland RM (2017) Adrenal responses of large whales: integrating fecal aldosterone as a complementary biomarker to glucocorticoids. Gen Comp Endocrinol 252:103–110

Cho I, Blaser MJ (2012) The human microbiome: at the interface of health and disease. Nat Rev Genet 13:260–270

Christiansen F, Vivier F, Charlton C, Ward R, Amerson A, Burnell S, Bejder L (2018) Maternal body size and condition determine calf growth rates in southern right whales. Mar Ecol Prog Ser 592:267–281

Christiansen F, Dawson SM, Durban JW, Fearnbach H and others (2020) Population comparison of right whale body condition reveals poor state of the North Atlantic right whale. Mar Ecol Prog Ser 640:1–16

Cooke JG (2020) *Eubalaena glacialis*. The IUCN Red List of Threatened Species 2020: e.T41712A162001243 (accessed 09 July 2020). www.iucnredlist.org/species/41712/162001243

Corkeron P, Hamilton P, Bannister J, Best P and others (2018) The recovery of North Atlantic right whales, *Eubalaena glacialis*, has been constrained by human-caused mortality. R Soc Open Sci 5:180892

Daoust PY, Coutoure E, Wimmer T, Bourque L (2018) Incident report: North Atlantic right whale mortality event in the Gulf of St. Lawrence, 2017. Collaborative report produced by Canadian Wildlife Health Cooperative, Marine Animal Response Society, and Fisheries and Oceans Canada. www.cwhc-rcsf.ca/docs/technical_reports/NARW_Incident_Report-%2020180405%20MD.pdf

Davies KTA, Brown MW, Hamilton PK, Knowlton AR, Taggart CT, Vanderlaan ASM (2019) Variation in North Atlantic right whale *Eubalaena glacialis* occurrence in the Bay of Fundy, Canada, over three decades. Endang Species Res 39:159–171

Davis GE, Baumgartner MF, Bonnell JM, Bell J and others (2017) Long-term passive acoustic recordings track the changing distribution of North Atlantic right whales (*Eubalaena glacialis*) from 2004 to 2014. Sci Rep 7: 13460

Denison ER, Rhodes RG, McLellan WA, Pabst DA, Erwin PM (2020) Host phylogeny and life history stage shape the gut microbiome in dwarf (*Kogia sima*) and pygmy (*Kogia breviceps*) sperm whales. Sci Rep10:15162

Doucette GJ, Mikulski CM, King KL, Roth PB and others (2012) Endangered North Atlantic right whales (*Eubalaena glacialis*) experience repeated, concurrent exposure to multiple environmental neurotoxins produced by marine algae. Environ Res 112:67–76

Durban JW, Moore MJ, Chiang G, Hickmott LS and others (2016) Photogrammetry of blue whales with an unmanned hexacopter. Mar Mamm Sci 32:1510–1515

Erwin PM, Rhodes RG, Kiser KB, Keenan-Bateman TF, McLellan WA, Pabst DA (2017) High diversity and unique composition of gut microbiomes in pygmy (*Kogia breviceps*) and dwarf (*K. sima*) sperm whales. Sci Rep 7:7205

Ezenwa VO, Gerardo NM, Inouye DW, Medina M, Xavier JB (2012) Animal behavior and the microbiome. Science 338:198–199

Fauquier D, Long K, Biedron I, Wilkin S and others (2020) Report of the Health Assessment Workshop for North Atlantic Right Whales (*Eubalaena glacialis*), June 24–26, 2019. NOAA Tech Memo NMFS-F/OPR-65. https://repository.library.noaa.gov/view/noaa/27432

Gowan TA, Ortega-Ortiz JG, Hostetler JA, Hamilton PK and others (2019) Temporal and demographic variation in partial migration of the North Atlantic right whale. Sci Rep 9:353

Hamilton PK, Cooper LA (2010) Changes in North Atlantic right whale (*Eubalaena glacialis*) cow–calf association times and use of the calving ground: 1993–2005. Mar Mamm Sci 26:896–916

Hamilton PK, Marx MK (2005) Skin lesions on North Atlantic right whales: categories, prevalence and change in occurrence in the 1990s. Dis Aquat Org 68:71–82

Hamilton PK, Knowlton AR, Marx MK, Kraus SD (1998) Age structure and longevity in North Atlantic right whales *Eubalaena glacialis* and their relation to reproduction. Mar Ecol Prog Ser 171:285–292

Hamilton P, Knowlton A, Marx M (2007) Right whales tell their own stories: the photo-identification catalog. In: Kraus S, Rolland R (eds) The urban whale: North Atlantic right whales at the crossroads. Harvard University Press, Cambridge, MA, p 75–104

Harcourt R, van der Hoop J, Kraus S, Carroll EL (2019) Future directions in *Eubalaena* spp.: comparative research to inform conservation. Front Mar Sci 5:530

Hlista BL, Sosik HM, Martin Traykovski LV, Kenney RD, Moore MJ (2009) Seasonal and inter-annual correlations between right-whale distribution and calving success and chlorophyll concentrations in the Gulf of Maine, USA. Mar Ecol Prog Ser 394:289–302

Hu YO, Ndegwa N, Alneberg J, Johansson S and others (2018) Stationary and portable sequencing-based approaches for tracing wastewater contamination in urban stormwater systems. Sci Rep 8:11907

Hu Y, Green GS, Milgate AW, Stone EA, Rathjen JP, Schwessinger B (2019) Pathogen detection and microbiome analysis of infected wheat using a portable DNA sequencer. Phytobiomes J 3:92–101

Hughes-Hanks JM, Rickard LG, Panuska C, Saucier JR, O'Hara TM, Dehn L, Rolland RM (2005) Prevalence of *Cryptosporidium* spp. and *Giardia* spp. in five marine mammal species. J Parasitol 91:1225–1228

Hunt KE, Rolland RA, Kraus SD, Wasser SK (2006) Analysis of fecal glucocorticoids in the North Atlantic right whale (*Eubalaena glacialis*). Gen Comp Endocrinol 148: 260–272

Hunt KE, Lysiak NS, Moore MJ, Rolland RM (2016) Longitudinal progesterone profiles in baleen from female North Atlantic right whales (*Eubalaena glacialis*) match known calving history. Conserv Physiol 4:cow014

International Whaling Commission (2010) Report of the Southern Right Whale Die-Off Workshop 15–18 March 2010, Centro Nacional Patagónico, Puerto Madryn, Argentina SC/62/Rep1

International Whaling Commission (2013) Report of the Southern Right Whale die-off workshop. J Cetacean Res Manag 12: 367–398

Jackson JA, Kennedy A, Moore M, Andriolo A and others (2020) Have whales returned to a historical hotspot of industrial whaling? The pattern of southern right whale *Eubalaena australis* recovery at South Georgia. Endang Species Res 43:323–339

Kellar NM, Speakman TR, Smith CR, Lane SM and others (2017) Low reproductive success rates of common bottlenose dolphins *Tursiops truncatus* in the northern Gulf of Mexico following the *Deepwater Horizon* disaster (2010–2015). Endang Species Res 33:143–158

Kemper C, Coughran D, Warneke R, Pirzl R, Watson M, Gales R, Gibbs S (2008) Southern right whale (*Eubalaena australis*) mortalities and human interactions in Australia, 1950–2006. J Cetacean Res Manag 10:1–8

Kenney RD, Mayo CA, Winn HE (2020) Migration and foraging strategies at varying spatial scales in western North Atlantic right whales: a review of hypotheses. J Cetacean Res Manag Spec Issue 2:251–260

Knowlton A, Kraus S, Kenney R (1994) Reproduction in North Atlantic right whales (*Eubalaena glacialis*). Can J Zool 72:1297–1305

Knowlton AR, Hamilton PK, Marx MK, Pettis HM Kraus SD (2012) Monitoring North Atlantic right whale *Eubalaena glacialis* entanglement rates: a 30 yr retrospective. Mar Ecol Prog Ser 466:293–302

Knowlton AR, Robbins J, Landry S, McKenna HA, Kraus SD, Werner TB (2016) Effects of fishing rope strength on the severity of large whale entanglements. Conserv Biol 30: 318–328

Kraus SD (1990) Rates and potential causes of mortality in the north Atlantic right whales (*Eubalaena glacialis*). Mar Mamm Sci 6:278–291

Kraus SD, Prescott JH, Knowlton AR, Stone GS (1986) Migration and calving of right whales (*Eubalaena glacialis*) in the western North Atlantic. Rep Int Whal Comm (Spec Issue) 10:139–144

Laist DW, Knowlton AR, Pendleton D (2014) Effectiveness of mandatory vessel speed limits for protecting North Atlantic right whales. Endang Species Res 23:133–147

Lane SM, Smith CR, Mitchell J, Balmer BC and others (2015) Reproductive outcome and survival of common bottlenose dolphins sampled in Barataria Bay, Louisiana, USA, following the Deepwater Horizon oil spill. Proc Proc R Soc B 282:20151944

Leaper R, Cooke J, Trathan P, Reid K, Rowntree V, Payne R (2006) Global climate drives southern right whale (*Eubalaena australis*) population dynamics. Biol Lett 2: 289–292

Ley RE (2010) Obesity and the human microbiome. Curr Opin Gastroenterol 26:5–11

Lysiak NSJ, Trumble SJ, Knowlton AR, Moore MJ (2018) Characterizing the duration and severity of fishing gear entanglement on a North Atlantic right whale (*Eubalaena glacialis*) using stable isotopes, steroid and thyroid hormones in Baleen. Front Mar Sci 5:168

Maul GE, Sergeant DE (1977) New Cetacean records from Madeira. Bocagiana. 43:1–8. http://publications.cm-funchal.pt/jspui/handle/100/1521

McFall-Ngai M, Hadfield MG, Bosch TC, Carey HV and others (2013) Animals in a bacterial world, a new imperative for the life sciences. Proc Natl Acad Sci USA 110: 3229–3236

Meyer-Gutbrod EL, Greene CH, Sullivan PJ, Pershing AJ (2015) Climate-associated changes in prey availability drive reproductive dynamics of the North Atlantic right whale population. Mar Ecol Prog Ser 535:243–258

Miller CA, Reeb D, Best PB, Knowlton AR, Brown MW, Moore MJ (2011) Blubber thickness in right whales *Eubalaena glacialis* and *Eubalaena australis* related with reproduction, life history status and prey abundance. Mar Ecol Prog Ser 438:267–283

Miller CA, Holm HC, Horstmann L, George JC, Fredricks HF, Van Mooy BA, Apprill A (2020) Coordinated transformation of the gut microbiome and lipidome of bowhead whales provides novel insights into digestion. ISME J 14:688–701

Moore M, Myers H (2019) High-tech fishing gear could help save critically endangered right whales. https://theconversation.com/high-tech-fishing-gear-could-help-save-critically-endangered-right-whales-115974

Moore M, Knowlton A, Kraus S, McLellan W, Bonde R (2004) Morphometry, gross morphology and available histopathology in Northwest Atlantic right whale (*Eubalaena glacialis*) mortalities (1970 to 2002). J Cetacean Res Manag 6:199–214

Moore MJ, Mitchell GH, Rowles TK, Early G (2020) Dead Cetacean? Beach, bloat, float, sink. Front Mar Sci 7:333

Nelson TM, Apprill A, Mann J, Rogers TL, Brown MV (2015) The marine mammal microbiome: current knowledge and future directions. Microbiol Aust 36:8–13

NOAA (2012) Process for injury determination distinguishing serious from non-serious injury of marine mammals. www.fisheries.noaa.gov/webdam/download/64668196

NOAA (2015) Injury to natural resources. In: Deepwater Horizon oil spill: draft programmatic damage assessment and restoration plan and draft programmatic environmental impact statement, National Oceanic and Atmospheric Administration. www.gulfspillrestoration.noaa.gov/wp-content/uploads/Chapter-4_Injury-to-Natural-Resources1.pdf (accessed 11 Nov 2015)

NOAA (2020) North Atlatnic right whale stock assessment reports. www.fisheries.noaa.gov/national/marine-mammal-protection/marine-mammal-stock-assessments

O'Hara T, Rolland R, Reeves R (2003) Report from Bowhead/Right Whale Comparative Health and Physiology Workshop, March 25–26, 2003. https://repository.library.noaa.gov/view/noaa/23704.1-30

Pace RM, Corkeron PJ, Kraus SD (2017) State–space mark–recapture estimates reveal a recent decline in abundance of North Atlantic right whales. Ecol Evol 7:8730–8741

Pace RM, Williams R, Kraus SD, Knowlton AR, Pettis HM (2021) Cryptic mortality in North Atlantic right whales. Conserv Sci Pract 3:e346

Parks SE, Clark CW, Tyack PL (2007) Short- and long-term changes in right whale calling behavior: the potential effects of noise on acoustic communication. J Acoust Soc Am 122:3725–3731

Payne R, Brazier O, Dorsey EM, Perkins JS, Rowntree VJ, Titus A (1983) External features in southern right whales (*Eubalaena australis*) and their use in identifying individuals. In: Payne R (ed) Communication and behavior of whales. Westview Press, Boulder, CO, p 371–445

Pershing AJ, Record NR, Monger BC, Mayo CA and others (2009) Model-based estimates of right whale habitat use in the Gulf of Maine. Mar Ecol Prog Ser 378:245–257

Pettis HM (2019) Final report on right whale visual health assessment. In: Hamilton PK, Knowlton AR, Hagbloom MN, Howe KR and others (eds) Maintenance of the North Atlantic right whale catalog, whale scarring and visual health databases, anthropogenic injury case studies, and near real-time matching for biopsy efforts, entangled, injured, sick, or dead right whales. Contract No. 1305M2-18-PNFFM-0108. Report to National Marine Fisheries Service, Woods Hole, MA, p 97–105

Pettis H, Rolland R, Hamilton P, Knowlton A, Kraus S, Brault S (2004) Visual health assessment of North Atlantic right whales (*Eubalaena glacialis*) using photographs. Can J Zool 82:8–19

Pettis H, Pace R, Hamilton P (2020) North Atlantic Right Whale Consortium 2019 Annual Report Card. www.narwc.org/report-cards.html

Pirotta V, Smith A, Ostrowski M, Russell D, Jonsen ID, Grech A, Harcourt R (2017) An economical custom-built drone for assessing whale health. Front Mar Sci 4:425

Plourde S, Lehoux C, Johnson CL, Perrin G, Lesage V (2019) North Atlantic right whale (*Eubalaena glacialis*) and its food: (I) a spatial climatology of *Calanus* biomass and potential foraging habitats in Canadian waters. J Plankton Res 41:667–685

Record N, Runge J, Pendleton D, Balch W and others (2019) Rapid climate-driven circulation changes threaten conservation of endangered North Atlantic right whales. Oceanography (Wash DC) 32:162–169

Reeves RR, Rolland R, Clapham PJ (2001) Causes of reproductive failure in North Atlantic right whales: new avenues of research. NEFSC Ref Doc 01-16:1–46

Reeves R, Smith T, Josephson E (2007) Near-annihilation of a species: right whaling in the North Atlantic. In: Kraus S, Rolland R (eds) The urban whale: North Atlantic right whales at the crossroads. Harvard University Press, Cambridge, MA, p 39–74

Rolland R, Moore M (2018) Health assessment of large whales. In: Gulland G, Dierauf L, Whitman K (eds) Marine mammal medicine. Taylor and Francis, Boca Raton, FL, p 835–848

Rolland RM, Hunt KE, Kraus SD, Wasser SK (2005) Assessing reproductive status of right whales (*Eubalaena glacialis*) using fecal hormone metabolites. Gen Comp Endocrinol 142:308–317

Rolland R, Hunt K, Doucette G, Rickard L, Wasser S, Kraus S, Rolland R (2007) The inner whale: hormones, biotoxins and parasites. In: Kraus S, Rolland R (eds) The urban whale: North Atlantic right whales at the crossroads. Harvard University Press, Cambridge, MA, p 232–272

Rolland RM, Parks SE, Hunt KE, Castellote M and others (2012) Evidence that ship noise increases stress in right whales. Proc R Soc B Biol Sci 279:1737

Rolland RM, Schick RS, Pettis HM, Knowlton AR, Hamilton PK, Clark JS, Kraus SD (2016) Health of North Atlantic right whales *Eubalaena glacialis* over three decades: from individual health to demographic and population health trends. Mar Ecol Prog Ser 542:265–282

Rolland RM, McLellan WA, Moore MJ, Harms CA, Burgess EA, Hunt KE (2017) Fecal glucocorticoids and anthropogenic injury and mortality in North Atlantic right whales *Eubalaena glacialis*. Endang Species Res 34: 417–429

Rowles T, Bradford A, Calambokidis J, Falcone E and others (2006) Draft report of the NOAA Large Whale Health Assessment Workshop held in Olympia, Washington on 8–9 December 2006. Report SC/59/DW2. International Whaling Commission Cambridge, p 1–7

Sanders JG, Beichman AC, Roman J, Scott JJ, Emerson D, McCarthy JJ, Girguis PR (2015) Baleen whales host a unique gut microbiome with similarities to both carnivores and herbivores. Nat Commun 6:8285

Schick RS, Kraus SD, Rolland RM, Knowlton AR and others (2013) Using hierarchical Bayes to understand movement, health, and survival in the endangered North Atlantic right whale. PLOS ONE 8:e64166

Schick RS, Kraus SD, Rolland RM, Knowlton AR and others (2016) Effects of model formulation on estimates of health in individual right whales (*Eubalaena glacialis*). In: Popper AN, Hawkins A (eds), The effects of noise on aquatic life II. Springer, Berlin, p 977–985

Schwacke LH, Smith CR, Townsend FI, Wells RS and others (2014) Health of common bottlenose dolphins (*Tursiops truncatus*) in Barataria Bay, Louisiana, following the Deepwater Horizon oil spill. Environ Sci Technol 48: 93–103

Seyboth E, Groch KR, Dalla Rosa L, Reid K, Flores PA, Secchi ER (2016) Southern right whale (*Eubalaena australis*) reproductive success is influenced by krill (*Euphausia superba*) density and climate. Sci Rep 6:28205

Sharp SM, McLellan WA, Rotstein DS, Costidis AM and others (2019) Gross and histopathologic diagnoses from North Atlantic right whale *Eubalaena glacialis* mortalities between 2003 and 2018. Dis Aquat Org 135:1–31

Silber GK, Adams JD, Fonnesbeck CJ (2014) Compliance with vessel speed restrictions to protect North Atlantic right whales. PeerJ 2:e399

Sironi M, Rowntree VJ, Di Martino M, Beltramino L, Rago V, Marón C, Uhart M (2018) Southern right whale mortalities at Península Valdés, Argentina: updated information for 2016–2017. Report SC/67B/CMP/06. International Whaling Commission, Cambridge

Sisson N, Long K (2018) Evaluating effectiveness of U.S. management measures for North Atlantic right whales, Summary of an Expert Working Group Meeting. https://repository.library.noaa.gov/view/noaa/23429 Pages:1–23

Smith CR, Rowles TK, Hart LB, Townsend FI and others (2017) Slow recovery of Barataria Bay dolphin health following the *Deepwater Horizon* oil spill (2013–2014), with evidence of persistent lung disease and impaired stress response. Endang Species Res 33:127–142

Stamation K, Watson M, Moloney P, Charlton C, Bannister J (2020) Population estimate and rate of increase of southern right whales *Eubalaena australis* in southeastern Australia. Endang Species Res 41:373–383

Stephen C (2014) Toward a modernized definition of wildlife health. J Wildl Dis 50:427–430

Tennessen JB, Parks SE (2016) Acoustic propagation modeling indicates vocal compensation in noise improves communication range for North Atlantic right whales. Endang Species Res 30:225–237

Thomas PT, Uhart M, McAloose D, Sironi M and others (2013) Workshop on the southern right whale die-off at Península Valdés, Argentina. Report SC/65a/BRG15. Interantional Whaling Commission, Cambridge

van der Hoop J, Moore M, Barco S, Cole T and others (2013) Assessment of management to mitigate anthropogenic effects on large whales. Conserv Biol 27:121–133 van der Hoop JM, Vanderlaan ASM, Cole TVN, Henry AG and others (2014) Vessel strikes to large whales before and after the 2008 Ship Strike Rule. Conserv Lett 8: 24–32

van der Hoop JM, Corkeron P, Kenney J, Landry S, Morin D, Smith J, Moore MJ (2016) Drag from fishing gear entangling North Atlantic right whales. Mar Mamm Sci 32: 619–642

van der Hoop J, Corkeron P, Moore M (2017a) Entanglement is a costly life-history stage in large whales. Ecol Evol 7: 92–106

van der Hoop JM, Nowacek DP, Moore MJ, Triantafyllou MS (2017b) Swimming kinematics and efficiency of entangled North Atlantic right whales. Endang Species Res 32:1–17

Van Waerebeek K, Baker AN, Felix F, Gedamke J and others (2007) Vessel collisions with small cetaceans worldwide and with large whales in the Southern Hemisphere, an initial assessment. Lat Am J Aquat Mamm 6:43–69

Venn-Watson S, Colegrove KM, Litz J, Kinsel M and others (2015) Adrenal gland and lung lesions in Gulf of Mexico common bottlenose dolphins (*Tursiops truncatus*) found dead following the *Deepwater Horizon* oil spill. PLOS ONE 10:e0126538

Wilson C, Sastre AV, Hoffmeyer M, Rowntree VJ and others (2016) Southern right whale (*Eubalaena australis*) calf mortality at Península Valdés, Argentina: Are harmful algal blooms to blame? Mar Mamm Sci 32:423–451

Yablokov AV (1994) Validity of whaling data. Nature 367: 108

Zappes CA, da Silva CV, Pontalti M, Danielski ML, Di Beneditto APM (2013) The conflict between the southern right whale and coastal fisheries on the southern coast of Brazil. Mar Policy 38:428–437

Editorial responsibility: Dave S. Rotstein,
Olney, Maryland, USA

Submitted: September 25, 2020; Accepted: January 6, 2021
Proofs received from author(s): February 22, 2021

Vol. 45: 251–268, 2021
https://doi.org/10.3354/esr01137

ENDANGERED SPECIES RESEARCH
Endang Species Res

Published July 29

Residency, demographics, and movement patterns of North Atlantic right whales *Eubalaena glacialis* in an offshore wind energy development in southern New England, USA

E. Quintana-Rizzo[1,5], S. Leiter[1], T. V. N. Cole[2], M. N. Hagbloom[1], A. R. Knowlton[1], P. Nagelkirk[1], O. O'Brien[1], C. B. Khan[2], A. G. Henry[2], P. A. Duley[2], L. M. Crowe[3], C. A. Mayo[4], S. D. Kraus[1]

[1]Anderson Cabot Center for Ocean Life, New England Aquarium, Boston, MA 02110, USA
[2]Northeast Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Woods Hole, MA 02543, USA
[3]Integrated Statistics, under contract to the Northeast Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Woods Hole, MA 02543, USA
[4]Center for Coastal Studies, Provincetown, MA 02657, USA
[5]*Present address:* Simmons University, Boston, MA 02115, USA

ABSTRACT: Offshore wind energy development is growing quickly around the world. In southern New England, USA, one of the largest commercial offshore wind energy farms in the USA will be established in the waters off Massachusetts and Rhode Island, an area used by the Critically Endangered North Atlantic right whale *Eubalaena glacialis*. Prior to 2011, little was known about the use of this area by right whales. We examined aerial survey data collected between 2011–2015 and 2017–2019 to quantify right whale distribution, residency, demography, and movements in the region. Right whale occurrence increased during the study period. Since 2017, whales have been sighted in the area nearly every month, with peak sighting rates between late winter and spring. Model outputs suggest that 23% of the species' population is present from December through May, and the mean residence time has tripled to an average of 13 d during these months. Age and sex ratios of the individuals present in the area are similar to those of the species as a whole, with adult males the most common demographic group. Movement models showed that southern New England is an important destination for right whales, including conceptive and reproductive females, and qualitative observations included animals feeding and socializing. Implementing mitigation procedures in coordination with these findings will be crucial in lessening the potential impacts on right whales from construction noise, increased vessel traffic, and habitat disruption in this region.

KEY WORDS: Migratory species · Alternative energy · Aerial surveys

---

1. INTRODUCTION

The management and conservation of migratory species is challenging, particularly in dynamic marine environments. Many factors influence a species' presence, so it is difficult to predict how and when a species may utilize an area and whether conservation actions are necessary. Anthropogenic stressors can also affect a species' presence or residency and impact the quality of suitable habitats throughout the migratory route needed for the species' breeding, food, and shelter (Runge et al. 2014). Thus, the effec-

---

*Corresponding author: tetequintana@comcast.net

Publisher: Inter-Research · www.int-res.com

tive conservation of migratory species requires an understanding of how, when, and which individuals use different migratory pathways and habitats as well as the potential stressors throughout their range.

The North Atlantic right whale *Eubalaena glacialis* (hereafter referred to as the right whale) is a Critically Endangered migratory species (Cooke 2020). It is also one of the most endangered cetaceans worldwide, with an estimated abundance of 356 individuals (Pettis et al. 2021). The population has been declining since 2010 (Pace et al. 2017, Pettis et al. 2020) due to mortality from entanglements in fixed fishing gear and vessel strikes (Corkeron et al. 2018, Sharp et al. 2019, Pace et al. 2021) and a 40% decrease in calving (Kraus et al. 2016a), including no births in 2018 (Pettis et al. 2020). This decrease in reproduction may be attributable to chronic stress from anthropogenic injury (van der Hoop et al. 2017) and climate-driven changes in food resources (Meyer-Gutbrod et al. 2018, Record et al. 2019).

Whaling records indicate that right whales once inhabited both sides of the North Atlantic (IWC Int 2001), but today the remaining population is seen almost exclusively along the east coast of the USA and Canada, from Florida to the Gulf of St. Lawrence, with infrequent sightings in the Gulf of Mexico and the eastern North Atlantic (Kraus & Rolland 2007, Firestone et al. 2008, Ward-Geiger et al. 2011). Since 2010, their presence has declined in and around once key habitats in the Gulf of Maine and Bay of Fundy (Davies et al. 2015, 2017), while sightings have increased in other areas including Cape Cod Bay, Massachusetts Bay, the Mid-Atlantic Bight, and the Gulf of St. Lawrence (Whitt et al. 2013, Davis et al. 2017, Mayo et al. 2018, Davies et al. 2019, Ganley et al. 2019, Charif et al. 2020). These shifts in distribution have been correlated with changes in oceanographic conditions and food supply (Record et al. 2019) and have resulted in increased exposure to anthropogenic impacts as the whales move into areas with little or no protective measures (Davies & Brillant 2019). The shifts have prompted the need for increased monitoring efforts to track right whale distribution, especially in areas where anthropogenic pressures are expanding.

Right whale movements across habitats have conservation implications (Brillant et al. 2015) nationally and internationally, as their travel and residency patterns expose them to various anthropogenic activities. Regulations to protect right whales have been implemented in the USA and Canada. Both countries have established critical habitats, which are areas considered to contain physical and biological features essential to the species' conservation (USA: NMFS 2016) or 'the habitat necessary for the survival or recovery of a listed wildlife species and that is identified as the species' critical habitat in the recovery strategy or in an action plan for the species' (Canada: Brown et al. 2009, Fisheries and Oceans Canada 2014). Within the USA, the Gulf of Maine–Georges Bank critical habitat is considered an important feeding habitat, and the southeastern coast is a critical habitat for calving (NMFS 2016). In Canada, the Bay of Fundy and Roseway Basin are critical feeding habitats (Fisheries and Oceans Canada 2014). These areas were considered to be of primary importance to the whales, but feeding and calving have also been observed outside the established critical habitats (Patrician et al. 2009, Foley et al. 2011). Thus, predicting the species' spatiotemporal distribution is vital in the management of human activities where whales and threats co-occur.

Right whales were first systematically recorded in southern New England (SNE) waters between 2011 and 2015 (Kraus et al. 2016b, Leiter et al. 2017, Stone et al. 2017). Little was known about the use of this area by right whales prior to this monitoring effort, although a large influx of 102 right whales was documented on 20 April 2010 by Northeast Fisheries Science Center (NEFSC) surveys (Khan et al. 2011), and models suggested the SNE region was suitable right whale habitat (Pendleton et al. 2012). SNE is near other right whale habitats, including the Great South Channel, Cape Cod Bay, and the mid-Atlantic migratory corridor (Schick et al. 2009, Whitt et al. 2013) connecting the northeastern feeding grounds with the calving grounds in the southeastern USA. The 2011–2015 monthly visual and acoustic monitoring effort found consistent use of the area by a significant portion of the right whale population, a strong correlation between season and presence, and a peak abundance in the spring (Kraus et al. 2016b, Leiter et al. 2017). Over one-third of the right whale population and 30% of the presumed living calving females known at the time were documented during these surveys (Leiter et al. 2017).

The regular presence of right whales in SNE deserves more attention. Since SNE will become one of the largest commercial offshore wind energy leases along the US east coast, the consequences of the construction and operation are relevant to the conservation of the species. The effects of offshore wind development on right whales are unknown (Madsen et al. 2006), but this enormous development could have a local impact on right whales at a critical time when they are becoming more reliant on the region (Leiter et al. 2017). The construction and maintenance of hundreds of wind turbines could cause habitat changes (Wilhelmsson et al. 2006) and influence oceanographic conditions and water column stratification (Broström 2008, Paskyabi & Fer 2012, Paskyabi 2015, Segtnan & Christakos 2015). Both construction and maintenance activities may also expose right whales to higher levels of vessel traffic as well as increased noise. Increased vessel traffic will result in a greater risk of vessel strikes with right whales. In addition, low-frequency noise from large ships (20–200 Hz) overlaps acoustic signals used by right whales (Hatch et al. 2012). Collectively, these perturbations could affect the use of this region by right whales as well as influence their migratory movements throughout the mid-Atlantic region (Schick et al. 2009).

Here, we present an extended assessment of the distribution, demography, residency, and movements of right whales observed in the SNE region over 2 survey periods (2011–2015 and 2017–2019). We discuss the management implications of this study and include recommendations for future conservation management plans for this and other offshore wind energy development areas.

2. MATERIALS AND METHODS

2.1. Field effort and right whale identifications

The study area included SNE waters from the shores of Martha's Vineyard and Nantucket, including Nantucket Shoals, Massachusetts, USA, to approximately 90 km south, and encompassed all the lease sites for Massachusetts and Rhode Island wind energy development. Geographically, the study area lies between 40.50° and 41.33° N latitude and 71.40° and 69.50° W longitude (Fig. 1A). The New England Aquarium (NEAq) conducted systematic aerial surveys in this region, while NEFSC and the Center for Coastal Studies (CCS) conducted directed surveys to areas of right whale presence. Although the level of effort, spatial extent, and configuration of the 3 survey platforms varied, the flights were line transect surveys conducted from a high-winged aircraft (Cessna 337 Skymaster O-2A, high-wing Cessna 336, or Havilland DHC-6 Twin Otter) with 2 experienced observers positioned on either side of the plane. Surveys were flown under visual flight rules at

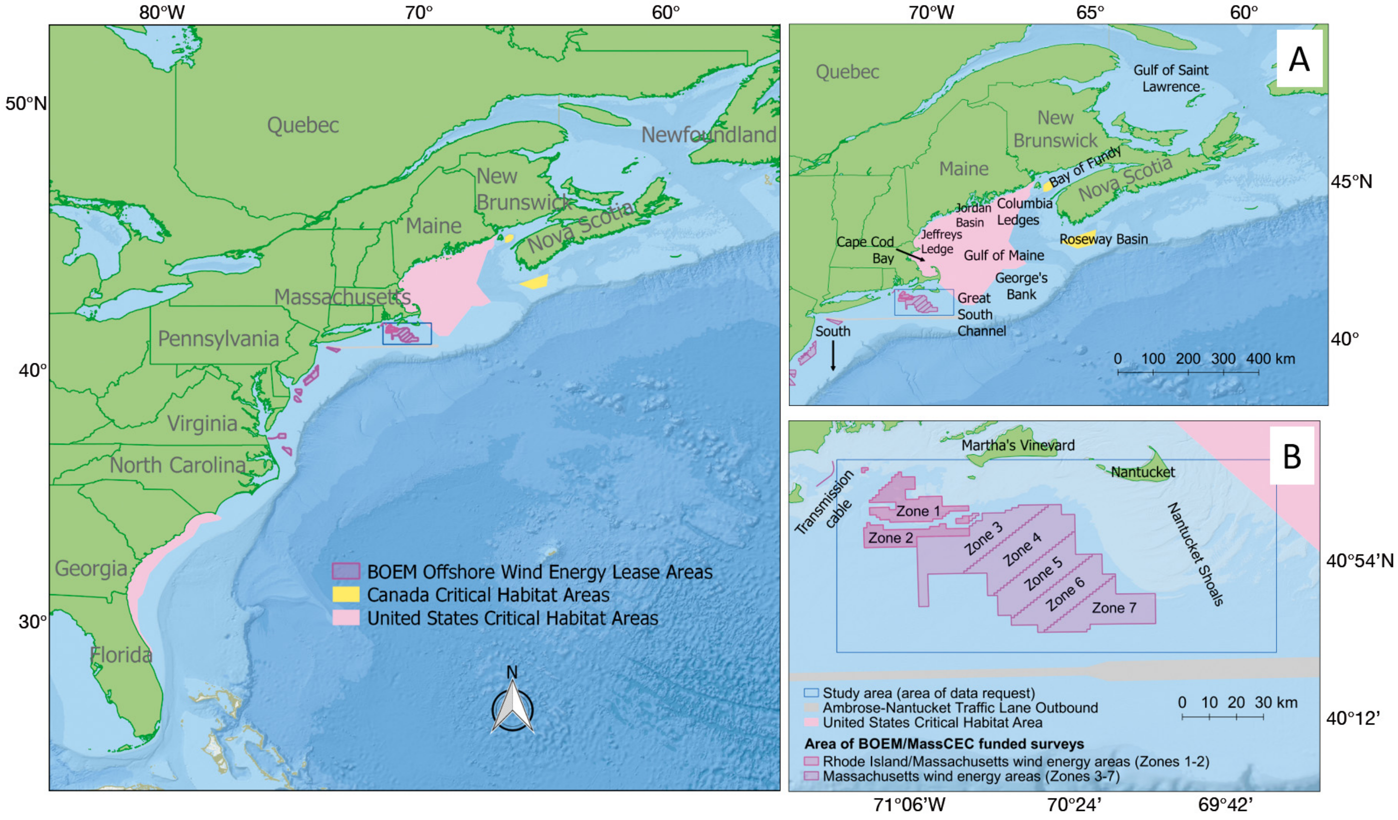


Fig. 1. Right whale critical habitats in the USA and Canada, and offshore wind energy lease areas. (A) Habitats studied in the analysis of right whale movement patterns. South covers the area from New York to Florida. (B) Study area south of Martha's Vineyard and Nantucket, Massachusetts, USA, which encompasses the Rhode Island–Massachusetts and Massachusetts wind energy areas. BOEM: Bureau of Ocean Energy Management; MassCEC: Massachusetts Clean Energy Center

an altitude of 229 to 305 m and a target groundspeed of 185 km h^{-1}. Preferred environmental conditions included a minimum ceiling of 610 m, visibility >9 km, wind speed <10 knots, and Beaufort sea state ≤4. Flight parameters (e.g. time, latitude, longitude, altitude, speed) were recorded every 2 to 5 s throughout the surveys, and when right whales were sighted, the plane broke from the trackline and circled the whales to obtain photographs for individual identification. The plane continued the line transect survey after obtaining images of all right whales present in the area. Sighting and photographic data were collected in accordance with North Atlantic Right Whale Consortium (NARWC) Sightings database guidelines (Kenney 2019). Individual right whales were identified by distinctive callosity patterns on their head, lips, and chin and by scars (Kraus et al. 1986). Right whale photographs were integrated into the NARWC Identification database (Hamilton et al. 2007) and matched to cataloged individuals.

2.2. Datasets and statistical analysis

The data were divided into 2 time periods, 2011–2015 (early years) and 2017–2019 (recent years). No surveys were conducted by NEAq in the study area in 2016. We reanalyzed portions of the 2011–2015 data from Leiter et al. (2017) because the study area was expanded in 2017–2019. The NARWC provided 3 datasets to support various analyses investigating right whale use in SNE (NARWC 2019, 2020). Dataset 1 included only right whale sightings and survey effort collected by the NEAq aerial surveys in the study area during both study periods. This dataset was used to identify clustered distribution areas and calculate sighting rates of right whales in SNE. Dataset 2 included the photographed sightings, demographics, and behavior of identified individual right whales collected during systematic surveys and directed effort conducted by all survey teams in SNE. Verification of individual right whale identifications for 2019 was not completed at the time of writing and was omitted from the analysis. Dataset 2 was used for residency and demographic analyses to calculate the percentage of right whales of the current population sighted in SNE, to summarize general behavioral activities, and to create a discovery curve of the individual right whales photographed in the study area. Discovery curves were created to obtain a cumulative count of distinct individuals over time and to provide insights into whether this population was opened or closed (Wilson et al. 1999). Behavioral activities were not quantified because the information was not always collected; however, observations of feeding and socializing were summarized. Surface or near-surface feeding was defined as an observation during which observers could see a right whale swimming open mouthed at or beneath the surface (Mayo et al. 2018). Socializing included surface active groups, which are defined as 2 or more whales rolling and touching at the surface (Kraus & Hatch 2001, Parks et al. 2007a). Dataset 3 included the sighting history of individual right whales observed during systematic surveys and directed effort in SNE by all contributors. This dataset was used to assess right whale movements to and from SNE and other locations in the North Atlantic during the 2011–2015 and 2017–2018 periods. Descriptive statistics were reported as mean ± SE for continuous variables and N (%) for categorical variables.

2.2.1. Distribution

Distribution and sighting rates were calculated using the standardized systematic survey data in Dataset 1. Effort was defined as the total kilometers flown including transects, circling, cross-legs, and transits (Kraus et al. 2016b, Leiter et al. 2017). Species identification confidence levels of definite (high confidence in species identification) or probable (moderate confidence, Kenney 2019) were included in the analysis. Sighting rates were calculated as the number of right whales sighted per 1000 km of survey effort on a per-month basis to examine temporal trends in the number of whales visiting the study area. Monthly sighting rates across all years were examined using a Kruskal-Wallis test, and multiple Mann-Whitney *U* post hoc tests were used to compare differences between years. The 2-tailed statistical tests were conducted using the SPSS 26.0 package (2019) at a significance level of 0.05. Temporal and spatial analyses of sighting rates assumed that non-systematic periods such as circling were distributed sufficiently homogeneously that a substantial bias was not incurred.

A hotspot analysis was used to delineate the seasonal clustered distribution of right whales within the study area for the 2 study periods (2011–2015 and 2017–2019) using QGIS 3.10.6 (QGIS Development Team 2018). The study area was divided into equally sized grids of 7 × 7 km cells. Sighting rates per survey (number of right whales sighted per 1000 km) were assigned to each corresponding cell, and a hotspot analysis was performed to test for statistically significant spatial clustering of right whales by seasons in the early and recent years of the study using the QGIS Hotspot Analysis plugin (Oxoli et al. 2017). This plugin implements the Getis-Ord Gi* statistic to detect atypical clusters of high (hotspots) or low (coldspots) values by looking at a cell value in the context of its neighbors' values (Getis & Ord 1992, Oxoli et al. 2017). Seasons were defined as winter (December–February), spring (March–May), summer (June–August), and fall (September–November). Only season–period combinations with greater than 10 right whale sightings were used, as smaller sample sizes are considered insufficient for statistical analysis (Ott 1994). Seasonal maps were compiled for each study period at 3 levels of confidence (99, 95, and 90%), and all clusters that were within the 90% confidence level were considered hotspots.

2.2.2. Demographics

NARWC (2020) provided sex and age class (calf, juvenile, adult, unknown) information for the individual right whales sighted in the study area (Dataset 2). Only juvenile (defined as whales that are 1–8 yr old) and adult (defined as whales that are 9 yr of age or older, were not seen as calves but initial sighting was at least 8 yr prior, or were known to be reproductive; Hamilton et al. 1995) age classes were examined. Unknowns and dependent calves were excluded because the number of sightings was too small ($n < 10$) for statistical comparisons. A *G*-test of independence was used to determine if the sex and age ratios differed from year to year, and the annual age and sex ratios were compared to the corresponding annual ratios of the population using individual *G*-tests of goodness of fit with a Bonferroni correction (after Mayo et al. 2018). Population ratios were calculated using the minimum number of right whales presumed alive in a given year following Knowlton et al. (1994).

Since right whales were present in this region at the time of year when conception is expected for this species (Cole et al. 2013), life history characteristics of the males and females were investigated. Paternity is determined through molecular analysis (Frasier et al. 2007), and for this study, genetic analysis of known fathers was only available for the first 3 yr. Both the proportion of reproductive females and the proportion of conceptive females compared to all identified females present in SNE were calculated for each year. Females that had given birth in the years prior to or in the year of a recorded sighting were considered reproductive (Kraus et al. 2001). Females were considered conceptive for a year beginning in March, 2 yr before giving birth (Cole et al. 2013). For instance, a female first sighted with a calf anywhere along the North Atlantic between December 2014 and November 2015 would be considered conceptive during the period 1 March 2013 through 1 March 2014.

2.2.3. Residence

Residence was defined as the minimum number of days that an individual whale was in SNE (Baracho-Neto et al. 2012). To determine the residency of right whales in the study area, maximum likelihood methods were used to determine the lagged identification rate, i.e. the probability that an individual right whale will be resighted in the study area after a time lag using Dataset 2 (Whitehead 2001). This method allows for non-random distribution of sampling effort (Whitehead 2007, 2009) and the incorporation of individual identification data obtained during both systematic and directed surveys.

Empirical lagged identification rate data were compared to a series of movement models representing closed and open populations implemented in the program SOCPROG 2.9 (Whitehead 2009) (Table 1a). These models provide an estimate of the number of visitors in the study area based on mark–recapture probabilities (Whitehead 2001). SOCPROG includes 2 closed population models, but only one of those models (A) was applied because SNE appeared to be an open population, as the discovery curve indicated that new right whales were identified in the study area over time, and the 2 models provided similar results to this dataset. The following pairs of open models are structurally identical but parameterized differently: B and D, C and F, and E and G (Table 1). This order represents the order in which the program generates the results when the models are run simultaneously. All models were run simultaneously so that the variance inflation factor could be taken from the most general model and applied to all of them (Whitehead 2009). Model selection was based on the lowest Akaike's information criterion (AIC) when the data were overdispersed (Whitehead 2007); otherwise, the lowest quasi-AIC (QAIC) was used, and model fits were bootstrapped 100 times to generate SEs for the lagged identification rate estimates.

The lagged identification rate was calculated from the best-fit model applied to sighting data collected from December to May, the period when previous

Table 1. (a) Models and parameters and (b) fits and comparison for lagged identification rate of all right whales, females, and males in southern New England during 2 time periods. AIC: Akaike's information criterion; QAIC: quasi-AIC

a.

Model	Model type and parameters
A	Closed (1/a1 = N or number of visitors)
B	Emigration/mortality (a1 = emigration rate; 1/a2 = N)
C	Emigration + reimmigration (a1 = emigration rate; a2/(a2 + a3) = proportion of population in study area at any time)
D	Emigration/mortality (a1 = N; a2 = mean residence time)
E	Emigration + reimmigration + mortality
F	Emigration + reimmigration (a1 = N; a2 = mean time in study area; a3 = mean time out of study area)
G	Emigration + reimmigration + mortality (a1 = N; a2 = mean time in study area; a3 = mean time out of study area; a4 = mortality rate)

b.

Model	All		Female		Male	
	AIC 2011–2015	QAIC 2017–2018	AIC 2011–2015	QAIC 2017–2018	AIC 2011–2015	QAIC 2017–2018
A	357.32	1490.84	154.68	504.23	357.50	496.68
B	356.30	1476.94	154.47	504.88	891.58	487.30
C	360.39	1458.85[a]	156.74	496.26[a]	356.94[a]	479.89[a]
D	356.30	1476.94	154.47	504.89	358.06	487.30
E	359.79	1466.59	157.70	497.96	359.06	486.63
F	351.20[a]	1458.85[a]	153.40[a]	496.26[a]	356.94[a]	479.89[a]
G	352.89	1460.84	523.78	502.68	358.72	482.91

[a] Best-fit model (with lowest AIC or QAIC value)

studies identified a high right whale presence in the area (Kraus et al. 2016b, Leiter et al. 2017). Residency was estimated for the 2 time periods (2011–2015 and 2017–2018) to determine if it changed over time. The lagged identification rates were calculated, and models fitted, for males and females separately to investigate whether the sexes exhibited different residency patterns. The number of right whale identifications for summer and fall was too low to calculate a separate lagged identification rate, but the percentages of individual right whales sighted in the summer and fall were calculated. These models have been used for cetaceans (e.g. Wimmer & Whitehead 2004, Dinis et al. 2016, Chabanne et al. 2017) and other migratory marine megafauna (e.g. manta rays: Deakos et al. 2011, whale sharks: McKinney et al. 2017, McCoy et al. 2018).

2.2.4. Movements

Dataset 3 was used to estimate the seasonal transition probabilities between SNE and other areas for both study periods. The analysis was limited to the movements between SNE and no more than 4 areas to ensure precise estimates given by the small number of habitat comparisons and the high number of identified individuals moving among areas (Whitehead 2009). The areas followed Brillant et al. (2015) and included, from north to south, the Gulf of St. Lawrence, Bay of Fundy, Gulf of Maine (including the Columbia and Jeffreys ledges and Jordan Basin), Cape Cod Bay, Great South Channel–Georges Bank, and the South (from New York to Florida) (Fig. 1B). The mid-Atlantic was combined with adjacent areas to the south to increase the sample size.

Transition probabilities were calculated using a parameterized Markov movement model in SOCPROG 2.9 (Whitehead 2009). This population-scale behavior model uses the locations and each time unit of photographically identified individuals to estimate the probability of moving from one area to another at a time lag (Whitehead 2001). This model can be used with identifications that are not distributed randomly or uniformly in space or time and that have no independent measure of effort (Whitehead 2001). The small number ($n < 10$) of seasonal right whale identifications in SNE in fall and summer 2011–2015 did not permit the estimation of transition probabilities for those seasons. A 30 d lag was used based on the assumption that an identified right whale in any location could reach any of these other habitats within this interval (Brillant et al. 2015, Davies et al. 2015) during the season of interest. Back-and-forth movements of right whales between southern New England and nearby areas were explored by examining the sighting histories of individual right whales.

3. RESULTS

3.1. Field effort, right whale identifications, and behavioral activities

The combined survey effort in southern New England covered 111 440 km between March 2011 and December 2019 (Table 2). The annual tally of right whales reported (not unique whale identifications) from all sightings varied between 28 and 418 (144 ± 49 whales). A total of 327 unique right whales were identified, with a mean number of 9 identifications per survey day. At least 16 of these whales were confirmed dead according to NARWC as of the beginning of December 2020. The discovery curve showed an increasing trend in the number of new individuals sighted, with no clear plateau signal (Fig. 2), and by the end of 2019, 87 % of the current population had been sighted in SNE throughout the study period. The discovery curve had a steep slope during the 2011–2015 surveys and was even steeper in 2017–2018, suggesting an open population or that sightings in the area were underestimated. Feeding was recorded on more occasions (n = 190 occasions) than socializing (n = 59 occasions). Feeding was observed in all seasons and years, whereas social behaviors were observed mainly in the winter and spring and were not observed in 2011 and 2017.

Table 2. Total tally of right whales recorded in all sightings (no ID included), unique ID, population percentage sighted in relation to the general right whale population (based on Pace et al. 2017 and Pettis et al. 2021 updated population estimates), and annual survey effort (km) in southern New England waters by main data contributors. NEAq: New England Aquarium; NEFSC: Northeast Fisheries Science Center; CCS: Center for Coastal Studies; NA: not available at the time of the data request; NC: not calculated (number of unique IDs not available); (–) no data

Year	Tally of right whales	Unique ID	% of population ± SE	NEAq (km)	NEFSC (km)	CCS (km)
2011	83	53	11 ± 1	4279	2455	327
2012	28	22	5 ± 1	16 042	1471	–
2013	32	20	4 ± 1	12 890	779	–
2014	44	43	9 ± 1	17 279	1763	–
2015	86	53	11 ± 1	9594	6761	357
2017	214	122	29 ± 2	18 867	2456	–
2018	418	202	53 ± 2	11 295	9732	–
2019	250	NA	NC	20729	NA	–

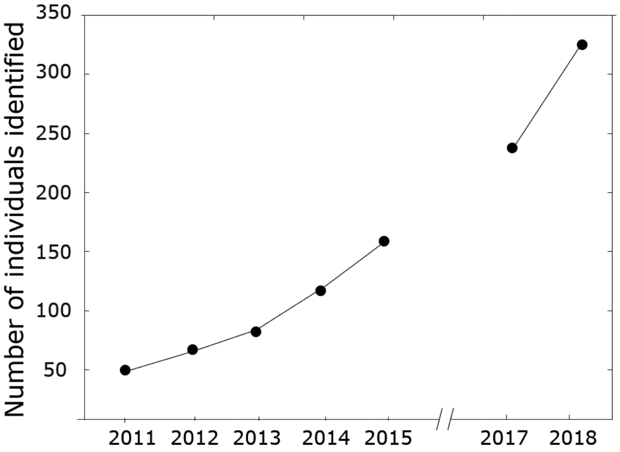


Fig. 2. Discovery curve for the number of uniquely identified individual right whales sighted in southern New England. The slope of the curve indicates an open population where not all individuals have been sampled. No field effort was conducted in 2016

3.2. Datasets and statistical analysis

3.2.1 Distribution

Sighting rates varied through time, suggesting that right whales have become more common in recent years and that their presence now extends beyond the December–May period in SNE. No right whales were reported in 2011 in Dataset 1, but the NEAq surveys did not start until October that year. Sighting rates varied in most other years (Fig. 3; Kruskal-Wallis test = 20.67, df = 6, p = 0.002). Pairwise comparisons showed that the sighting rates of right whales were not significantly different among the early years of the study, and the sighting rates of most of those years were lower than those of recent years (Fig. 3). Sighting rates were not statistically different in 2015, 2017, and 2018 (Fig. 3). Right whale sightings by month were highest from January to April during the early years of the study, but in recent years, right whales were sighted in most months of the year, with notably high sighting rates in December 2018 and August 2019 (Fig. 4).

The seasonal clustered distribution of right whales varied in space and time and extended into wind

A: Mann-Whitney *U*-test statistical values

p-values	Year	2012	2013	2014	2015	2017	2018	2019
	2012		49.50	56.00	16.00	26.50	18.00	7.50
	2013	0.96		56.00	15.00	27.50	19.00	10.50
	2014	0.75	0.75		22.00	41.00	30.00	10.00
	2015	0.21	0.17	0.34		27.00	18.00	9.00
	2017	0.04*	0.04*	0.10	0.95		43.00	18.50
	2018	0.01*	0.01*	0.04*	0.39	0.39		24.00
	2019	0.002*	0.006*	0.002*	0.11	0.03*	0.15	

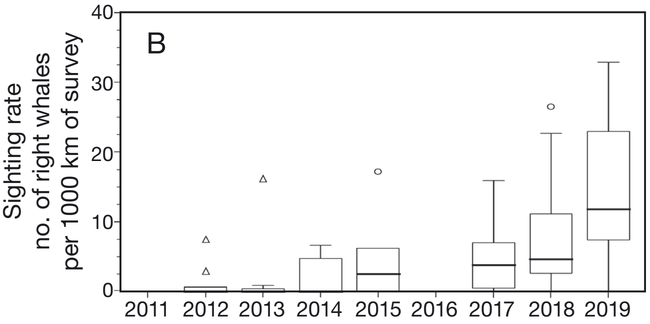
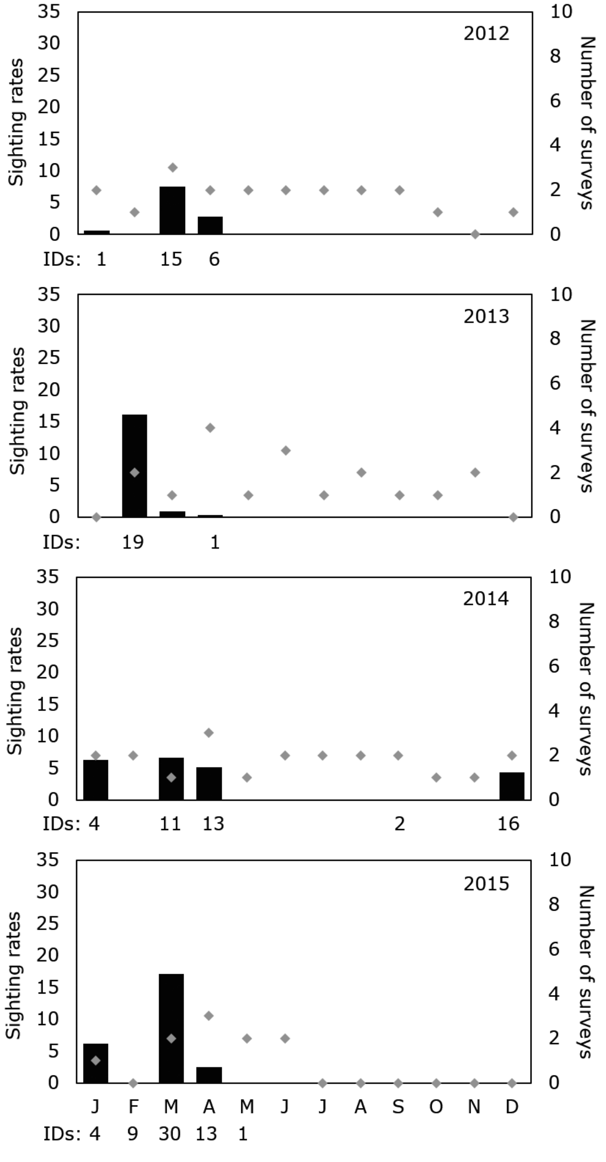


Fig. 3. (A) Mann-Whitney *U*-test comparisons and (B) central tendency and variability of sighting rates of right whales. No right whale sightings were reported in 2011, and no field effort was conducted in 2016 in Dataset 1 (sightings and survey effort collected during aerial surveys conducted by the New England Aquarium). The solid line drawn across each box represents the median sighting rate of that year. The lower boundary is the 25th percentile, and the upper boundary is the 75th percentile of a box. Lines on the top and bottom of each box represent the largest and smallest frequency sighting rates, respectively, excluding outliers (o) and extreme values (Δ). $^*p < 0.05$



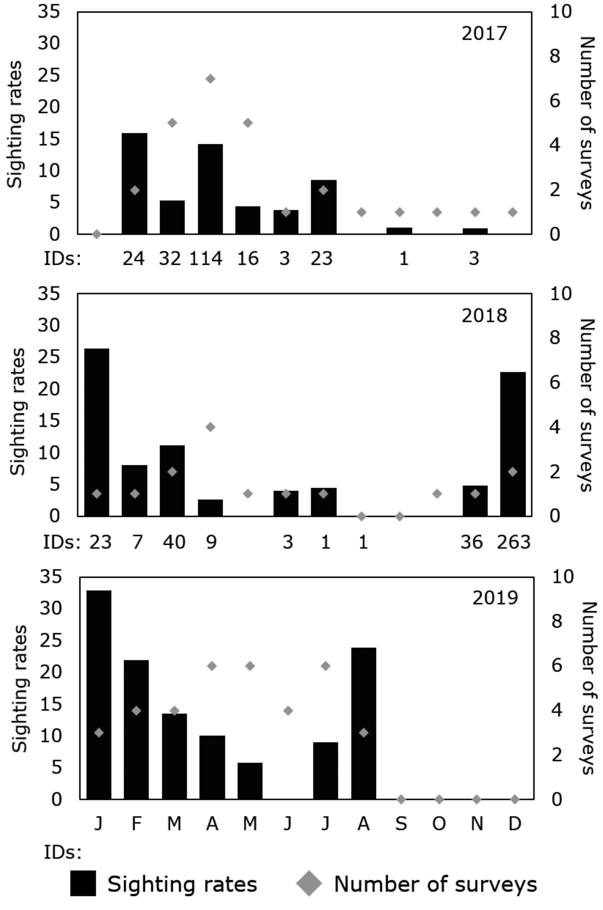


Fig. 4. Monthly sighting rates of right whales and monthly aerial surveys conducted in the study area in Dataset 1 (sightings and survey effort collected during aerial surveys conducted by the New England Aquarium). Sighting rate is defined as the number of right whales per 1000 km of survey. The number of IDs, including resightings, is included for those months in which IDs were available in Dataset 2 (IDs collected by all survey teams). The 2019 IDs were not available at the time of the data request

energy lease sites. In the 2011–2015 winters, right whale sightings increased in the study area and were more concentrated in the northeastern wind energy areas and the southern portion of Nantucket Shoals (Fig. 5A). However, in the 2017–2019 winters, the sightings spanned to the southeastern portion of the shoals (Fig. 5B). In the spring, right whale distribution shifted to the west in both study periods, although in the early years, their distribution was further south of Nantucket (Fig. 5C,D). Summer sightings were only recorded during the 2017–2019 period, with right whales sighted in nearshore waters off Nantucket and along Nantucket Shoals (Fig. 5E).

3.2.2. Demographics

The ratio of adults to juveniles in SNE was the same as in the population as a whole during the study. Adult whales were observed significantly more than juveniles, with an annual mean of 70% adults and 30% juveniles. The adult:juvenile ratio was significantly different from year to year ($G = 20.61$, χ^2 df = 6, $p < 0.002$), but the annual ratios were not significantly different from the yearly population age ratios (Table 3), indicating that the age ratio of the whales visiting the study area followed the age ratio of the population. Sex was confirmed for 93% of the identifi-

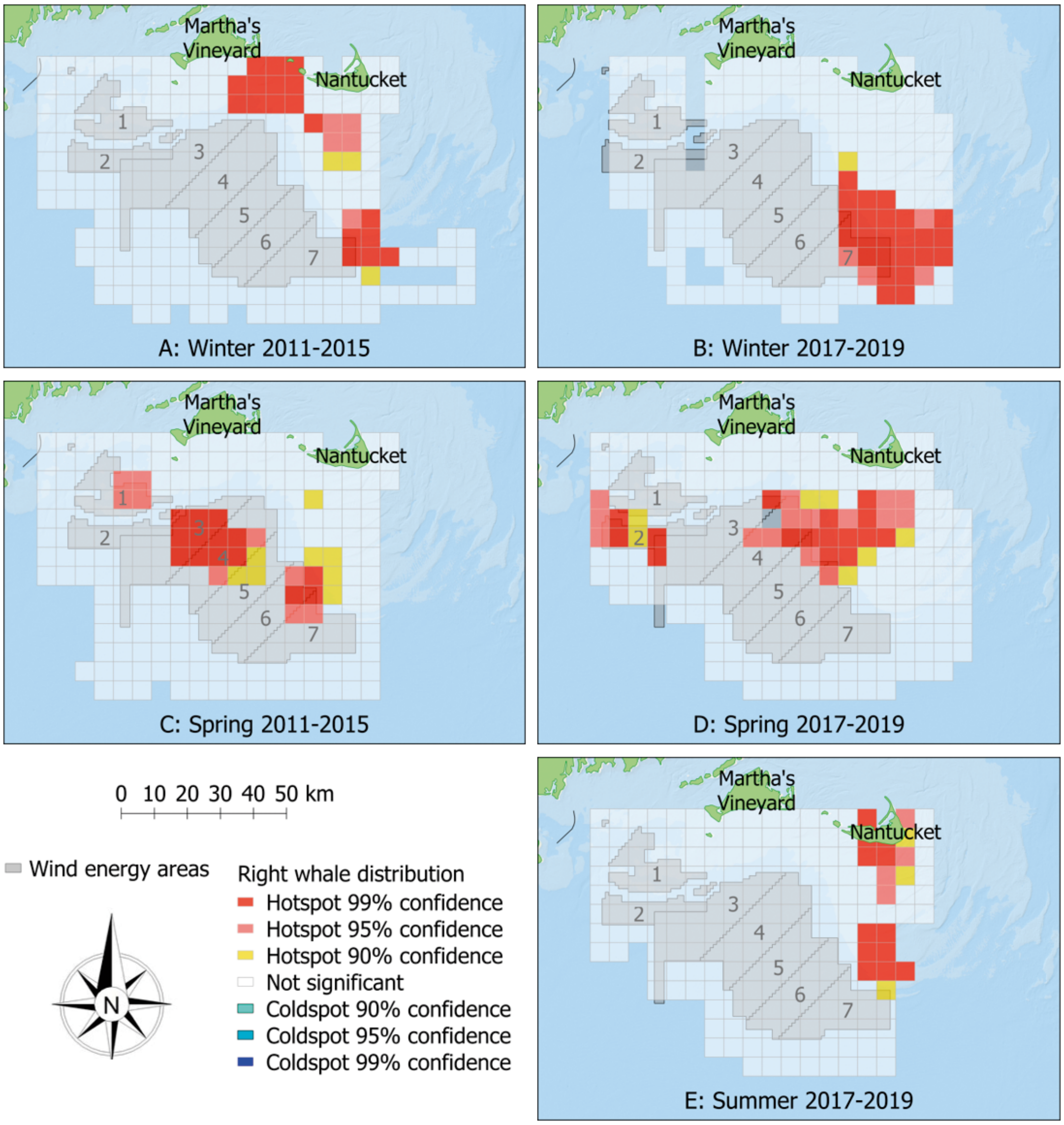


Fig. 5. Hotspot analysis of right whale seasonal distribution in the study area (A,C: 2011–2015; B,D,E: 2017–2019), with hotspots based on significantly higher values than surrounding areas. No coldspots were identified. Wind energy area lease zones are identified by numbers. Additional details of the study area are shown in Fig. 1

Table 3. Annual numbers of unique adult, juvenile, male, and female right whales sighted in southern New England (SNE), and statistical results of age ratio and sex ratio comparisons to the population ratios (NARWC 2020) using a *G*-test of goodness of fit with Bonferroni corrected p-values. Annual total numbers of whales of different age and gender classes are not equal because demographic parameters were not always known for all individuals

Year	Adult	Juvenile	SNE vs. population age ratios *G*-test (df)	p	Male	Female	SNE vs. population sex ratios *G*-test (df)	p
2011	28	20	1.96 (1)	1.00	26	24	0.82 (1)	1.00
2012	11	8	2.21 (1)	1.00	12	7	0.18 (1)	1.00
2013	11	8	2.45 (1)	1.00	10	8	0.06 (1)	1.00
2014	24	18	2.62 (1)	0.21	26	17	0.08 (1)	1.00
2015	30	18	2.89 (1)	0.49	29	20	0.02 (1)	1.00
2017	81	34	3.64 (1)	0.28	66	49	0.04 (1)	1.00
2018	156	38	5.00 (1)	1.00	117	72	1.00 (1)	1.00

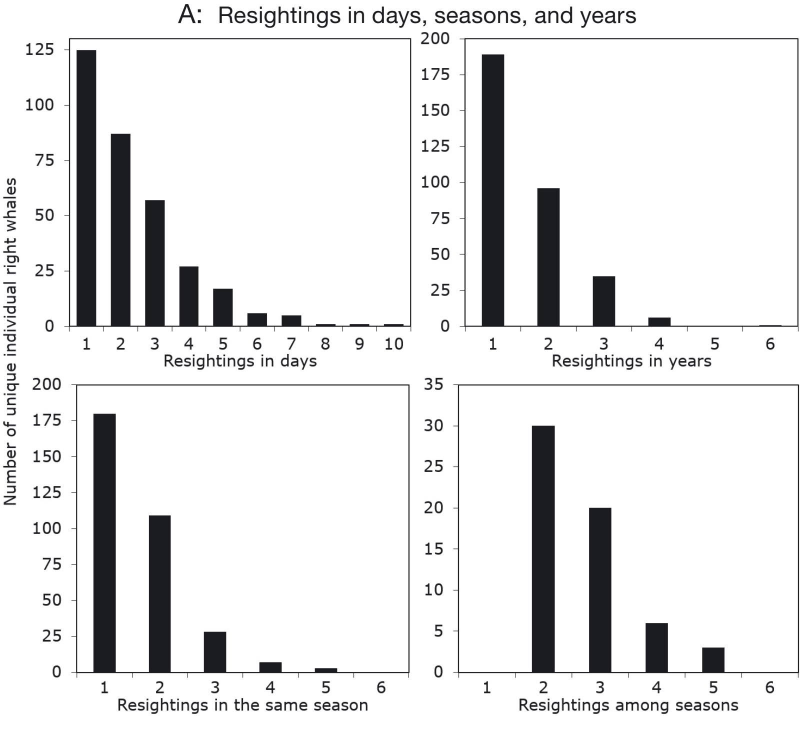
able right whale individuals. Of these, 181 were males and 125 were females. The sex ratios did not vary significantly from year to year (*G* = 2.04, df = 6, p = 0.92). The mean annual percentage of males and females was 57 and 39%, respectively. The observed sex ratio and the population sex ratio did not vary significantly (Table 3).

Both reproductive females and conceptive females were seen in the study area. Forty-five of the 108 reproductively active females (42%) known to be alive during the study were sighted in SNE, and 17 were resighted in multiple years. The overall yearly proportions of reproductively active females varied from 0.25 to 0.57 (0.41 ± 0.05). In the case of conceptive females, only 4 females were identified in 4 years (2011, 2012, 2017, 2018), and their yearly proportion varied from 0 to 0.14 (0.03 ± 0.02). Except for 1 conceptive female which was sighted twice, the others were sighted only once in the study area during their conception period. The genetic information of known fathers was only available for 2011–2013. Of the 13 known fathers, only 2 were sighted (once) in SNE but not during the conceptive period.

Dependent calf sightings were uncommon in SNE, and only descriptive statistics are provided. A total of 89 right whale calves were born in the population between 2011 and 2019, but only 6 different calves (inferred by the presence of known mothers) were recorded during the study in SNE (4 in 2011, 1 in 2015, 1 in 2019). Three calves were sighted twice in the same year.

3.2.3. Residence

Individual sighting frequency over the study period varied between 1 and 10 d, suggesting different degrees of residency (Fig. 6). Most right whales (62%, n = 202) were sighted more than once over the course of the study, and 42% of those whales were sighted in between 2 and 6 years (2 ± 0.05 years) (Fig. 6). One whale was sighted nearly every year except in 2013. Within a season, 147 whales were sighted multiple



B: Unique IDs and resightings by year

Parameter	2011	2012	2013	2014	2015	2017	2018
Unique IDs	53	22	20	43	53	122	202
Resightings in the same season	12	0	0	3	2	43	87
Resightings among seasons	0	0	0	0	2	13	44

Fig. 6. Different resighting patterns of uniquely identified right whales at different time scales including (A) during the same season and among seasons and (B) by year in southern New England between 2011 and 2018. No field effort was conducted in 2016

times (≤5), and 59 whales were sighted several times (≤3) in different seasons of the same year. Summer and fall sightings were only common in recent years, and 14 individuals were sighted more than once during this period. Whales resighted the most times included individuals of both sexes as well as adults and juveniles, although the 3 most sighted animals were all males (2 adults and 1 juvenile sighted 8–10 times).

Model F (emigration + reimmigration) was the best-fit model to describe the residency of the right whale population in the study area (Table 1b) from December to May, indicating that whales enter, leave, and reenter the study area during this period. In the early years, the model indicated that, on average, 54 ± 31 whales were in the study area at any one time during those months and that an individual remained there for an average period of 9 ± 7 d (Table 4). However, in recent years, the number of whales estimated to be in the study area during December to May was 65 ± 18 right whales, and the residency for both sexes was approximately 13 ± 12 d (Table 4). However, these results need to be taken with caution, as bootstrap estimates of the SEs around the estimates were in some cases 1.5 times the mean. Model C (emigration + reimmigration) was also the best fit to explain the emigration rate and proportion of females and males in the study area (Table 1). This model indicated that the emigration rate of females is about 5 times higher than that of males and that 23 % of the population could be present in the study area from December to May.

3.2.4. Movements

The transition probabilities of individual whales varied throughout the study. In the winter and spring, the probability of any right whale emigrating from the study area was 3 times higher in 2011–2015 than in 2017–2018 (Table 5). In the early winters, the Gulf of Maine and Cape Cod Bay were the top-ranking destinations for right whales sighted in SNE, with transition probabilities ranging from 0.21 to 0.30 (Table 5). In the same period, the Gulf of Maine, Cape Cod Bay, and the Great South Channel–Georges Bank were the most likely destinations along the US coast for all emigrating right whales (Table 5). However, in recent winters, the Great South Channel–Georges Bank (destination probability, *Pi* = 0.45) and SNE (*Pi* = 0.47) ranked high among the most likely destinations for right whales within the USA. In the spring, other areas were more visited. During the 2011–2015 spring, the South (New York–Florida) was the top-ranking destination for right whales emigrating from SNE, as well as other regions within the USA, but whales sighted in the SNE region also had a high probability of staying in the study area (0.70). In the 2017–2018 spring, the probability of right whales traveling to the South changed from 0.69 to 0.30 (Table 5), while Cape Cod Bay (*Pi* = 0.55), SNE (*Pi* = 0.49), and the Gulf of Maine (*Pi* = 0.44) ranked highly as destinations. In recent summers, SNE and the Gulf of St. Lawrence were the high-ranking destinations (Table 5).

Sighting histories of a small percentage of right whales (n = 14, <5 %) identified in the study area showed movement back and forth between areas, mainly between SNE and Cape Cod Bay and between SNE and the South (New York). Eleven right whales, including 6 adult males, 3 adult females, and 2 juvenile males, were first sighted in Cape Cod Bay (≥1 time), then once in SNE, and then again in Cape Cod Bay (≥1 time). The number of days between sightings of a whale at these 2 areas ranged from 3 to 42 d. The other 3 right whales were first sighted in SNE, then in either Cape Cod Bay or the South (New

Table 4. Parameters of the model(s) ± standard error that best fit the lag identification rates of all right whales including females and males in southern New England, December–May, during the study periods 2011–2015 and 2017–2018. Time in/out: time spent in/outside of the study area; (–) not applicable

Model type and parameters	2011–2015			2017–2018		
	All	Female	Male	All	Female	Male
F: Emigration + reimmigration						
Number of visitors	54 ± 31	14 ± 7	18 ± 33	65 ± 18	28 ± 13	36 ± 9
Time in (d)	9 ± 7	4 ± 3	5 ± 43	13 ± 12	15 ± 24	18 ± 51
Time out (d)	63 ± 42	21 ± 24	41 ± 163	50 ± 46	64 ± 70	97 ± 136
C: Emigration + reimmigration						
Emigration rate	–	–	0.25 ± 2.06	0.10 ± 0.91	0.33 ± 1.39	0.06 ± 1.53
Proportion of population in study area at any time	–	–	0.09 ± 0.0001	0.23 ± 0.001	0.14 ± 0.0001	0.17 ± 0.0002

Table 5. Seasonal transition probabilities of right whales moving between southern New England (SNE) and other right whale areas along the North Atlantic. Destination probabilities (columns) are shown as *Pi*, and origin probabilities (rows) are shown as *Pe*, including the probability of staying within the original region of the sighting (diagonal). There were no data for summer destination 2011–2015; GSL: Gulf of St. Lawrence; BOF: Bay of Fundy; GOM: Gulf of Maine; CCB: Cape Cod Bay; GSB: Great South Channel–Georges Bank; SOU: South (New York–Florida)

2011–2015

Winter destination

Origin	GSL[a]	BOF[a]	GOM	CCB	SNE	GSB	SOU	*Pe*
GSL								
BOF								
GOM			0.80	0.03	0.08	0.04	0.04	0.20
CCB			<0.01	0.30	0.16	0.53	<0.01	0.70
SNE			0.21	0.29	0.33	0.11	0.06	0.67
GSB			0.16	0.14	0.11	0.59	0.08	0.49
SOU			0.08	0.03	0.001	0.01	0.08	0.13
Pi			0.45	0.50	0.36	0.68	0.17	

Spring destination

Origin	GSL[a]	BOF[a]	GOM	CCB	SNE	GSB	SOU	*Pe*
GSL								
BOF								
GOM			0.34	0.14	0.14	0.06	0.32	0.66
CCB			0.04	0.82	0.03	0.06	0.04	0.18
SNE			<0.01	0.07	0.72	0.08	0.14	0.29
GSB			0.14	0.09	0.05	0.55	0.19	0.47
SOU			0.07	0.16	0.16	0.12	0.41	0.51
Pi			0.24	0.46	0.39	0.32	0.69	

2017–2018

Winter destination

Origin	GSL[b]	BOF[a]	GOM	CCB	SNE	GSB	SOU	*Pe*
GSL								
BOF								
GOM								
CCB				0.69	0.04	0.15	0.12	0.31
SNE				0.02	0.80	0.18	<0.01	0.20
GSB				0.12	0.28	0.61	<0.01	0.40
SOU				0.13	0.15	0.13	0.60	0.40
Pi				0.27	0.47	0.45	0.12	

Spring destination

Origin	GSL[b]	BOF[a]	GOM	CCB	SNE	GSB	SOU	*Pe*
GSL								
BOF								
GOM			0.19	0.44	0.09	0.10	0.17	0.81
CCB			0.24	0.73	<0.01	0.02	<0.01	0.27
SNE			<0.01	0.04	0.89	0.01	0.06	0.11
GSB			0.09	0.03	0.17	0.64	0.07	0.36
SOU			0.10	0.04	0.23	0.06	0.58	0.42
Pi			0.44	0.55	0.49	0.19	0.30	

Summer destination

Origin	GSL	BOF	GOM[b]	CCB[a]	SNE	GSB[b]	SOU[a]	*Pe*
GSL	0.88	<0.01			0.12			0.12
BOF	0.09	0.72			0.19			0.28
GOM								
CCB								
SNE	0.12	0.05			0.82			0.87
GSB								
SOU								
Pi	0.21	0.05			0.31			

[a]No sightings; [b]Small sample size, thus no probabilities calculated

York), and then again in SNE (1 adult male, 1 juvenile male, 1 adult female). The gap between sightings of an individual moving between these areas varied between 19 and 78 d. The gap in resighting times is likely more of a reflection of survey effort than of the whales' movements among locations.

4. DISCUSSION

This 8 yr analysis of sightings revealed that right whales have become more common in SNE waters, with sightings now documented in nearly every month of the year. Sighting rates were highest in the span from winter through early spring and sometimes even during the summer months (e.g. August 2019). Our effort included off-transect periods such as circling, cross-legs, and transits (Leiter et al. 2017). Thus, sighting rates estimated by this analysis should be compared only to studies using a similar analytical approach. Close to a quarter of the population may be in this area at any given time between December and May, and the annual percentage of right whales identified varied between 4 and 53% (13 ± 4%) of the minimum right whale population. SNE is also an important habitat used by all demographic groups because the age and sex ratios are similar to those in the overall species population, and the estimated residency duration for females and males tripled during the study period. The apparent increased use of this habitat could be related to an increased field effort in recent years, which resulted in a higher number of identifications, and/or to dramatic climate-driven ecosystem changes that have occurred in the past decade (Record et al. 2019). Migratory species such as right whales are particularly affected by climate change because they rely on highly productive seasonal habitats (Robinson et al. 2009).

Right whales exhibit partial migration (Gowan et al. 2019), a term used to describe a species in which a proportion of a population stays resident in a habitat(s) and another proportion migrates to another habitat(s) (Chapman et al. 2011). It is a widespread phenomenon in invertebrates (Menz et al. 2019), fish (Chapman et al. 2012), birds (Lundberg 1988), and mammals (Cagnacci et al. 2011, Martin et al. 2018, Berg et al. 2019). In the case of right whales, all demographic groups have the potential to migrate to the wintering grounds off the southeastern USA, but the migration appears to be condition dependent and varies across demographic groups and years. Females may overwinter in the feeding areas in the north and skip the breeding grounds in the south in the years immediately preceding and following calving to increase their energy stores for future reproduction (Gowan et al. 2019). On the other hand, juveniles and adult males may travel to the southern wintering grounds following years of higher prey availability in a northern fall feeding ground (Gowan et al. 2019).

The mixture of movement patterns within the population and the geographical location of SNE suggests that the area could be a feeding location for whales that stay in the mid-Atlantic and north during the winter–spring months and a stopover site for whales migrating to and from the calving grounds. For example, a female right whale initially tagged off the coast of Virginia in March 2021 traveled for 13 d to SNE, where she stayed for 3 d before traveling north towards Cape Cod Bay (D. Engelhaupt pers. comm.). Because of the complex movements displayed by the species, our use of the term residence describes the minimum time a right whale could spend in SNE regardless of the overall movement that the whale exhibited at that time. It does not suggest that right whales overwinter in SNE.

Our findings show that SNE is an important transition region, as the whales that utilized the area moved to and from critical habitats including Cape Cod Bay, the Gulf of Maine, and the Great South Channel–Georges Bank, and in the summer, many traveled on to the Gulf of St. Lawrence. Florida and Georgia were more frequent destinations when calving rates were higher (Pace et al. 2017) in the early study period, but the recent low transition rates could be due to a lack of births in 2018 or changes in survey efforts and right whale movements. The sightings of SNE whales in Canadian waters and multiple USA locations, including the mid-Atlantic, emphasize the need for protecting coastal areas that serve as migratory corridors.

Right whales may utilize SNE as a feeding ground more often than as a social or mating ground, although behaviors linked to both activities have been observed in the area. Feeding was recorded on more occasions than socializing, and it was observed in all seasons, whereas surface active groups were observed mainly in the winter and spring. Preliminary results of oceanographic surveys conducted in waters near right whale sightings suggest that their diet includes multiple zooplankton species including *Calanus finmarchius* and *Centropages* sp. (Quintana-Rizzo et al. 2018). Evidence of feeding throughout the seasons provides support for the extension of US feeding critical habitats into SNE waters.

Almost 50% of reproductive females utilized this area within the study period, which is an important consideration for the species' conservation since the overall population has declined significantly (Pace et al. 2017, Corkeron et al. 2018). Conceptive females were not often seen, and their proportional presence was not as high as in the inferred mating ground identified by Cole et al. (2013) over a decade ago. However, large numbers of conceptive females are not required for mating to occur because mating groups often consist of many males and 1 female (Kraus & Hatch 2001). Few calves were seen in SNE, in contrast to Cape Cod Bay, where calf sightings have increased and up to 40% of the calves born in a given year can be sighted (Mayo et al. 2018).

Individual right whales were sighted more frequently in Cape Cod Bay than in SNE in the winter and spring, and some whales move back and forth between the feeding habitats. The relative importance of the 2 areas for the whales is difficult to assess since differences in the frequency of apparent habitat use are likely confounded by differences in survey coverage. Cape Cod Bay is a much smaller area surrounded by land on 3 sides, and comprehensive surveys are conducted weekly during the primary period of right whale presence there between January and April, whereas SNE is an extensive oceanic area, and surveys were conducted only a few times per month throughout the year.

The year-round productivity of Nantucket Shoals (PCCS 2005) may influence the presence of right whales, even in low numbers. Indeed, the shoals appear to be a hotspot for right whales throughout most of the year. The shoals extend eastward and southeastward of Nantucket Island (Fig. 1B; Freire et al. 2015). The shoals and Nantucket Sound form one of the largest tidal dissipation areas in the Gulf of Maine and New England regions (Chen et al. 2018). The tidal dissipation creates a local tidal pump that serves as the primary driver for the relatively high phytoplankton biomass in the shoals' shallow dune-like regions all year (Hu et al. 2008, Saba et al. 2015), which presumably correlates to zooplankton prey for right whales.

In recent years, right whale sightings in SNE waters in winter were concentrated in the eastern portion of the area, near Nantucket Shoals, and in and near Zones 6 and 7 of the Massachusetts wind energy area. In the spring, right whale sightings increased in the northern parts of the wind energy areas and shifted generally westward, but their specific locations and extents varied with time. Late spring aggregations of right whales were recently detected outside of the study area, near the Ambrose–Nantucket shipping lanes south of the Massachusetts wind energy areas (Fig. 1B), by NEAq and NEFSC aerial surveys. This demonstrates that right whale aggregations vary in space and time and can be formed in nearby locations from which the whales could easily move to the wind energy areas. In recent summers, right whale sightings increased in the Nantucket coastal and shoal waters, but the observation efforts also became more frequent. Sightings in these Nantucket locations were common in the summer of 2020 and extended into the early fall, as suggested by observations of right whales during the NEFSC surveys (NEFSC unpubl. data). The 2019 and 2020 identifications were unavailable at the time of our data request, but preliminary results suggest that a high number of juveniles were present in SNE waters at this time in contrast to 2017 and 2018 (Quintana-Rizzo et al. 2019a,b). Additional data collection over the coming years will reveal whether or not this pattern continues.

The presence of right whales in SNE throughout all seasons is important to determine appropriate management actions. The study area is bracketed by 2 right whale seasonal management areas (SMAs); these are regulatory protection zones along the US east coast in which vessels larger than 300 gross tons must slow to 10 knots or less when transiting (NMFS 2008). To protect aggregations of right whales outside of the SMAs, the National Marine Fisheries Service has voluntary dynamic management areas (DMAs), which are triggered when 3 or more whales are sighted within close proximity to each other. DMAs last for 15 d from the date of the sighting(s) that triggered them (NMFS 2008). It requests that ships avoid DMAs or transit through them at 10 knots or less. A recent assessment of the automatic identification system data of vessel traffic for these DMAs indicates very low mariner cooperation with speed reduction requests (NMFS 2020). In 2017 and 2018, the annual number of DMAs doubled from the annual average of 3 DMAs in the 2011–2016 period. In 2019, the number of triggered or extended DMAs reached a peak, with an active DMA in every month except October (NEFSC unpubl. data).

The presence of right whales in SNE during all seasons is an important consideration for the planning and execution of offshore wind development. The historical seasonal migratory pattern should not be used alone to determine time-sensitive actions in this habitat. Monitoring and mitigation plans should include protocols for the likely presence of right whales throughout the year (Whitt et al. 2013). Their increasing summer and fall presence deserves special attention since this will overlap with the current schedule for pile driving for turbine foundations in the next few years, the phase of construction considered to have the greatest acoustic impact (Madsen et al. 2006, Thompson et al. 2010), which could potentially affect right whale behavior. This timing was originally selected based on the observed seasonality of right whales in SNE (Leiter et al. 2017), but our findings show that their seasonal occurrence has changed. Management and mitigation procedures should be adapted and reevaluated continually in relation to right whales' use of the area.

Although the effects of offshore wind energy development on right whales are unknown, it has been reported that baleen whales avoid impulsive sounds with noise levels similar to those of pile-driving activities (Madsen et al. 2006, Stone & Tasker 2006). Migrating baleen whales such as the bowhead whale *Balaena mysticetus*, a distant cousin of the right whale, avoided airguns at approximately 20 km (Richardson et al. 1999). Minke whales rapidly flee from military sonar exposures (Dolman & Simmonds 2010), and their numbers decline during naval activity (Parsons et al. 2000). The effects of noise associated with vessel traffic during the construction and maintenance of the wind turbines are also unclear, but right whales have not previously exhibited behavioral responses to approaching vessels (Nowacek et al. 2004). However, analyses of right whale fecal samples suggest that noise from large commercial vessels increases their stress levels (Rolland et al. 2012). Although right whales may be able to vocally adapt to increased low-frequency noise to some degree through a shift in vocalization frequency and duration (Parks et al. 2007b, 2009, 2011), the above findings suggest that the whales could potentially be negatively affected by disturbances from sound and noise related to wind energy development. Increased vessel traffic associated with the construction and maintenance of turbines also increases the risk of whales being struck.

Implementing mitigation measures by all lease-holding companies will be crucial. The first leasing company to start pile-driving activities in the Massachusetts wind energy area has agreed to implement enhanced mitigation procedures to detect and protect right whales from early winter to mid-May, to avoid pile driving from January to April, and to maintain a comprehensive monitoring effort during the other months of the year that construction might take place (Vineyard Wind, NGO Agreement 2019). Mitigation procedures will include using real-time acoustic monitoring, having certified protected species observers on a vessel stationed at the pile-driving site, and using vessel surveys during daylight hours within a 10 km range of the construction site (Vineyard Wind, NGO Agreement 2019). However, conservation and management efforts will need to identify specific indicators of potential impacts to reduce uncertainty, especially as the offshore wind energy industry grows and expands (Hill & Arnold 2012, Madsen et al. 2015). Abundance and distribution studies will not be enough to understand potential changes in right whale patterns considering the large-scale shifts that the species is experiencing. Examples of indicators exist in studies conducted in Europe (Köppel 2017, Bispo et al. 2019), where wind energy development has a long history. Studies designed to examine the consequences of acoustic exposure to construction noise are urgently needed. The area of the potential effect of acoustic exposure can extend far beyond the immediate vicinity of the proposed development and cause behavioral disturbances in animals in a large area (Thomsen et al. 2006). Work is also needed to determine if wind farms alter the habitat's physical and oceanographic characteristics (Wilhelmsson et al. 2006, Broström 2008, Paskyabi & Fer 2012, Paskyabi 2015, Carpenter et al. 2016). This may have cascading impacts on the food chain in the region, which could potentially displace right whales to other areas. Estimating the potential impacts of offshore wind farms on right whales or their cause-and-effect relationships will be challenging at a time in which whale numbers and distributions are changing, but this is necessary to inform appropriate strategies for future wind energy development.

Acknowledgements. Funding for survey effort was provided by the Bureau of Ocean Energy Management under Cooperative Agreement M17AC00002 and the Massachusetts Clean Energy Center (MassCEC). NEAq surveys were conducted under NOAA permits no. 14233 (2011–2015) and no. 19674 (2017–2019) issued to Scott D. Kraus. NOAA surveys were conducted under research permits no. 17355 June 2013–June 2018 and no. 21371 after June 2018. NOAA Fisheries funded the publication of this paper. The work includes data collected and processed by multiple institutions — our sincere thanks to the contributors of the North Atlantic Right Whale Consortium and to the many observers who collected and processed sighting data at different organizations. At NEAq, we acknowledge the work of A. Bostwick, J. Anderson, J. Taylor, S. Mussoline, K. Stone, and T. Montgomery. At NEFSC, we recognize the work of A. Ogilvie, J. Gatzke, K. Vale, C. Accardo, and K. Slivka. At CCS, we thank A. James, L. Ganley, and P. Hughes. Surveys were possible with the coordination of Avwatch, in particular C. Kluckhuhn, T. Laue, R. Jackson, B. Strakele, M. Cortese, and D. Heikkila. We thank D. LeRoi for his technical assistance. H. Pettis, P. Hamilton, and R. Kenney provided helpful support during the data request. R. Kenney calculated the survey effort of the aerial teams working in SNE. M. Zani was instrumental in identifications and catalog work completed in 2011–2015. J. Roberts, C. Orphanides, and an anonymous reviewer provided very useful comments to improve the manuscript. E.Q.R. thanks N. Bolgen for his support; D. Engelhaupt for sharing information on the movements of a tagged right whale; H. Whitehead for the valuable discussions on the movement and residence models even in the middle of the pandemic; and S. Brillant, A. Vanderlaan, and M. Smithson for insightful discussions in the early stages of the manuscript. This work is dedicated to the North Atlantic right whale.

LITERATURE CITED

Baracho-Neto C, Neto E, Rossi-Santos M, Wedekin L, Neves M, Lima F, Faria D (2012) Site fidelity and residence times of humpback whales (*Megaptera novaeangliae*) on the Brazilian coast. J Mar Biol Assoc UK 92:1783–1791

Berg J, Hebblewhite M, Clair CC, Merrill E (2019) Prevalence and mechanisms of partial migration in ungulates. Front Ecol Evol 7:325

Bispo R, Bernadino J, Coelho H, Costa JL (eds) (2019) Wind energy and wildlife impacts. Balancing energy sustainability with wildlife conservation. Springer, Cham

Brillant SW, Vanderlaan ASM, Rangeley RW, Taggart CT (2015) Quantitative estimates of the movement and distribution of North Atlantic right whales along the northeast coast of North America. Endang Species Res 27: 141–154

Broström G (2008) On the influence of large wind farms on the upper ocean circulation. J Mar Syst 74:585–591

Brown MW, Fenton D, Smedbol K, Merriman C, Robichaud-Leblanc K, Conway JD (2009) Recovery strategy for the North Atlantic right whale (*Eubalaena glacialis*) in Atlantic Canadian waters. Species at Risk Act recovery strategy series. Fisheries and Oceans Canada, Ottawa

Cagnacci F, Focardi S, Heurich M, Stache A and others (2011) Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. Oikos 120:1790–1802

Carpenter JR, Merckelbach L, Callies U, Clark S, Gaslikova

L, Baschek B (2016) Potential impacts of offshore wind farms on North Sea stratification. PLOS ONE 11:e0160830

Chabanne DBH, Finn H, Bejder L (2017) Identifying the relevant local population for environmental impact assessments of mobile marine fauna. Front Mar Sci148

Chapman BB, Brönmark C, Nilsson JÅ, Hansson LA (2011) The ecology and evolution of partial migration. Oikos 120:1764–1775

Chapman BB, Hulthén K, Brodersen J, Nilsson PA, Skov C, Hansson LA, Brönmark C (2012) Partial migration in fishes: causes and consequences. J Fish Biol 81:456–478

Charif RA, Shiu Y, Muirhead CA, Clark CW, Parks SE, Rice AN (2020) Phenological changes in North Atlantic right whale habitat use in Massachusetts Bay. Glob Change Biol 26:734–745

Chen Z, Curchitser E, Chant R, Kang D (2018) Seasonal variability of the cold pool over the Mid-Atlantic Bight continental shelf. J Geophys Res C Oceans 123:8203–8226

Cole TVN, Hamilton P, Henry AG, Duley P, Pace RM III, White BN, Frasier T (2013) Evidence of a North Atlantic right whale *Eubalaena glacialis* mating ground. Endang Species Res 21:55–64

Cooke JG (2020) *Eubalaena glacialis*. The IUCN Red List of Threatened Species 2020:e.T41712A162001243. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T41712A162001243.en (accessed 24 Nov 2020)

Corkeron P, Hamilton P, Bannister J, Best P and others (2018) The recovery of North Atlantic right whales, *Eubalaena glacialis*, has been constrained by human-caused mortality. R Soc Open Sci 5:180892

Davies KTA, Brillant SW (2019) Mass human-caused mortality spurs federal action to protect endangered North Atlantic right whales in Canada. Mar Policy 104:157–162

Davies KTA, Vanderlaan ASM, Smedbol RK, Taggart CT (2015) Oceanographic connectivity between right whale critical habitats in Canada and its influence on whale abundance indices during 1987–2009. J Mar Syst 150: 80–90

Davies KTA, Brown MW, Hamilton PK, Knowlton AR, Taggart CT, Vanderlaan ASM (2019) Variation in North Atlantic right whale *Eubalaena glacialis* occurrence in the Bay of Fundy, Canada, over three decades. Endang Species Res 39:159–171

Davis GE, Baumgartner MF, Bonnell JM, Bell J and others (2017) Long-term passive acoustic recordings track the changing distribution of North Atlantic right whales (*Eubalaena glacialis*) from 2004 to 2014. Sci Rep 7:13460

Deakos MH, Baker JD, Bejder L (2011) Characteristics of a manta ray *Manta alfredi* population off Maui, Hawaii, and implications for management. Mar Ecol Prog Ser 429:245–260

Dinis A, Alves F, Nicolau C, Ribeiro C, Kaufmann M, Cañadas A, Freitas L (2016) Bottlenose dolphin *Tursiops truncatus* group dynamics, site fidelity, residency and movement patterns in the Madeira Archipelago (North-East Atlantic). Afr J Mar Sci 38:151–160

Dolman S, Simmonds M (2010) Towards best environmental practice for cetacean conservation in developing Scotland's marine renewable energy. Mar Policy 34: 1021–1027

Firestone J, Lyons SB, Wang C, Corbett JJ (2008) Statistical modeling of North Atlantic right whale migration along the mid-Atlantic region of the eastern seaboard of the United States. Biol Conserv 141:221–232

Fisheries and Oceans Canada (2014) Recovery strategy for the North Atlantic right whale (*Eubalaena glacialis*) in Atlantic Canadian waters. Species at Risk Act recovery strategy series. Fisheries and Oceans Canada, Ottawa

Foley HJ, Holt RC, Hardee RE, Nilsson PB and others (2011) Observations of a western North Atlantic right whale (*Eubalaena glacialis*) birth offshore of the protected southeast US critical habitat. Mar Mamm Sci 27:E234–E240

Frasier TR, Hamilton PK, Brown MW, Conger LA and others (2007) Patterns of male reproductive success in a highly promiscuous whale species: the endangered North Atlantic right whale. Mol Ecol 16:5277–5293

Freire R, Pe'eri S, Madore B, Rzhanov Y, Alexander L, Parrish CE, Lippmann TC (2015) Monitoring near-shore bathymetry using a multi-image satellite-derived bathymetry approach. US Hydrographic Conference 2015

Ganley LC, Brault S, Mayo CA (2019) What we see is not what there is: estimating North Atlantic right whale *Eubalaena glacialis* local abundance. Endang Species Res 38:101–113

Getis A, Ord JK (1992) The analysis of spatial association by use of distance statistics. Geogr Anal 24:189–206

Gowan TA, Ortega-Ortiz JG, Hostetler JA, Hamilton PK and others (2019) Temporal and demographic variation in partial migration of the North Atlantic right whale. Sci Rep 9:353

Hamilton PK, Marx MK, Kraus SD (1995) Weaning in North Atlantic right whales. Mar Mamm Sci 11:386–390

Hamilton PK, Knowlton AR, Marx MK (2007) Right whales tell their own stories: the photo-identification catalog. In: Kraus SD, Rolland RM (eds) The urban whale: North Atlantic right whales at the crossroads. Harvard University Press, Cambridge, MA, p 75–104

Hatch LT, Clark CW, Van Parijs SM, Frankel AS, Ponirakis DW (2012) Quantifying loss of acoustic communication space for right whales in and around a US national marine sanctuary. Conserv Biol 26:983–994

Hill D, Arnold R (2012) Building the evidence base for ecological impact assessment and mitigation. J Appl Ecol 49:6–9

Hu SD, Townsend W, Chen C, Cowles G, Beardsley RC, Rubao J, Houghton RW (2008) Tidal pumping and nutrient fluxes on Georges Bank: a process-oriented modeling study. J Mar Syst 74:528–544

IWC Int (International Whaling Commission) (2001) Report of the workshop on the comprehensive assessment of right whales: a worldwide comparison. J Cetacean Res Manag 1–35. Available at https://journal.iwc.int/index.php/jcrm/article/view/270

Kenney RD (2019) The North Atlantic Right Whale Consortium database: a guide for users and contributors, version 6. North Atlantic Right Whale Consortium Ref Doc 2019-02. University of Rhode Island, Narragansett, RI

Khan C, Cole T, Duley P, Henry A, Gatzke J (2011) North Atlantic right whale sighting survey (NARWSS) and right whale sighting advisory system (RWSAS) 2010 results summary. US Dep Commer, Northeast Fish Sci Cent Ref Doc 11-05

Knowlton AR, Kraus SD, Kenney RD (1994) Reproduction in North Atlantic right whales (*Eubalaena glacialis*). Can J Zool 72:1297–1305

Köppel J (2017) Wind energy and wildlife interactions. Presentations from the CWW2015 conference. Springer, Cham

Kraus SD, Hatch JJ (2001) Mating strategies in the North Atlantic right whale (*Eubalaena glacialis*). J Cetacean Res Manag Spec Issue 2:237–244

Kraus SD, Rolland RM (2007) The urban whale syndrome. In: Kraus SD, Rolland RM (eds) The urban whale: North Atlantic right whales at the crossroads. Harvard University Press, Cambridge, MA, p 488–513

Kraus SD, Moore KE, Price CA, Crone MJ, Watkins WA, Winn HE, Prescott JH (1986) The use of photographs to identify individual North Atlantic right whales (*Eubalaena glacialis*). Rep Int Whal Comm Spec Issue 10:145–151

Kraus SD, Hamilton P, Kenney RD, Knowlton A, Slay CK (2001) Reproductive parameters of the North Atlantic right whale. J Cetacean Res Manag Spec Issue 2:231–236

Kraus SD, Kenney RD, Mayo CA, McLellan WA, Moore MJ, Nowacek DP (2016a) Recent scientific publications cast doubt on North Atlantic right whale future. Front Mar Sci 3:137

Kraus SD, Leiter S, Stone K, Wikgren B and others (2016b) Northeast large pelagic survey collaborative aerial and acoustic surveys for large whales and sea turtles. OCS Study BOEM 2016-054. US Department of the Interior, Bureau of Ocean Energy Management, Sterling, VA

Leiter SM, Stone KM, Thompson JL, Accardo CM and others (2017) North Atlantic right whale *Eubalaena glacialis* occurrence in offshore wind energy areas near Massachusetts and Rhode Island, USA. Endang Species Res 34: 45–59

Lundberg P (1988) The evolution of partial migration in birds. Trends Ecol Evol 3:172–175

Madsen PT, Wahlberg M, Tougaard J, Lucke K, Tyack P (2006) Wind turbine underwater noise and marine mammals: implications of current knowledge and data needs. Mar Ecol Prog Ser 309:279–295

Martin J, Tolon V, Morellet N, Santin-Janin H and others (2018) Common drivers of seasonal movements on the migration — residency behavior continuum in a large herbivore. Sci Rep 8:7631

Mayo CA, Ganley L, Hudak CA, Brault S, Marx MK, Burke E, Brown MW (2018) Distribution, demography, and behavior of North Atlantic right whales (*Eubalaena glacialis*) in Cape Cod Bay, Massachusetts, 1998–2013. Mar Mamm Sci 34:979–996

McCoy E, Burce R, David D, Aca EQ and others (2018) Long-term photo-identification reveals the population dynamics and strong site fidelity of adult whale sharks to the coastal waters of Donsol, Philippines. Front Mar Sci 5:271

McKinney JA, Hoffmayer ER, Holmberg J, Graham RT and others (2017) Long-term assessment of whale shark population demography and connectivity using photo-identification in the western Atlantic Ocean. PLOS ONE 12: e0180495

Menz MH, Reynolds D, Gao B, Hu G, Chapman J, Wotton KR (2019) Mechanisms and consequences of partial migration in insects. Front Ecol Evol 7:403

Meyer-Gutbrod EL, Greene CH, Davies KTA (2018) Marine species range shifts necessitate advanced policy planning: the case of the North Atlantic right whale. Oceanography 31:19–23

NARWC (North Atlantic Right Whale Consortium) (2019) North Atlantic Right Whale Consortium Sightings database 4/15/2019. Anderson Cabot Center for Ocean Life at the New England Aquarium, Boston, MA

NARWC (2020) North Atlantic Right Whale Consortium Identification database 6/19/2020. Anderson Cabot Center for Ocean Life at the New England Aquarium, Boston, MA

NMFS (National Marine Fisheries Service) (2008) Endangered fish and wildlife; final rule to implement speed restrictions to reduce the threat of ship collisions with North Atlantic right whales. US Dep Commer, 50 CFR 224, Fed Reg 73:60173–60191

NMFS (2016) Endangered and threatened species; critical habitat for endangered North Atlantic right whale. Fed Reg 81:4838–4874

NMFS (2020) North Atlantic right whale (*Eubalaena glacialis*) vessel speed rule assessment. National Marine Fisheries Service, Office of Protected Resources, Silver Spring, MD. https://media.fisheries.noaa.gov/2021-01/FINAL_NARW_Vessel_Speed_Rule_Report_Jun_2020.pdf?null

Nowacek DP, Johnson MP, Tyack PL (2004) North Atlantic right whales (*Eubalaena glacialis*) ignore ships but respond to alerting stimuli. Proc R Soc B 271:227–231

Ott RL (1994) An introduction to statistical methods and data analysis. Duxbury Press, Belmont, CA

Oxoli D, Prestifilippo G, Bertocchi D, Zurbaràn M (2017) Enabling spatial autocorrelation mapping in QGIS: the Hotspot Analysis plugin. Geoing Ambient e Mineraria 2: 45–50

Pace RM III, Corkeron PJ, Kraus SD (2017) State–space mark–recapture estimates reveal a recent decline in abundance of North Atlantic right whales. Ecol Evol 7: 8730–8741

Pace RM, Williams R, Kraus SD, Knowlton AR, Pettis HM (2021) Cryptic mortality of North Atlantic right whales. Conserv Sci Pract 2021:e346

Parks SE, Brown MW, Conger LA, Hamilton PK and others (2007a) Occurrence, composition, and potential functions of North Atlantic right whale (*Eubalaena glacialis*) surface active groups. Mar Mamm Sci 23:868–887

Parks SE, Clark CW, Tyack PL (2007b) Short- and long-term changes in right whale calling behavior: the potential effects of noise on acoustic communication. J Acoust Soc Am 122:3725–3731

Parks SE, Urazghildiiev I, Clark CW (2009) Variability in ambient noise levels and call parameters of North Atlantic right whales in three habitat areas. J Acoust Soc Am 125: 1230–1239

Parks SE, Johnson M, Nowacek D, Tyack PL (2011) Individual right whales call louder in increased environmental noise. Biol Lett 7:33–35

Parsons ECM, Birks I, Evans PGH, Gordon JG, Shrimpton JH, Pooley S (2000) The possible impacts of military activity on cetaceans in West Scotland. Eur Res Cetaceans 14: 185–190

Paskyabi MB (2015) Offshore wind farm wake effect on stratification and coastal upwelling. Energy Procedia 80: 131–140

Paskyabi MB, Fer I (2012) Upper ocean response to large wind farm effect in the presence of surface gravity waves. Energy Procedia 24:245–254

Patrician MR, Biedron IS, Esch HC, Wenzel FW and others (2009) Evidence of a North Atlantic right whale calf (*Eubalaena glacialis*) born in northeastern US waters. Mar Mamm Sci 25:462–477

PCCS (Provincetown Center for Coastal Studies) (2005) Toward an ocean vision for the Nantucket Shelf Region Part I. Review of the environmental characteristics of the Nantucket Shelf Region. Part II. Management options for resource protection and sustainable uses. Provincetown Center for Coastal Studies Coastal Solutions Initiative, Provincetown, MA

Pendleton DE, Sullivan PJ, Brown MW, Cole TVN and others (2012) Weekly predictions of North Atlantic right whale *Eubalaena glacialis* habitat reveal influence of prey abundance and seasonality of habitat preferences. Endang Species Res 18:147–161

Pettis HM, Pace RM III, Hamilton PK (2020) North Atlantic Right Whale Consortium 2019 annual report card. Report to North Atlantic Right Whale Consortium. NARWC, Boston, MA

Pettis HM, Pace RM III, Hamilton PK (2021) North Atlantic Right Whale Consortium 2020 annual report card. Report to North Atlantic Right Whale Consortium. NARWC, Boston, MA

QGIS Development Team (2018) QGIS geographic information system. Open-Source Geospatial Foundation. https://www.qgis.org

Quintana-Rizzo E, Kraus S, Baumgartner MF (2018) Megafauna aerial surveys in the wind energy areas of Massachusetts and Rhode Island with emphasis on large whales. Progress report submitted to the Massachusetts Clean Energy Center. New England Aquarium Anderson Cabot Center for Ocean Life, Boston, MA

Quintana-Rizzo E, O'Brien O, Baumgartner MF (2019a) Megafauna aerial surveys in the wind energy areas of Massachusetts and Rhode Island with emphasis on large whales. Monthly report No. 26: August 2019. Prepared for MassCEC, Boston, MA. New England Aquarium Anderson Cabot Center for Ocean Life, Boston, MA

Quintana-Rizzo E, O'Brien O, Baumgartner MF (2019b) Megafauna aerial surveys in the wind energy areas of Massachusetts and Rhode Island with emphasis on large whales. Monthly report No. 27: September 2019. Prepared for MassCEC, Boston, MA. New England Aquarium Anderson Cabot Center for Ocean Life, Boston, MA

Record NR, Runge JA, Pendleton DE, Balch WM and others (2019) Rapid climate-driven circulation changes threaten conservation of endangered North Atlantic right whales. Oceanography 32:162–169

Richardson WJ, Miller GW, Greene CR (1999) Displacement of migrating bowhead whales by sounds from seismic surveys in shallow waters of the Beaufort Sea. J Acoust Soc Am 106:2281

Robinson R, Crick HQP, Learmonth JA, Maclean IMD and others (2009) Travelling through a warming world: climate change and migratory species. Endang Species Res 7:87–99

Rolland RM, Parks SE, Hunt KE, Castellote M and others (2012) Evidence that ship noise increases stress in right whales. Proc R Soc B 279:2363–2368

Runge CA, Martin TG, Possingham HP, Willis SG, Fuller RA (2014) Conserving mobile species. Front Ecol Environ 12:395–402

Saba VS, Hyde KJW, Rebuck ND, Friedland KD, Hare JA, Kahru M, Fogarty MJ (2015) Physical associations to spring phytoplankton biomass interannual variability in the US northeast continental shelf. J Geophys Res Biogeosci 120:205–220

Schick RS, Halpin PN, Read AJ, Slay CK and others (2009) Striking the right balance in right whale conservation. Can J Fish Aquat Sci 66:1399–1403

Segtnan OH, Christakos K (2015) Effect of offshore wind farm design on the vertical motion of the ocean. Energy Procedia 80:213–222

Sharp SM, McLellan WA, Rotstein DS, Costidis AM and others (2019) Gross and histopathologic diagnoses from North Atlantic right whale *Eubalaena glacialis* mortalities between 2003 and 2018. Dis Aquat Org 135:1–31

Stone CJ, Tasker ML (2006) The effects of seismic airguns on cetaceans in UK waters. J Cetacean Res Manag 8:255–263

Stone KM, Leiter SM, Kenney RD, Wikgren BC, Thompson JL, Taylor JKD, Kraus SD (2017) Distribution and abundance of cetaceans in a wind energy development area offshore of Massachusetts and Rhode Island. J Coast Conserv 21:527–543

Thompson PM, Lusseau D, Barton T, Simmons D, Rusin J, Helen B (2010) Assessing the responses of coastal cetaceans to the construction of offshore wind turbines. Mar Pollut Bull 60:1200–1208

Thomsen F, Lüdemann K, Kafemann R, Piper W (2006) Effects of offshore wind farm noise on marine mammals and fish. Biola, Hamburg, on behalf of COWRIE

van der Hoop J, Corkeron P, Moore M (2017) Entanglement is a costly life-history stage in large whales. Ecol Evol 7:92–106

Ward-Geiger LI, Knowlton AR, Amos AF, Pitchford TD, Mase-Guthrie B, Zoodsma BJ (2011) Recent sightings of the North Atlantic right whale in the Gulf of Mexico. Gulf Mex Sci 29:74–78

Whitehead H (2001) Analysis of animal movement using opportunistic individual identifications: applications to sperm whales. Ecology 82:1417–1432

Whitehead H (2007) Selection of models of lagged identification rates and lagged association rates using AIC and QAIC. Commun Stat Simul Comput 36:1233–1246

Whitehead H (2009) SOCPROG programs: analyzing animal social structures. Behav Ecol Sociobiol 63:765–778

Whitt AD, Dudzinski K, Laliberté JR (2013) North Atlantic right whale distribution and seasonal occurrence in nearshore waters off New Jersey, USA, and implications for management. Endang Species Res 20:59–69

Wilhelmsson D, Malm T, Ohman MC (2006) The influence of offshore windpower on demersal fish. ICES J Mar Sci 63:775–784

Wilson B, Hammond PS, Thompson PM (1999) Estimating size and assessing trends in a coastal bottlenose dolphin population. Ecol Appl 9:288–300

Wimmer T, Whitehead H (2004) Movements and distribution of northern bottlenose whales, *Hyperoodon ampullatus*, on the Scotian Slope and in adjacent waters. Can J Zool 82:1782–1794

Editorial responsibility: Ana Cañadas,
Durham, North Carolina, USA
Reviewed by: J. Roberts and 1 anonymous referee

Submitted: January 3, 2021
Accepted: May 27, 2021
Proofs received from author(s): July 13, 2021

Current Biology

Report

Decreasing body lengths in North Atlantic right whales

Highlights

- Whales with severe entanglements in fishing gear are stunted
- Whales whose mothers were entangled while nursing are stunted
- Body lengths have been decreasing since 1981
- Cumulative impacts in addition to entanglements may contribute to stunted growth

Authors

Joshua D. Stewart, John W. Durban,
Amy R. Knowlton, ...,
Wayne L. Perryman, Carolyn A. Miller,
Michael J. Moore

Correspondence

joshua.stewart@noaa.gov

In brief

Stewart et al. examine trends in body lengths in endangered North Atlantic right whales using aerial photogrammetry. They show that whales that have experienced severe entanglements in fishing gear are shorter than whales with no documented entanglements, and that body lengths of right whales have been decreasing over the past four decades.

Stewart et al., 2021, Current Biology *31*, 1–6
July 26, 2021
https://doi.org/10.1016/j.cub.2021.04.067

CellPress

Please cite this article in press as: Stewart et al., Decreasing body lengths in North Atlantic right whales, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.04.067

Current Biology

CellPress

Report

Decreasing body lengths in North Atlantic right whales

Joshua D. Stewart,[1,7,8,*] John W. Durban,[2,3] Amy R. Knowlton,[4] Morgan S. Lynn,[2] Holly Fearnbach,[5] Jacob Barbaro,[2] Wayne L. Perryman,[2] Carolyn A. Miller,[6] and Michael J. Moore[6]

[1]National Research Council Postdoctoral Fellow for Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, La Jolla Shores Drive, La Jolla, CA, 92037, USA

[2]Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, La Jolla Shores Drive, La Jolla, CA, 92037, USA

[3]Southall Environmental Associates, Inc., Soquel Dr., Aptos, CA, 95003, USA

[4]Anderson Cabot Center for Ocean Life, New England Aquarium, Boston, MA, 02110, USA

[5]Marine Mammal Research Program, SR3, SeaLife Response, Rehabilitation and Research, S 216th St., Des Moines, WA, 98198, USA

[6]Department of Biology, Woods Hole Oceanographic Institution, Woods Hole Rd., Woods Hole, MA, 02543, USA

[7]Twitter: @NOAAFish_WCRO

[8]Lead contact

*Correspondence: joshua.stewart@noaa.gov

https://doi.org/10.1016/j.cub.2021.04.067

SUMMARY

Whales are now largely protected from direct harvest, leading to partial recoveries in many previously depleted species.[1] However, most populations remain far below their historical abundances and incidental human impacts, especially vessel strikes and entanglement in fishing gear, are increasingly recognized as key threats.[2] In addition, climate-driven changes to prey dynamics are impacting the seasonal foraging grounds of many baleen whales.[2] In many cases these impacts result directly in mortality. But it is less clear how widespread and increasing sub-lethal impacts are affecting life history, individual fitness, and population viability. We evaluated changes in body lengths of North Atlantic right whales (NARW) using aerial photogrammetry measurements collected from crewed aircraft and remotely operated drones over a 20-year period (Figure 1). NARW have been monitored consistently since the 1980s and have been declining in abundance since 2011 due primarily to deaths associated with entanglements in active fishing gear and vessel strikes.[3] High rates of sub-lethal injuries and individual-level information on age, size and observed entanglements make this an ideal population to evaluate the effects that these widespread stressors may have on individual fitness. We find that entanglements in fishing gear are associated with shorter whales, and that body lengths have been decreasing since 1981. Arrested growth may lead to reduced reproductive success[4,5] and increased probability of lethal gear entanglements.[6] These results show that sub-lethal stressors threaten the recoveries of vulnerable whale populations even in the absence of direct harvest.

RESULTS AND DISCUSSION

We combined age and length data collected from crewed aircraft in 2000–2002 and from remotely operated drones in 2016-2019 in a growth model mirroring a previous analysis of the 2000–2002 data.[7] We modified the 2-phase Gompertz growth equation to include model-estimated effects on asymptotic length for: (a) birth year, (b) duration of entanglements with attached fishing gear, (c) whether a whale's mother experienced a severe entanglement injury while nursing that whale, and (d) the number of lactation events a female whale experienced, which is known to be one of the most significant energetic expenditures for right whales.[8] We considered the cumulative effects of covariates from birth until age 10 (or until the time of measurement if it occurred prior to age 10), as the expected length at age 10 is more than 95% of the estimated asymptotic length and constraints to growth after that point would be unlikely to measurably affect whale lengths.

Across all years we collected 202 length measurements of 129 individual whales: 133 measurements from crewed aircraft and 69 from remotely operated drones. 76 whales were measured once, 36 twice (in separate years), 14 three times, and 3 four times. The ages of measured whales ranged from <1 to 37 years old, including whales born from 1981 to 2019. Eleven whales in our dataset were observed with attached gear; 8 of those whales were measured once, 2 were measured twice, and 1 was measured four times. Gear entanglement durations (midpoints) ranged from 65 to 334 days. Seven measured whales had known severe maternal entanglement injuries; 1 of those whales was measured twice. No whales in our dataset had both a maternal entanglement injury and an entanglement with attached gear. Nine measured whales had one lactation event, and 1 whale had two lactation events prior to age 10.

Birth year had the greatest effect on the estimated asymptotic length of NARW (99.8% of posterior distribution <0). The estimated

Please cite this article in press as: Stewart et al., Decreasing body lengths in North Atlantic right whales, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.04.067

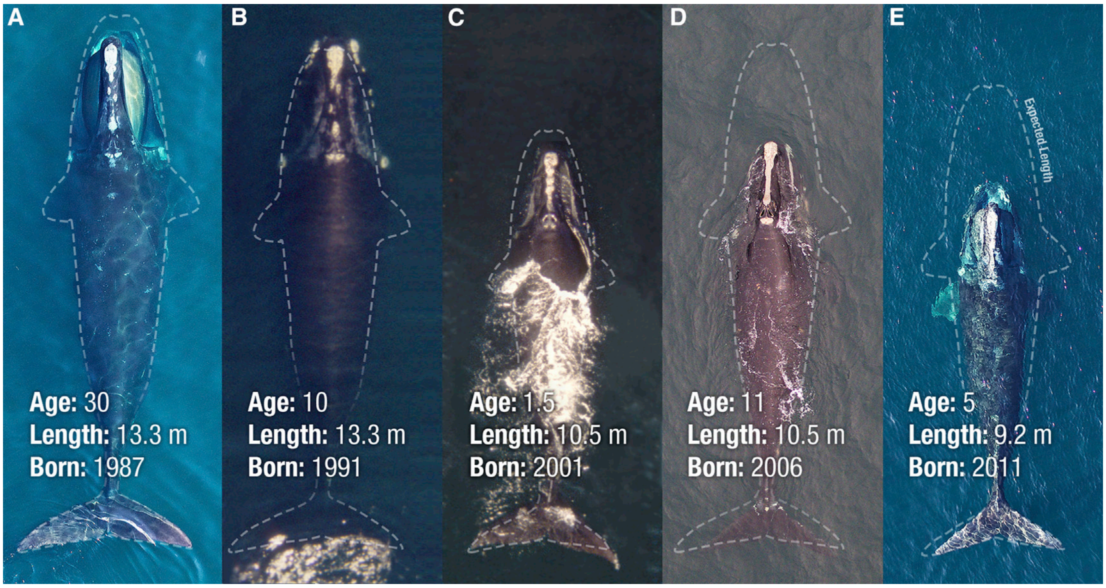


Figure 1. Stunted North Atlantic right whales

A scaled photo illustration comparing the body lengths of (A) Whale 1703, imaged in 2017 at age 30 using a remotely operated drone, (B) Whale 2145, imaged in 2001 at age 10 from a crewed aircraft, (C) Whale 3180, imaged in 2002 at age 1.5 from a crewed aircraft, (D) Whale 3617, imaged in 2017 at age 11 using a drone, and (E) Whale 4130, imaged in 2016 at age 5 using a drone. The dashed outline in each panel represents the median model-estimated body length for a whale of the same age born in 1981 with no history of entanglements or maternal entanglements. Note the entanglement scarring around the caudal peduncle in (D). Figure design by Madeline Wukusick.

effect of birth year was an asymptotic length 0.025 m (95% credible intervals 0.01–0.04) shorter than the baseline asymptotic length per year born after 1981. With the maximum effect of birth year applied, a whale born in 2019 is expected to reach a maximum length approximately 1 m shorter than a whale born in 1981 (Figure 2). This corresponds to a 7.3% decline in maximum body length. Known entanglements of a whale with attached gear (97.4% of posterior distribution <0) and entanglements of its mother during nursing (99.7% of posterior distribution <0) also had negative effects on expected maximum length, of approximately −0.64 m (4.7% length reduction) and −0.69 m (5.0% length reduction), respectively. The effect of entanglement with attached gear was applied as a continuous effect, so a whale with an entanglement duration that is half the maximum duration is expected to experience half of that negative effect on asymptotic length, or an expected asymptotic length 0.32 m shorter than baseline. There was no significant effect of the number of lactation events (61.2% of posterior distribution >0) on expected maximum length of right whales (Figure 3). The estimates of error around the model-estimated mean length-at-age were different across altimeter types. GPS altimeter measurements had the highest error (median 0.63, 95% CI 0.26–1.01 m), followed by laser altimeter measurements (0.52, 0.19–0.77 m) and radar altimeter measurements (0.27, 0.01–0.48 m).

Our results demonstrate that NARW born in recent years have experienced stunted growth, and over the same period that we detected this effect they have experienced increasing rates of entanglement.[3] As a result, NARW appear to have less energy to devote to early growth. A portion of the estimated length reduction was directly attributable to entanglements, but the effect size of entanglements was smaller than the effect size of birth year. We posit that the birth year effects on asymptotic length represent the cumulative effects of dynamic and hard-to-observe impacts on individual NARW that may include unrecorded entanglements, shifting prey seascapes, vessel strikes, and foraging interference from vessel traffic (Figure 4). For example, entanglements of NARW are imperfectly observed, and many whales have evidence of entanglement injuries without direct observations of attached gear; in these scar-only cases it is impossible to determine the duration of those entanglements.[9] Even direct observations of attached gear events have only approximate entanglement durations (we considered the midpoint between minimum and maximum possible duration of each entanglement) and there is almost certainly a large amount of noise introduced into our analyses as a result of these imperfect observations. Consequently, while our analyses detected a negative effect of entanglements on whale length, we cannot rule out a larger true effect size than our estimate; for example, if entanglements that were not recorded in our dataset contributed to restricted growth that was instead reflected in birth year effects.

The abundance of *Calanus finmarchicus*, a primary copepod prey item for NARW, has fluctuated in the Gulf of Maine over the past 40 years (Figure 4), apparently driving reproductive output in the NARW population.[11] *C. finmarchicus* is a subarctic species, and its distribution is expected to shift poleward as the North Atlantic warms,[12] leading to projected abundance declines in the Gulf of Maine.[13] There has not been a steady decline in *C. finmarchicus* abundance coincident with the decreasing NARW body lengths reported here. However, in the past decade, sighting rates of NARW on their typical foraging grounds have declined, and the timing and geographic distribution of peak

Please cite this article in press as: Stewart et al., Decreasing body lengths in North Atlantic right whales, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.04.067

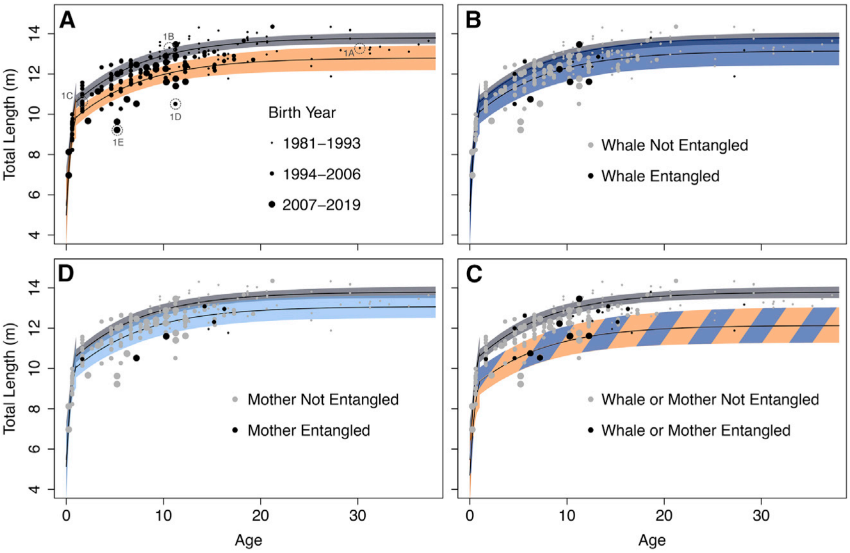


Figure 2. Growth curves for North Atlantic right whales

The gray curve in each panel represents the expected length at age for a typical NARW born in 1981 that experiences no entanglements and does not have an entangled mother while nursing. Solid lines represent median estimates and colored curves represent 95% Bayesian credible intervals for the mean length at age of whales with covariate effects applied.

(A) The expected length at age for a typical whale born in 2019 that experiences no entanglements and does not have an entangled mother while nursing (orange curve). Black points are observed lengths of known-age whales, with point size indicating the birth year of the whale (in three ranges for clarity; all panels). The dashed circles and corresponding labels indicate the whales pictured in Figure 1 panels A–E.

(B) The expected length at age for a typical whale born in 1981 that experiences a severe attached-gear entanglement (maximum effect size of a 334-day entanglement duration applied; dark blue curve). Light gray points are whales with no observed attached-gear entanglements; black points are whales with observed attached-gear entanglements. Note that duration of entanglement is not indicated.

(C) The expected length at age for a typical whale born in 1981 whose mother is entangled while that whale is nursing (light blue curve). Black points are whales whose mothers were detected with a severe entanglement injury while the measured whale was a nursing calf.

(D) The expected length at age for a typical whale born in 2019 that experiences a severe entanglement (maximum effect size; orange and blue striped curve). In other words, the cumulative effects of birth year and entanglements. Black points are whales with observed attached-gear entanglements or whales whose mother was known to have a severe entanglement injury while the measured whale was nursing, as these effect sizes were comparable. See model diagnostics in Figures S1–S3.

C. finmarchicus densities have been shifting.[14] These changes may indicate a deteriorating foraging environment in the Gulf of Maine. Given that NARW are dependent on hyper-dense patches of copepods to maximize foraging efficiency,[15] coarse regional indices of *C. finmarchicus* abundance (e.g., Figure 4) may not adequately represent foraging conditions that could affect growth rates. Other anthropogenic factors such as increasing vessel noise could also be interfering with foraging behavior and restricting NARW growth[16] (Figure 4).

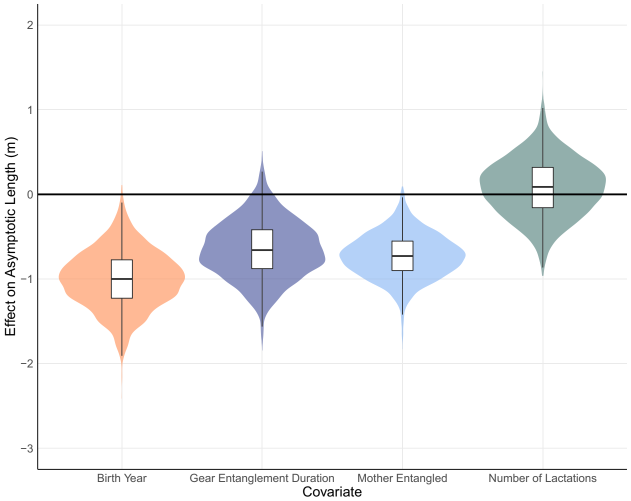


Figure 3. Covariate effects on asymptotic length of North Atlantic right whales

Violin plots represent the Bayesian posterior distributions of the estimated effect (in meters) of each covariate on the asymptotic length parameter in the 2-phase Gompertz growth equation. The interior boxplots represent the median effect size (horizontal black line), the 50% posterior density intervals (white box) and the 95% credible intervals (vertical black line). The effects of birth year, gear entanglement duration, maternal entanglement, and number of lactations are scaled to the maximum effect size as the minimum covariate values for each of these is zero. We considered an effect significant if >95% of posterior draws were below (or above) zero.

In baleen whales, larger maternal size and body condition are associated with faster calf growth rates and larger calves.[4,5] Decreasing body size may therefore be associated with smaller calves and lower calf survivorship, or potentially delayed first calving and lower reproductive success in females. NARW exhibit generally poor body condition compared to other populations of right whales,[17,18] which could contribute to synergistic negative effects where females in poor condition produce smaller calves that ultimately reach smaller maximum sizes, further contributing to reduced calf growth and declining calf condition. In addition, our results suggest that sub-lethal entanglements constrain overall body size in NARW, which may in turn make them less resilient to future entanglements by reducing their absolute energetic reserves and increasing the probability of a lethal entanglement.[6]

Mortality from vessel strikes and entanglements in fishing gear are thought to be a major driver of the current NARW population decline,[3] but the observed changes in body lengths also indicate a troubling trend that may have further negative effects on population viability in this critically endangered species, with chronic sub-lethal health effects slowing growth and potentially reducing reproductive success. Changes in body size can also be a leading indicator of population collapse,[19–21] further highlighting the ongoing and compounding threats to the NARW population. Implementing solutions to reduce entanglements and other anthropogenic impacts could give North Atlantic right whales increased

Please cite this article in press as: Stewart et al., Decreasing body lengths in North Atlantic right whales, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.04.067

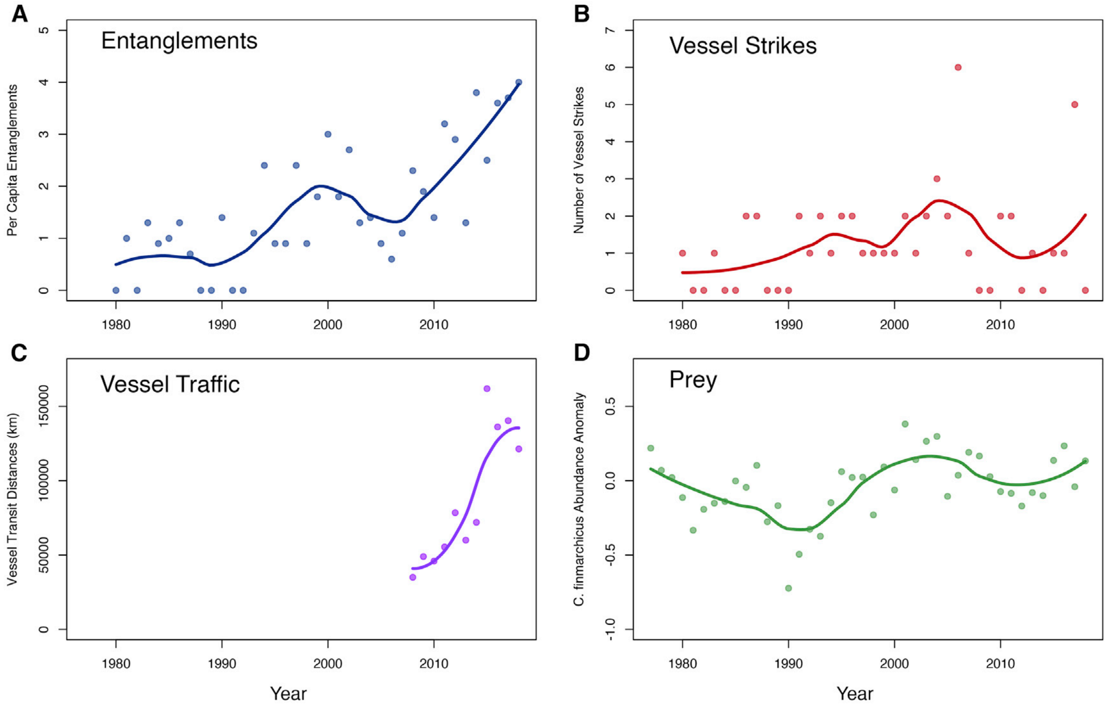


Figure 4. Possible cumulative impacts affecting right whale growth

Time series of potential stressors that could affect right whale energy budgets and foraging success.

(A) Number of new serious entanglements (attached gear or severe injuries) observed each year, standardized by the number of individual whales observed during field surveys; source ref.[9]

(B) Number of vessel strikes resulting in blunt trauma or deep lacerations observed each year. Note that vessel strikes are raw counts and not per capita rates; source ref.[10]

(C) Cumulative vessel transit distances (in kilometers) within three special management areas that are NARW foraging hotspots: Cape Cod Bay, Race Point, and Great South Channel; source NMFS Right Whale Vessel Speed Rule Assessment, June 2020.

(D) *Calanus finmarchicus* abundance anomalies for the Gulf of Maine; source NOAA Ecosystem Dynamics and Assessment Branch ecodata. The lines in each panel are a loess smooth to the annual data.

resilience to adapt to changing prey dynamics and other climate-related impacts while maintaining population viability.

Changes to life history traits, such as growth rates and age or size at maturity, are well documented in heavily exploited species (in particular fishes).[22] Body size changes in mammals (both positive and negative) are also expected under changing climate conditions.[23,24] Our results suggest that humans are impacting the demographic characteristics of endangered and protected marine mammals through indirect and incidental pressures on vulnerable populations. Entanglements in fishing gear are a growing problem for migratory baleen whale species and a wide variety of marine mammals.[25] Extensive survey effort for the NARW population allowed the sub-lethal effects of entanglements to be directly (if imperfectly) estimated, but it is likely that other marine mammal species that experience chronic entanglements are being similarly affected.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
    - ○ Lead Contact
    - ○ Materials Availability
    - ○ Data and Code Availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2021.04.067.

ACKNOWLEDGMENTS

Hollis Europe and Brandon Tao contributed to drone photogrammetry data collection in 2018 and 2019, respectively. Technical support from Don LeRoi, Aerial Imaging Solutions, significantly contributed to the successes of both the crewed and drone photographic sampling efforts. All photo-identification data were processed by the New England Aquarium. Life history, entanglement and vessel strike events for identified individuals were provided with approval from the North Atlantic Right Whale Consortium. We thank Peter Corkeron and Sean Hayes for supporting data collection efforts in Cape Cod Bay. We are grateful to the NOAA Fisheries Office of Science and Technology for supporting the development and application of photogrammetry drones and to the

NOAA Office of Marine and Aviation Operations for supporting photogrammetry operations. We appreciate the efforts of the Atlantic Large Whale Disentanglement Network in documenting entanglement sightings. We thank Sean Hayes, Allison Henry, and Caroline Good for their assistance in locating additional data sources of entanglements, vessel strikes and vessel traffic. We are grateful for feedback on earlier version of this manuscript by Jim Carretta, Tomoharu Eguchi, Dave Weller, and two anonymous reviewers. Photogrammetry data from 2016-2019 were collected with support from NOAA grant NA14OAR4320158. Funding to the New England Aquarium for curation of the photo-identification catalog is provided by NOAA Contract 1305M2-18-P-NFFM-0108. This analysis was performed while J.D.S. held an NRC Research Associateship award at the NOAA Southwest Fisheries Science Center.

AUTHOR CONTRIBUTIONS

J.D.S., J.W.D., and M.J.M. conceived the analysis; J.W.D., M.J.M., and H.F. conceived the study; J.W.D., M.J.M., A.R.K., H.F., and W.L.P. obtained funding for data collection; J.W.D., M.S.L., M.J.M., H.F., J.B., A.R.K., C.A.M., and W.L.P. collected and processed data; J.D.S. analyzed data and drafted the manuscript; all authors edited and revised the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: February 16, 2021
Revised: April 12, 2021
Accepted: April 26, 2021
Published: June 3, 2021

REFERENCES

1. Magera, A.M., Mills Flemming, J.E., Kaschner, K., Christensen, L.B., and Lotze, H.K. (2013). Recovery trends in marine mammal populations. PLoS ONE *8*, e77908.
2. Thomas, P.O., Reeves, R.R., and Brownell, R.L. (2016). Status of the world's baleen whales. Mar. Mamm. Sci. *32*, 682–734.
3. National Marine Fisheries Service (2019). North Atlantic Right Whale (*Eubalaena glacialis*) (Western Atlantic Stock. NOAA Mar. Mammal Stock Assess).
4. Christiansen, F., Vivier, F., Charlton, C., Ward, R., Amerson, A., Burnell, S., and Bejder, L. (2018). Maternal body size and condition determine calf growth rates in Southern right whales. Mar. Ecol. Prog. Ser. *592*, 267–282.
5. Christiansen, F., Dujon, A.M., Sprogis, K.R., Arnould, J.P.Y., and Bejder, L. (2016). Noninvasive unmanned aerial vehicle provides estimates of the energetic cost of reproduction in humpback whales. Ecosphere *7*, 1–18.
6. van der Hoop, J.M., Corkeron, P., Henry, A.G., Knowlton, A.R., and Moore, M.J. (2017). Predicting lethal entanglements as a consequence of drag from fishing gear. Mar. Pollut. Bull. *115*, 91–104.
7. Fortune, S.M.E., Trites, A.W., Perryman, W.L., Moore, M.J., Pettis, H.M., and Lynn, M.S. (2012). Growth and rapid early development of North Atlantic right whales (*Eubalaena glacialis*). J. Mammal. *93*, 1342–1354.
8. Fortune, S.M.E., Trites, A.W., Mayo, C.A., Rosen, D.A.S., and Hamilton, P.K. (2013). Energetic requirements of North Atlantic right whales and the implications for species recovery. Mar. Ecol. Prog. Ser. *478*, 253–272.
9. Knowlton, A.R., Hamilton, P.K., Marx, M.K., Pettis, H.M., and Kraus, S.D. (2012). Monitoring North Atlantic right whale E*ubalaena glacialis* entanglement rates: A 30 yr retrospective. Mar. Ecol. Prog. Ser. *466*, 293–302.
10. Moore, M.J., Rowles, T.K., Fauquier, D.A., Baker, J.D., Biedron, I., Durban, J.W., Hamilton, P.K., Henry, A.G., Knowlton, A.R., McLellan, W.A., et al. (2021). REVIEW: Assessing North Atlantic right whale health: threats, and development of tools critical for conservation of the species. Dis. Aquat. Organ. *143*, 205–226.
11. Meyer-Gutbrod, E.L., Greene, C.H., Sullivan, P.J., and Pershing, A.J. (2015). Climate-associated changes in prey availability drive reproductive dynamics of the North Atlantic right whale population. Mar. Ecol. Prog. Ser. *535*, 243–258.
12. Reygondeau, G., and Beaugrand, G. (2011). Future climate-driven shifts in distribution of *Calanus finmarchicus*. Glob. Change Biol. *17*, 756–766.
13. Grieve, B.D., Hare, J.A., and Saba, V.S. (2017). Projecting the effects of climate change on *Calanus finmarchicus* distribution within the U.S. Northeast Continental Shelf. Sci. Rep. *7*, 6264.
14. Record, N.R., Runge, J.A., Pendleton, D.E., Balch, W.M., Davies, K.T.A., Pershing, A.J., et al. (2019). Rapid climate-driven circulation changes threaten conservation of endangered North Atlantic right whales. Oceanography (Wash. D.C.) *32*, 162–169.
15. Kenney, R.D., Mayo, C.A., and Winn, H.E. (2001). Migration and foraging strategies at varying spatial scales in western North Atlantic right whales: a review of hypotheses. J. Cetacean Res. Manag. *2*, 251–260.
16. Blair, H.B., Merchant, N.D., Friedlaender, A.S., Wiley, D.N., and Parks, S.E. (2016). Evidence for ship noise impacts on humpback whale foraging behaviour. Biol. Lett. *12*.
17. Christiansen, F., Dawson, S., Durban, J., Fearnbach, H., Miller, C., Bejder, L., Uhart, M., Sironi, M., Corkeron, P., Rayment, W., et al. (2020). Population comparison of right whale body condition reveals poor state of the North Atlantic right whale. Mar. Ecol. Prog. Ser. *640*, 1–16.
18. Miller, C.A., Reeb, D., Best, P.B., Knowlton, A.R., Brown, M.W., and Moore, M.J. (2011). Blubber thickness in right whales *Eubalaena glacialis* and *Eubalaena australis* related with reproduction, life history status and prey abundance. Mar. Ecol. Prog. Ser. *438*, 267–283.
19. Clements, C.F., and Ozgul, A. (2016). Including trait-based early warning signals helps predict population collapse. Nat. Commun. *7*, 10984.
20. Calkins, D.G., Becker, E.F., and Pitcher, K.W. (1998). Reduced body size of female steller sea lions from a declining population in the Gulf of Alaska. Mar. Mamm. Sci. *14*, 232–244.
21. Guthrie, R.D. (2003). Rapid body size decline in Alaskan Pleistocene horses before extinction. Nature *426*, 169–171.
22. Hutchings, J.A., and Baum, J.K. (2005). Measuring marine fish biodiversity: Temporal changes in abundance, life history and demography. Philos. Trans. R. Soc. B Biol. Sci. *360*, 315–338.
23. Isaac, J.L. (2009). Effects of climate change on life history: Implications for extinction risk in mammals. Endanger. Species Res. *7*, 115–123.
24. Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L., and Heinsohn, R. (2011). Declining body size: a third universal response to warming? Trends Ecol. Evol. *26*, 285–291.
25. Read, A.J. (2008). The looming crisis: Interactions between marine mammals and fisheries. J. Mammal. *89*, 541–548.
26. Durban, J.W., Fearnbach, H., Perryman, W.L., and Leroi, D.J. (2015). Photogrammetry of killer whales using a small hexacopter launched at sea. J. Unmanned Veh. Syst. *3*, 131–135.
27. Dawson, S.M., Bowman, M.H., Leunissen, E., and Sirguey, P. (2017). Inexpensive aerial photogrammetry for studies of whales and large marine animals. Front. Mar. Sci. *4*, 1–7.
28. Perryman, W.L., and Lynn, M.S. (1993). Identification of geographic forms of common dolphin (*Delphinus delphis*) from aerial photogrammetry. Mar. Mamm. Sci. *9*, 119–137.
29. Miller, C.A., Best, P.B., Perryman, W.L., Baumgartner, M.F., and Moore, M.J. (2012). Body shape changes associated with reproductive status, nutritive condition and growth in right whales Eubalaena glacialis and E. australis. Mar. Ecol. Prog. Ser. *459*, 135–156.
30. Perryman, W.L., and Lynn, M.S. (2002). Evaluation of nutritive condition and reproductive status of migrating gray whales (*Eschrichtius robustus*) based on analysis of photogrammetric data. J. Cetacean Res. Manag. *4*, 155–164.
31. Kraus, S.D., Moore, K.E., Price, C.A., Crone, M.J., Watkins, W.A., Winn, H.E., et al. (1986). The use of photographs to identify individual North Atlantic right whales (*Eubalaena glacialis*). Rep. Int. Whaling Comm. *10*, 145–151.

Please cite this article in press as: Stewart et al., Decreasing body lengths in North Atlantic right whales, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.04.067

32. North Atlantic Right Whale Consortium (2020). North Atlantic Right Whale Consortium Identification Database 09/18/2020 (Anderson Cabot Cent. Ocean Life New Engl. Aquarium).

33. Knowlton, A.R., Robbins, J., Landry, S., McKenna, H., Kraus, S.D., and Werner, T.B. (2016). Effects of fishing gear strength on the severity of large whale entanglements. Conservation Biology *30*, 318–328.

34. van der Hoop, J., Corkeron, P., and Moore, M. (2016). Entanglement is a costly life-history stage in large whales. Ecol. Evol. *7*, 92–106.

35. Kato, H. (1988). Ossification Pattern of the Vertebral Epiphyses in the Southern Minke Whale (Sci. Reports Whales Res. Inst.), pp. 11–19.

36. Moran, M.M., Bajpai, S., George, J.C., Suydam, R., Usip, S., and Thewissen, J.G.M. (2014). Intervertebral and Epiphyseal Fusion in the Postnatal Ontogeny of Cetaceans and Terrestrial Mammals. J. Mamm. Evol. *22*, 93–109.

37. Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Proc. 3rd Int. Work. Distrib. Stat. Comput *124*.

38. R Core Team (2016). R: A language and environment for statistical computing (R Foundation for Statistical Computing).

39. Gelman, A., and Rubin, D.B. (1992). Inference from Iterative Simulation Using Multiple Sequences. Stat. Sci. *7*, 457–472.

Please cite this article in press as: Stewart et al., Decreasing body lengths in North Atlantic right whales, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.04.067

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
R	The R Project for Statistical Computing	V4.0.0
Just Another Gibbs Sampler (JAGS)	Plummer 2013	V4.2.0
Other		
126mm Reconnaissance Camera	Chicago Aerial	KA-76A
Remotely Operated Hexacopter	Aerial Imaging Solutions	APH-22
Digital Camera System	Olympus	E-PM2; 25mm Zuiko Lens

RESOURCE AVAILABILITY

Lead Contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Joshua Stewart (joshua.stewart@noaa.gov)

Materials Availability

This study did not generate new unique reagents

Data and Code Availability

All data and R code to replicate these analyses are available at http://github.com/stewart6/NARW-Growth.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Aerial photogrammetry measurements were collected from free-ranging North Atlantic Right Whales under NOAA National Marine Fisheries Service permits 21371, 17355 and 17355-01.

METHOD DETAILS

From 2000-2002, we used a fixed-winged, crewed airplane to collect aerial images of North Atlantic right whales (NARW) in the Bay of Fundy, Canada.[7] A 126mm format military reconnaissance camera captured images on film from approximately 250 m altitude. From 2016-2019 we flew a remotely controlled hexacopter drone at altitudes of approximately 50 m to collect images of NARW in Cape Cod Bay, U.S.A,[17] taking digital images using a 25mm lens mounted on an Olympus camera with micro 4/3 sensor.[26] Both methods achieved flat images that were undistorted across the entire frame. We collected altitude measurements using radar altimeters in 2000-2002,[7] drone GPS in 2016[17] and a laser altimeter[27] mounted on the vertical gimbal of the drone camera in 2017-2019. We established length estimates from image measurements by using altimetry data to convert image sensor distances to distances on the real scale.[7,26] We only selected images for use in length measurements when a whale was fully visible and appeared to be in flat orientation parallel to the water surface. In general, variability in repeated-measurements of total lengths of cetaceans is low, with average coefficients of variation typically ranging from approximately 1%–3%.[27–29] While altimeter inaccuracies can lead to both positive and negative length measurement errors, any movement or curvature of an animal will result in the animal appearing shorter from above than it actually is. To minimize this negative bias, and following previous studies using aerial photogrammetry to estimate cetacean lengths, we selected the longest measurement of each whale in cases of multiple measurements of an individual within a single sampling season[7,28,30]

We individually identified whales from aerial images based on their callosity patterns,[31] with known ages and birth years for individual whales provided by the Right Whale Consortium.[32] Directly observed entanglements with attached gear, as well as indirect evidence of entanglements (e.g., scarring) have been recorded for NARW since 1980.[9,32] Scarring patterns can provide approximate information about the severity of an entanglement injury (minor, moderate or severe),[33] but it is impossible to establish the duration of an entanglement based on scarring alone. Entanglements with attached gear provide quantitative—although still

Please cite this article in press as: Stewart et al., Decreasing body lengths in North Atlantic right whales, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.04.067

imperfect—information about entanglement duration. We estimated the minimum and maximum duration of entanglements with attached gear based on a whale's sighting records.[33] The minimum duration was calculated as the number of days between the date that a whale was first observed with gear attached and the date that a whale was last observed with gear attached. If a whale was first seen with attached gear on the same day that the gear was removed by a disentanglement team or shed by its next sighting, the minimum duration was recorded as one day. The maximum duration was calculated as the number of days between the most recent date that a whale was observed without attached gear prior to the first observation with attached gear, and the first observation without attached gear after the last observation with attached gear. For example, consider a whale that was seen on February 1st with no attached gear, March 10th with attached gear, May 1st with attached gear, and July 10th with no attached gear. The minimum entanglement duration would be March 10th – May 1st (52 days), and the maximum entanglement duration would be February 1st – July 10th (160 days). To account for the uncertainty in true entanglement duration, we used the midpoint between the minimum and maximum durations as our best estimate of entanglement duration. Growth rates in NARW slow considerably after age 10[7], so we used mid-point entanglement durations for any measured whale in our aerial photogrammetry dataset seen with attached gear during the first 10 years of life to represent a cumulative entanglement burden during early growth. If a length measurement was taken prior to age 10, we used the entanglement duration midpoint prior to that measurement. Entanglement duration was included as a continuous effect on asymptotic length (see model description below).

Maternal size and condition have been demonstrated to substantially impact calf growth rates in several populations of baleen whales, including southern hemisphere right whales.[4,5] This suggests that entanglements of a female with a dependent, nursing calf could affect calf growth if maternal energy stores are lost to excess drag from an entanglement.[34] In our dataset of aerial photogrammetry measurements, we had no records of measured whales whose mothers had an observed entanglement with attached gear while the measured whale was a nursing calf. However, there were three records of measured whales whose mothers were seen with attached gear that first appeared while the measured whale was < 1 year old and likely still nursing and eight records of measured whales whose mother was detected with attached gear or severe injuries that may have occurred when the calf was < 1 year old.[32] For measured whales whose mother had evidence of a severe entanglement injury or attached gear known to or likely to have occurred while the measured whale was nursing, we included a fixed effect of maternal entanglement on asymptotic length.

Lactation is an extremely costly life history event for right whales.[8] The energetic burden of supporting dependent calves could in theory reduce the amount of energy a female whale can devote to its own growth. We therefore considered the number of lactation events that a whale experienced[32] prior to age 10 as a continuous effect on the expected asymptotic length of that whale. If a whale was measured prior to age 10, we considered the number of lactation events experienced prior to measurement, similar to our handling of entanglement durations. For entanglement duration and number of lactation events, we scaled the covariate values associated with each measured whale to 1 by dividing the observed covariate by the maximum covariate value.

QUANTIFICATION AND STATISTICAL ANALYSIS

We based our growth model on the two-phase Gompertz growth function that was fit previously to age and length data for North Atlantic right whales collected between 2000 and 2002:[7]

$$S_t = Ae^{-ce^{-kt}}$$

where S is the expected length at age t, A is asymptotic length, c is the constant of integration, and k is the growth rate. This equation is fit separately in two phases to whales < 1 year old (Phase 1) and > 1 year old (Phase 2). We modified this equation to apply covariate effects to asymptotic length, such that:

$$S_{t,i} = A_i e^{-ce^{-kt}}$$

$$A_i = \widehat{A} + O_i$$

$$O_i = \sum_{j=1}^{n} Cov.Eff_{j,i}$$

$$Cov.Eff_{j,i} \sim N[Cov_{j,i} * \beta_j, \sigma_j]$$

where S is the expected length at age t for individual i, A is expected asymptotic length for individual i, $\widehat{A}$ is the asymptotic length shared across all whales before covariate effects are applied, and O is the asymptotic length offset for individual i. Cov is the covariate j (e.g., birth year, entanglement duration, etc.) experienced by whale i, and β is the model-estimated effect of covariate j. We introduce process error by allowing the estimated covariate effect $Cov.Eff$ to vary around the expected covariate effect with an independently estimated standard deviation σ for each covariate j. O is then calculated by summing the covariate effects $Cov.Eff$ for each

Please cite this article in press as: Stewart et al., Decreasing body lengths in North Atlantic right whales, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.04.067

individual *i.* We chose to apply covariate effects to asymptotic length because growth rate and asymptotic length are typically highly correlated in growth models, making it inappropriate to apply the same covariate to both parameters simultaneously. Whales are expected to have determinate growth due to the fusing of growth plates,[35,36] and we therefore applied covariate effects to asymptotic length rather than growth rate. This was based on the assumption that reduced early growth would lead to a truncated maximum attainable length for an individual, rather than slower growth that could eventually result in a similar maximum length to unaffected whales. In other words, we assume that the length a whale reaches by age 10-15 is likely to be close to the maximum size that whale can achieve. We applied the same model-estimated offset on asymptotic length to both growth phases. Our limited sample size of whales age < 1 (less than 10% of measured whales) contained no whales with attached gear or known maternal entanglements, and all but four measured calves were born in 2001, making the estimation of independent covariate effects for each growth phase impossible.

Previous analyses of NARW growth incorporated lengths from both aerial photogrammetry and necropsies from stranded whales. We excluded necropsied individuals from our analysis because we were investigating potentially small changes in body length as a result of covariate effects. Changes in body length are known to occur in stranded whales that have been towed to shore (stretching), and correction factors for these stretching effects are approximate.[7] As a result, our sample size of whales < 1 year old was smaller than in previous studies, so we applied an informative prior to $\widehat{A}$, *k,* and *c* for both Phase 1 & 2 based on the estimated parameters from the same Gompertz 2-phase growth equation fit using length data from both photogrammetry and necropsies:[7]

$$\widehat{A}_{\text{Phase1}} \sim N[11.93,\ 2.83]$$

$$\widehat{A}_{\text{Phase2}} \sim\ N[13.82, 0.28]$$

$$k_{Phase1} \sim N[2.325,\ 1.25]$$

$$k_{Phase2} \sim N[0.13,\ 0.03]$$

$$C_{Phase1} \sim N[1.017,\ 0.195]$$

$$\text{C}_{\text{Phase2}} \sim\ N[0.33,\ 0.02]$$

where each prior is normally distributed around a mean with standard deviation. This allowed parameter estimates to depart from the provided informative priors if there was sufficient information in the data to estimate a different value, but helped align baseline estimates of growth parameters with previous studies if there were insufficient data to produce a new estimate (see Figure S1 & Table S1).

To account for different aerial photogrammetry platforms that used different methods to calculate aircraft altitude (radar altimeter, GPS altimeter, and laser altimeter), we applied three separate model-estimated error terms to individual observations of length data, such that:

$$s_{t,i} \sim N[S_{t,i}, \sigma_{pt,i}]$$

where *s* is the measured length of individual *i* at age *t*, which is normally distributed around the expected length *S* of individual *i* based on its age *t* and applied covariate effects, with a unique standard deviation σ for each photogrammetry platform *p*, which is applied based on the platform used to measure individual *i* at time *t*.

We constructed and fit these models using the JAGS Bayesian modeling software[37] run via R.[38] We ran three chains, each of 100,000 iterations with a burn-in period of 50,000 iterations and a thinning interval of 50, for a total of 3,000 draws from the posterior distribution. Model convergence was determined based on visual inspection of chains and $\widehat{R}$ values < 1.05, which indicates that an infinite number of iterations would lead to potential reduction of posterior intervals by less than 5%.[39] We considered covariate effects to be significant if 95% of posterior draws for the estimated effect were < 0 for negative effects or > 0 for positive effects. To determine whether the model was specified appropriately, we performed posterior predictive checks on all 202 length measurements in our dataset. We applied the model-estimated covariate effects to the recorded covariates for each whale, and sampled from those mean values using the model-estimated observation error terms specific to the platforms used to image each whale. We then compared observed values to the 95% posterior prediction intervals (Figures S2 and S3).

Current Biology, Volume *31*

Supplemental Information

Decreasing body lengths in North Atlantic right whales

Joshua D. Stewart, John W. Durban, Amy R. Knowlton, Morgan S. Lynn, Holly Fearnbach, Jacob Barbaro, Wayne L. Perryman, Carolyn A. Miller, and Michael J. Moore

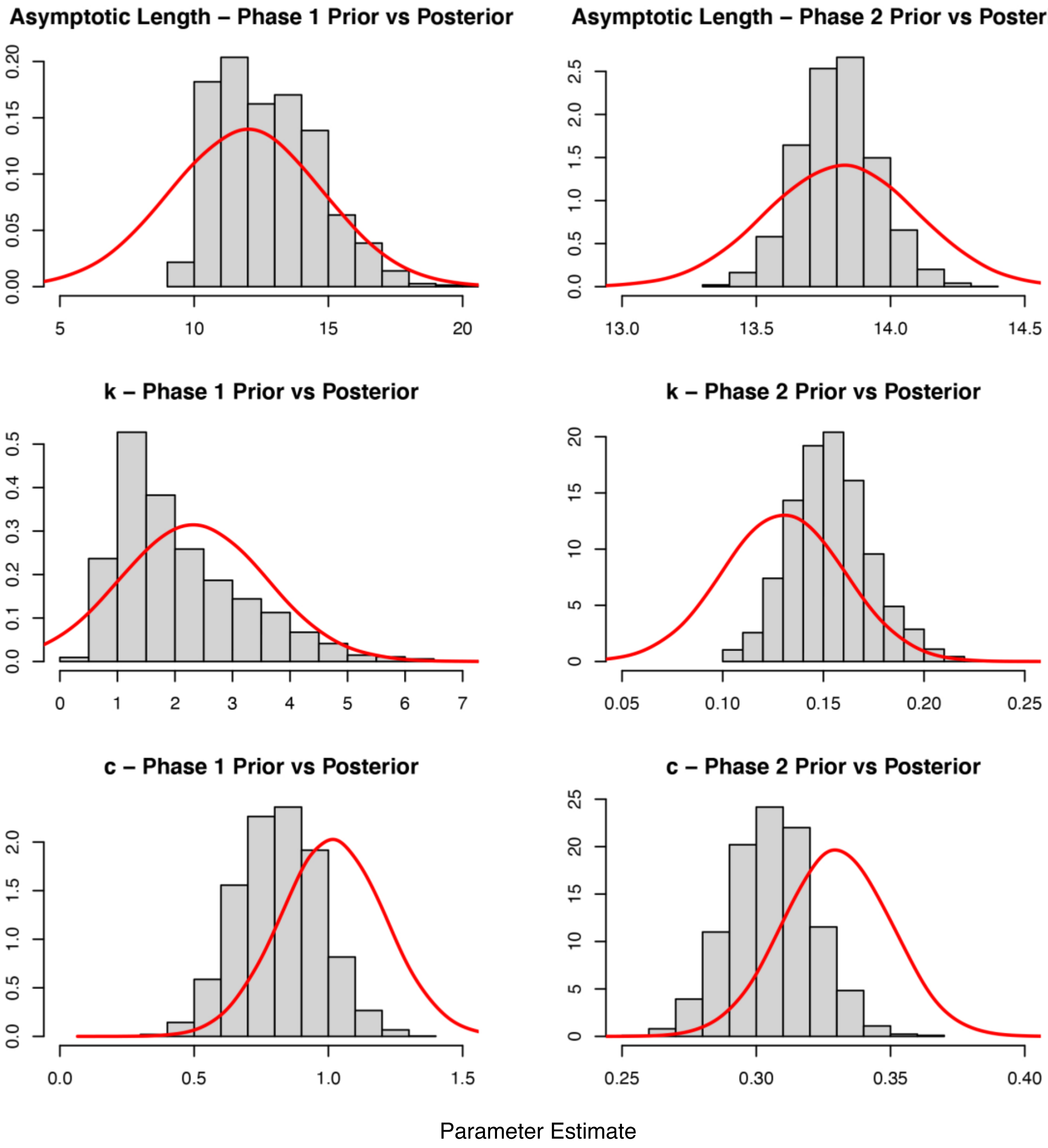


Figure S1. Priors versus posteriors for growth parameters in the Gompertz 2-Phase growth model, **Related to STAR Methods & Figure 2.** Red curves indicate the Bayesian priors used in the model, which are based on previous estimates of these parameters using aerial photogrammetry data from 2000-2002 and necropsy data. Gray histograms indicate the model posterior estimates for each parameter.

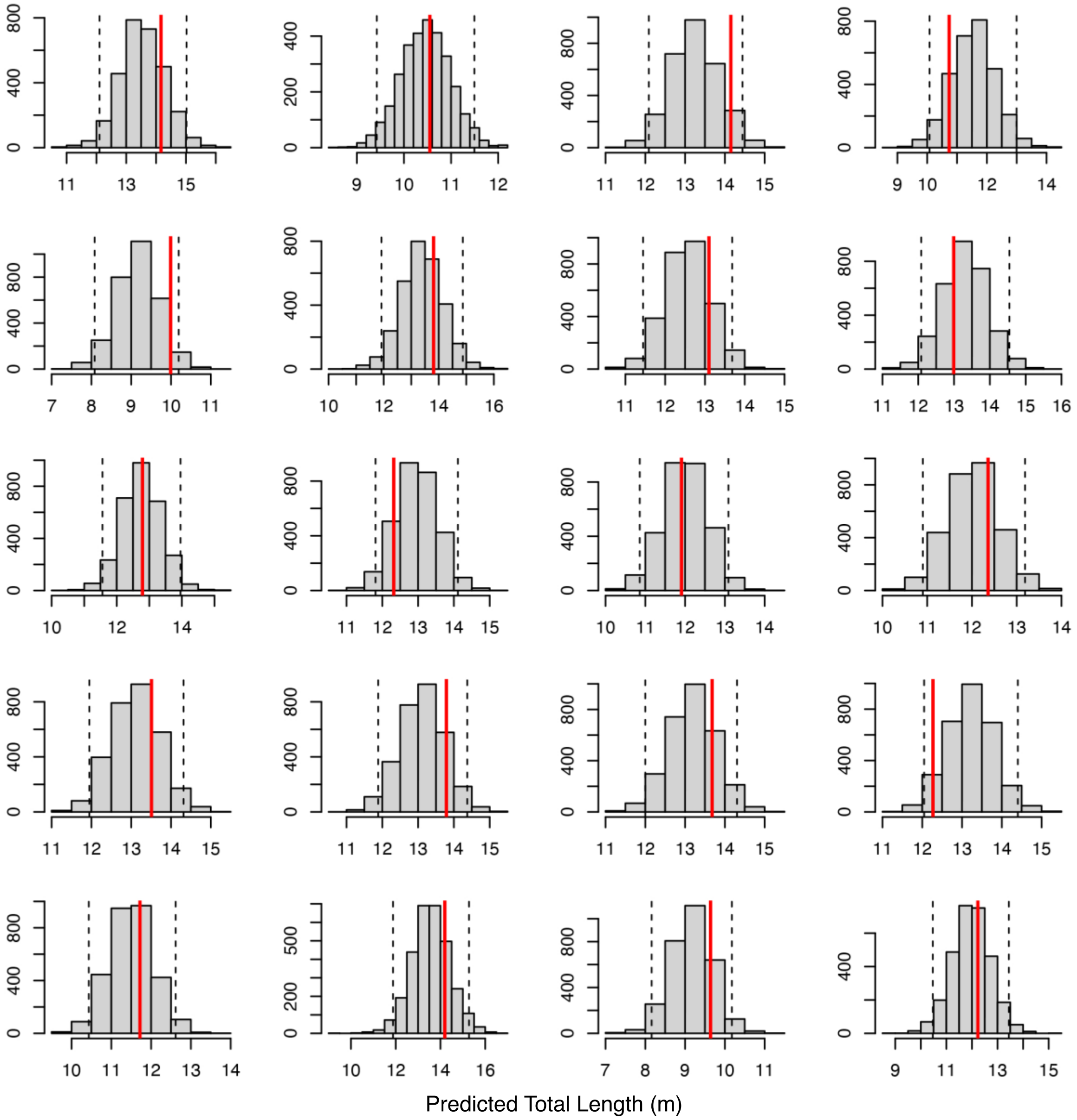


Figure S2. Posterior predictive checks of 20 randomly selected length-at-age observations, Related to STAR Methods & Figure 2. The gray histograms indicate the model-estimated range of predicted lengths for a whale based on its age and observed covariate values (birth year, entanglement history, maternal entanglements, number of lactations). The vertical red line indicates the observed length of that whale, and the vertical dashed lines indicate the 95% prediction intervals. 195 out of 202 observed lengths (96.5%) fell within the 95% posterior prediction intervals based on whales' ages and recorded covariate values.

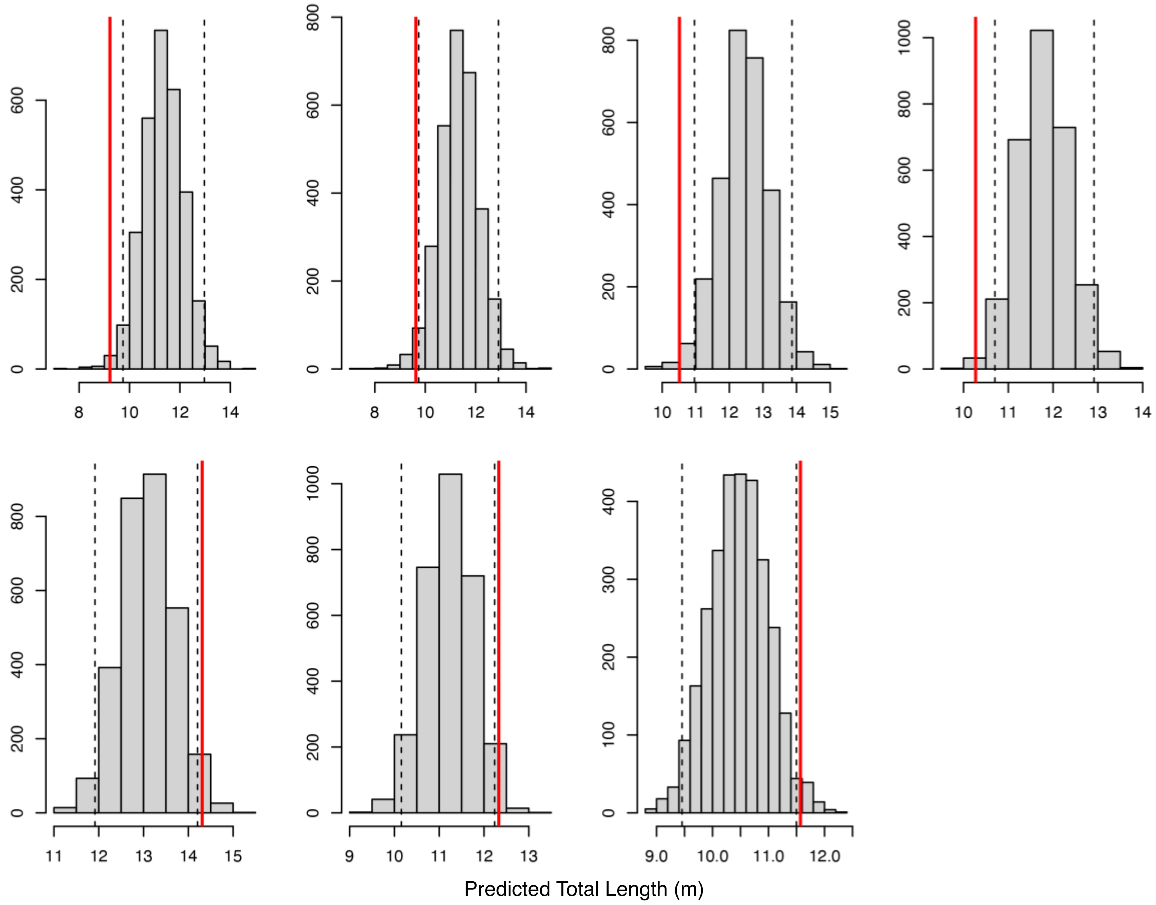


Figure S3. Posterior predictive distributions of seven whales whose observed lengths were outside of the 95% prediction intervals (but within the full posterior prediction distributions), Related to STAR Methods & Figure 2. Whales in the top row were born between 1996 and 2011 (whale IDs 2601, 3617, 4130 & 4140), and whales in the bottom row were born between 1987 and 2001 (whale IDs 1706, 2709 & 3110). The gray histograms indicate the model-estimated range of predicted lengths for a whale based on its age and observed covariate values (birth year, entanglement history, maternal entanglements, number of lactations). The vertical red line indicates the observed length of that whale, and the vertical dashed lines indicate the 95% prediction intervals. None of these seven whales had recorded attached-gear entanglements, maternal entanglements, or lactation events prior to age 10.

Parameter	**Phase 1 Estimate (95% CI)**	**Phase 2 Estimate (95% CI)**
$\hat{A}$	12.55 (10.04 – 16.78)	13.80 (13.52 – 14.10)
k	1.77 (0.71 – 4.80)	0.15 (0.12 – 0.20)
c	0.82 (0.53 – 1.13)	0.31 (0.28 – 0.34)

Table S1. Posterior estimates of growth curve parameters for the Gompertz 2-Phase growth model, Related to STAR Methods & Figure 2. Values are median estimates with 95% Bayesian credible intervals in parentheses. Note that $\hat{\boldsymbol{A}}$ is the baseline asymptotic length, before covariate effects are applied.