Vol. 581: 165–181, 2017
https://doi.org/10.3354/meps12315

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published October 13

North Atlantic right whale foraging ecology and its role in human-caused mortality

Mark F. Baumgartner[1,*], Frederick W. Wenzel[2], Nadine S. J. Lysiak[3], Melissa R. Patrician[4]

[1]Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA
[2]NOAA Northeast Fisheries Science Center, Woods Hole, MA 02543, USA
[3]Biology Department, University of Massachusetts Boston, Boston, MA 02125, USA
[4]Ship Operations, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

ABSTRACT: Endangered North Atlantic right whales *Eubalaena glacialis* suffer from unacceptably high rates of ship strikes and fishing gear entanglements, but little is known of the role that diving and foraging behavior plays in mediating human-caused mortality. We conducted a study of right whale foraging ecology by attaching tags to whales for short periods of time (hours), tracking their movements during daytime, and repeatedly sampling oceanographic conditions and prey distribution along the whales' tracks. Right whales were tagged from late winter to late fall in 6 regions of the Gulf of Maine and southwestern Scotian Shelf from 2000 to 2010. The diving behavior of the tagged whales was governed by the vertical distribution of their primary prey, the copepod *Calanus finmarchicus*. On average, right whales tagged during spring spent 72% of their time in the upper 10 m (within the draft of most large commercial vessels), indicating the need for expanded ship speed restrictions in western Gulf of Maine springtime habitats. One out of every 4 whales dove to within 5 m of the sea floor during the short time they were tagged, spending as much as 45% of their total tagged time in this depth stratum. Right whales dove to the sea floor in each habitat studied except for one (where only 1 whale was tagged). This relatively high incidence of near-bottom diving raises serious concerns about the continued use of floating ground lines in pot and trap gear in coastal Maine and Canadian waters.

KEY WORDS: *Eubalaena glacialis* · *Calanus finmarchicus* · Diving behavior · Entanglement · Ship strike

INTRODUCTION

The North Atlantic right whale *Eubalaena glacialis* is a unique predator, having the largest ratio of predator-to-prey body mass in the animal kingdom (Tucker & Rogers 2014). The evolution of baleen and ram filter feeding has allowed a roughly 50 000 kg, 14 m long predator to consume copepods that are only ~1 mg in weight and a few millimeters in length (see Baumgartner et al. 2007 for a review of how and why right whales feed this way). North Atlantic right whales feed primarily on the late juvenile developmental stages of the copepod *Calanus finmarchicus* (Wishner et al. 1988, 1995, Murison & Gaskin 1989, Mayo & Marx 1990, Baumgartner et al. 2003a), but supplement their diet with other zooplankton such as *Pseudocalanus* spp., *Centropages typicus*, and euphausiids (Collett 1909, Watkins & Schevill 1976, Mayo & Marx 1990). To survive, right whales must seek out and feed on extremely dense aggregations of copepods organized into vertically compressed layers (Baumgartner & Mate 2003). While feeding thresholds of 10^3 copepods m^{-3} have been estimated (Mayo & Marx 1990, Baumgartner & Mate 2003),

*Corresponding author: mbaumgartner@whoi.edu

Publisher: Inter-Research · www.int-res.com

copepod abundance measured in proximity to right whales within these compressed layers can exceed 10^5 copepods m^{-3} (Mayo & Marx 1990, Beardsley et al. 1996, Baumgartner & Mate 2003, Parks et al. 2012). The mechanisms that lead to the formation of these highly aggregated layers of copepods are poorly understood, but likely involve interactions between ocean physics, copepod behavior, and, during late winter and spring, phytoplankton vertical distribution (Baumgartner et al. 2007).

North Atlantic right whales are seriously endangered, with an estimated 458 animals remaining alive in 2015 (Pace et al. 2017). Commercial whaling between the 12th and 18th centuries decimated the population, leading to the first attempts at international protection in 1935. Since routine population monitoring and stranding networks were established in the 1970s and 1980s, unacceptably high rates of mortality from fishing gear entanglements and ship strikes have been continuously observed (Knowlton et al. 2012, van der Hoop et al. 2013, Kraus et al. 2016). Hayes et al. (2017) estimated that the minimum rate of human-caused mortality and serious injury to right whales averaged 5.7 animals yr^{-1} between 2010 and 2014 (4.7 and 1.0 animals yr^{-1} attributed to fishing gear entanglements and ship strikes, respectively), well above the 'potential biological removal' rate of 1.0 animal yr^{-1} mandated under the US Marine Mammal Protection Act. Knowlton et al. (2012) reported that 83% of all right whales had been entangled at least once in their life, and of these animals, 59% had been entangled more than once. There is no evidence to indicate that management actions enacted in the US prior to 2009 to reduce fishing gear entanglements have been effective (Pace et al. 2014). Recent management actions to reduce vessel speeds in known right whale habitats and to shift shipping lanes around whale high-use areas appear to have reduced, but not eliminated, ship strikes (Laist et al. 2014, van der Hoop et al. 2015).

The role that diving and foraging behavior plays in increasing the risks posed by anthropogenic activities to whales is not well known. For example, the amount of time whales spend at or near the surface has a strong influence on their risk of being hit by a ship. Baumgartner & Mate (2003) found that reproductively active females (pregnant females and females accompanied by calves) spend more time at the surface in the summer than other demographic groups, which potentially makes this critical segment of the population more susceptible to ship strikes. Parks et al. (2012) observed near-surface feeding behavior in Cape Cod Bay that put all right whales at particular risk from ship strikes. Ropes suspended in the water column as part of fixed fishing gear pose a significant hazard to right whales. Some fisheries use ground lines that float above the sea floor between traps or pots (e.g. Brillant & Trippel 2010), and these lines pose an entanglement risk to right whales (Johnson et al. 2005). Despite anecdotal evidence of muddy heads, documented near-bottom prospecting dives, and previous well-founded speculation about near-bottom feeding (Winn et al. 1995, Mate et al. 1997, Baumgartner & Mate 2003, S. Kraus pers. comm.), the spatial and temporal extent of near-seafloor diving is unknown in right whales, making risk assessment across habitats difficult.

We initiated a study of right whale diving behavior to better understand both foraging ecology and the risks posed by human activities focused in particular strata of the water column. The present study builds upon the summertime right whale foraging ecology study of Baumgartner & Mate (2003), using the same study design but collecting observations in other seasons and habitats. Archival tags were attached to right whales during daytime, and the animals were tracked closely in space and time to permit repeated observations of their prey, oceanographic conditions, and water depth along the whales' swim tracks. These observations were used to characterize (1) seasonal changes in right whale diving behavior, (2) the relationship between right whale diving behavior and the vertical distribution of their prey, (3) strategies to optimize foraging time, and (4) time spent in surface and near-bottom depth strata where the risk of ship strikes and entanglement in floating ground lines, respectively, are greatest.

MATERIALS AND METHODS

Archival tags consisted of a time-depth recorder (TDR; Wildlife Computers MK7, 2000–2001; MK9, 2004–2010), an acoustic transmitter (Vemco V22P, 2001–2010; no acoustic transmitter was used in 2000), and a radio transmitter (Telonics CHP-1P, 2000–2007; MOD-050, 2010). The TDR measured depth and conductivity (to determine if the tag was above or below the sea surface) at 1 s intervals; depth was measured at 2 and 0.5 m resolution during 2001–2002 and 2004–2010, respectively. To assess pressure errors in the TDR instruments, we attached tags to the vertical profiling instrument package (see below) to collect collocated depth measurements with a calibrated conductivity-temperature-depth

(CTD) instrument (Seabird SBE19 plus). Errors in the TDRs were significant, yet consistent among all instruments; errors increased 2.0–2.5 m per 50 m. Errors from the calibration casts were used to subsequently adjust depth measurements from the TDR instruments deployed on whales.

The tags' acoustic transmitters facilitated tracking submerged whales at close range (<1 km) using a hand-held directional hydrophone and an acoustic receiver. We have found this tracking method to be superior to radio tracking for our study, since it allows environmental sampling to occur much closer in space and time to the whale than when radio tracking. Each acoustic transmitter emitted a 10 ms, 36 kHz pulse at 165 dB (re 1 µPa at 1 m) roughly once every second. The frequency response of the transmitters, data on the behavior of right whales tagged with and without transmitters, and justification for the use of this active acoustic source on baleen whales can be found in Baumgartner & Mate (2003) and Baumgartner et al. (2008). Tags were deployed during daylight hours from 4.5–7.5 m rigid-hulled inflatable boats using a 9 m long telescoping aluminum pole, and attached to the whale's skin via a suction cup. Detachment was controlled using a zinc foil plug in the suction cup that corroded over 1–3 h and eventually allowed seawater to flood the suction cup. Upon detachment, syntactic or polyvinyl chloride foam incorporated in the tag provided buoyancy so that the tag could return to the surface and be recovered for data retrieval. Our sampling design called for attachment durations of 1–3 h because (1) right whales engage in repetitive stereotypical feeding behavior that can be adequately observed over relatively short time scales (hours; Baumgartner & Mate 2003), and (2) short attachment durations created an opportunity for several animals to be tagged (serially) in a single day, thus increasing the sample size as well as our chances of making reasonable inferences about the foraging behavior of the right whale population.

Once tagged, whales were tracked at close range (<1 km) from the tagging boat using the acoustic transmitter/receiver system and the naked eye. Care was taken to track tagged whales at sufficient distance to mitigate behavioral responses to the boat, but close enough to allow behavioral observations and to accurately collect surfacing locations. Upon a tagged whale's surfacing after a long dive or every few minutes for whales that surfaced more frequently, the tracking boat would stop at a surfacing location and record the position with a Global Positioning System (GPS) receiver. Roughly every 10–15 min, the most recent position would be transmitted by radio to a nearby oceanographic vessel, and the vessel would subsequently move to that location to measure the water depth with an echosounder and conduct a cast with a vertical profiling instrument package. This package consisted of a CTD (Seabird Electronics, SBE 19 plus) and optical plankton counter (OPC; Focal Technologies, OPC-1T; Herman 1988, 1992) during the 2000 and 2001 field seasons. A chlorophyll fluorometer (Wetlabs, WETStar WS3S), video plankton recorder (VPR; Seascan model AutoVPR in 2005, digital AutoVPR in 2006–2010; Davis et al. 1992, 1996), and altimeter (Benthos, PSA-916) were added in 2005, and a bottom contact switch (Woods Hole Oceanographic Institution custom built) was added in 2006. These instruments provided vertical profiles of temperature (CTD), salinity (CTD), chlorophyll fluorescence (fluorometer), particle size and abundance (OPC), light attenuance (OPC), and zooplankton abundance and community composition (VPR). Casts were conducted from the surface to within several meters of the sea floor prior to 2006; during and after 2006, casts were conducted to within ~1 m of the sea floor. No VPR data are available for 2006, as the digital AutoVPR (DAVPR) malfunctioned for all casts that year.

The VPR captures digital images of a small volume of water 23–30 times s^{-1}, and is adept at estimating the abundance of large-bodied copepods such as *Calanus finmarchicus*. Regions of interest, defined as areas in the images with high brightness and contrast, were automatically extracted using AutoDeck software (Seascan) and visually inspected to identify and classify zooplankton. Taxon-specific abundance estimates were derived from the VPR using zooplankton counts from these manually classified regions of interest as well as empirical estimates of the image volume (11 ml for the AutoVPR used in 2005, 2.1 ml for the DAVPR used in 2007–2010). Comparable estimates of late-stage *C. finmarchicus* abundance were estimated from the OPC by counting all particles of 1.5–2.0 mm equivalent circular diameter and applying the calibration equation of Baumgartner (2003). The Baumgartner (2003) calibration equation was developed from zooplankton samples collected during the summer in the Bay of Fundy and the southwestern Scotian Shelf (Roseway Basin), where the *C. finmarchicus* population is dominated by copepods in the C5 developmental stage. Because C4 copepodids may occur in higher abundance during the spring in the western Gulf of Maine, the calibration equation of Baumgartner (2003) may underestimate the abundance of late-stage *C. finmarchicus* in this region. Fortunately, C4 and C5 copepodids are imaged and counted equally well by the VPR, so VPR-derived estimates of late-stage *C. finmarchicus* abundance may be more accurate in locations where C4 copepodids are numerous. For each cast with both OPC and VPR data, whichever instrument provided the higher measurements of *C. finmarchicus* abundance was used in subsequent analyses. *C. finmarchicus* vertical distribution derived from both the OPC and VPR was summarized in 2.5 m depth strata from the surface to the sea floor; maximum abundances in all 2.5 m depth strata sampled during a cast are reported below.

Baumgartner & Mate (2003) defined right whale dives as any vertical excursion below 50 m, and described the descent, at-depth, and ascent portions of a right whale feeding dive using vertical speed criteria; however, these criteria assume deep diving and relatively fast descents and ascents, which do not occur during shallow feeding dives in late winter and spring. We therefore defined a right whale dive as any vertical excursion that occurs between respiration bouts (characterized by periods of very short and very shallow dives, and TDR-measured conductivity anomalies indicating the tag was in air). We further defined the descent, at-depth, and ascent portions as follows: (1) the descent began and ended when the vertical descent speed first rose above and fell below 0.0 m s^{-1} (i.e. initiation occurs when the whale descends from the surface, and termination occurs when the whale stops swimming downward), (2) the ascent began and ended the last time the vertical ascent speed rose above and fell below 0.0 m s^{-1}, respectively (i.e. initiation occurs when the whale begins swimming upward toward the surface for the last time, and termination occurs when the whale stops swimming upward at the surface), and (3) the duration at depth was defined as the period between termination of the descent and initiation of the ascent. For the 154 summer right whale dives reported by Baumgartner & Mate (2003), the new dive definitions increased the time of ascent termination by an average 7.9 s (SD = 6.8 s), decreased the time of descent initiation by an average 8.1 s (SD = 5.3 s), and shortened the duration at depth by an average 15.9 s (SD = 9.1 s). The 2 dive definitions yielded highly correlated results for both ascent termination time (r^2 = 0.9657, $p < 0.0001$) and descent initiation time (r^2 = 0.9994, $p < 0.0001$). Since these changes are trivial, all dive characteristics, including those observed in 2000–2001 and reported by Baumgartner & Mate (2003), were calculated here with these new criteria.

A simple model was used to explore how variations in the vertical distribution of copepod layers influence right whale diving behavior. The model assumed that each right whale diving sequence consisted of a period of commuting from the surface to the foraging depth and back to the surface again (T_c), a period spent at the foraging depth (T_d), and a period of respiration at the surface (T_s). Dive sequences were repeated n times per unit of time T (e.g. h^{-1}), yielding

$$T = n(T_c + T_d + T_s) \tag{1}$$

The commuting time (T_c) was considered a function of the depth (D) and the ascent/descent rate (r; this can be considered an average of the ascent and descent rate, since these rates can differ based on a whale's buoyancy; see Nowacek et al. 2001 and Baumgartner & Mate 2003):

$$T_c = \frac{2D}{r} \tag{2}$$

The surface interval (T_s) was assumed to be a fraction (α) of the time submerged (T_c + T_d) as follows:

$$T_s = \alpha(T_c + T_d) \tag{3}$$

The fraction of time spent at the foraging depth per unit time (e.g. h^{-1}), a quantity right whales presumably wish to optimize to maximize their prey ingestion at the foraging depth, was then as follows:

$$F_d = \frac{nT_d}{T} = \frac{1}{1+\alpha} - \frac{2nD}{rT} \tag{4}$$

which can be rearranged and differentiated to yield:

$$\frac{\partial T_d}{\partial D} = \frac{2}{r}\left[\frac{(1+\alpha)F_d}{1-(1+\alpha)F_d}\right] \tag{5}$$

The parameter α was estimated from the percent surfacing time (PCST after Dolphin 1987) measured by Baumgartner & Mate (2003) for right whales tagged in the Bay of Fundy and Roseway Basin. PCST is calculated as

$$\mathrm{PCST} = \frac{T_s}{T_c + T_d + T_s} \tag{6}$$

from which α can be calculated as

$$\alpha = \frac{\mathrm{PCST}}{1-\mathrm{PCST}} \tag{7}$$

Baumgartner & Mate (2003) reported average PCST for 11 animals (excluding calves, females with calves, and pregnant females) as 21.2% (SD = 4.1%, range = 15.8–30.1%), corresponding to α = 0.2690; this value was used in calculations below. PCST did not change significantly between the 2 most sampled habitats, i.e. the Bay of Fundy and Great South Channel (2-sample t-test: $t = 0.556$, $p = 0.5824$); PCST averaged 19.6 % for 22 animals (excluding calves and females with calves) tagged in the Great South Channel (SD = 9.1 %, range = 6.5–44.5 %). Baumgartner & Mate (2003) also reported average ascent and descent rates of 1.47 and 1.40 m s^{-1}, respectively, so r = 1.45 m s^{-1} was used in calculations below. Inferences drawn from the model are not dependent on these specific parameter values; variation in these parameters does not affect the study results and conclusions. Unless otherwise noted, results are presented as means ± SD.

Table 1. Summary of North Atlantic right whale *Eubalaena glacialis* tagging dates, locations, and average tag attachment durations. Only tagging events lasting ≥30 min are included

Region	n	Month(s)	Year(s)	Duration (min)
Cape Cod Bay	2	March	2006	52
Great South Channel	22	May, June	2004–2007, 2010	86
Stellwagen Bank	1	August	2005	71
Bay of Fundy	26	July, August	2000–2001	96
Roseway Basin	2	August	2001	93
Jeffreys Ledge	2	December	2006	131

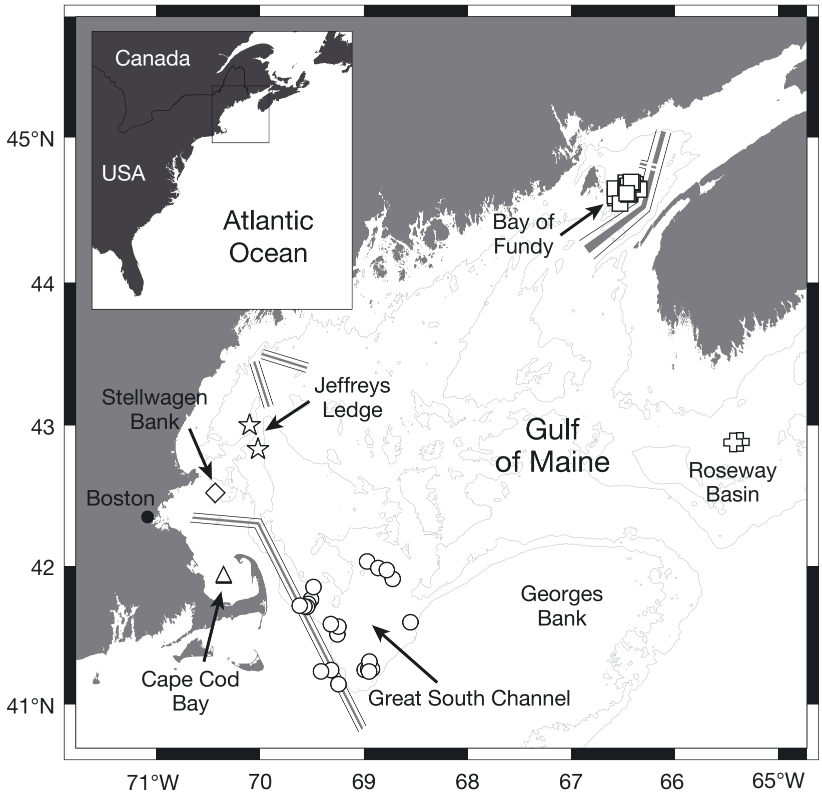

Fig. 1. Tagging locations of all North Atlantic right whales *Eubalaena glacialis* with tag attachment durations of ≥30 min (n = 55) in Cape Cod Bay (△), Great South Channel (○), Bay of Fundy (□), Roseway Basin (✜), Stell-wagen Bank (◇), and Jeffreys Ledge (☆). Shipping lanes approaching Saint John (New Brunswick), Portland (Maine), and Boston (Massachusetts) are shown

RESULTS

Tagging operations took place in 6 regions (Table 1, Fig. 1), but most whales were tagged in just 2 habitats: the Great South Channel and the Bay of Fundy. Between 2000 and 2010, 113 whales were tagged, but of these, only 55 (49 %) had attachment durations greater than 30 min. In the Great South Channel, 57 whales were tagged, of which 22 (39 %) had attachments over 30 min, and in the Bay of Fundy, 48 whales were tagged, of which 26 (54 %) had attachments over 30 min. Short attachments were attributable to poor skin condition, variations in tag design, and changes in suction cup stiffness. Of the 55 tagging events with attachment durations over 30 min, most were between 1 and 2 h in duration (n = 33); mean duration was 91 ± 60 min, the median duration was 81 min, and the interquartile range was 57–98 min. All analyses to follow were conducted with the 55 animals tagged for >30 min.

Right whales tagged in the Great South Channel exhibited significant variability in diving behavior (Figs. 2, 3a, & 4a). Many tagged whales remained at shallow depths: 64 % of whales (14 of 22) spent >80 % of their total tagged time shallower than 15 m (Fig. 4a, e.g. Fig. 2c). Maximum late-stage *Calanus finmarchicus* abundance in the upper 15 m near these shallow-diving whales was very high (Fig. 4b; OPC: 14 900 ± 14 400 copepods m^{-3}, range = 5200–62 900, n = 14 whales; VPR: 25 800 ± 9800 copepods m^{-3}, range = 6700–44 800, n = 12 whales), suggesting that the observed periods of shallow diving were primarily associated with feeding. Of the remaining 8 whales, all but 1 dove repeatedly to depths below 50 m (Fig. 3a), spending an average of 46 % of the total time they were tagged between 50 m and the sea floor (range = 27–70 %). Seven of the 22 whales

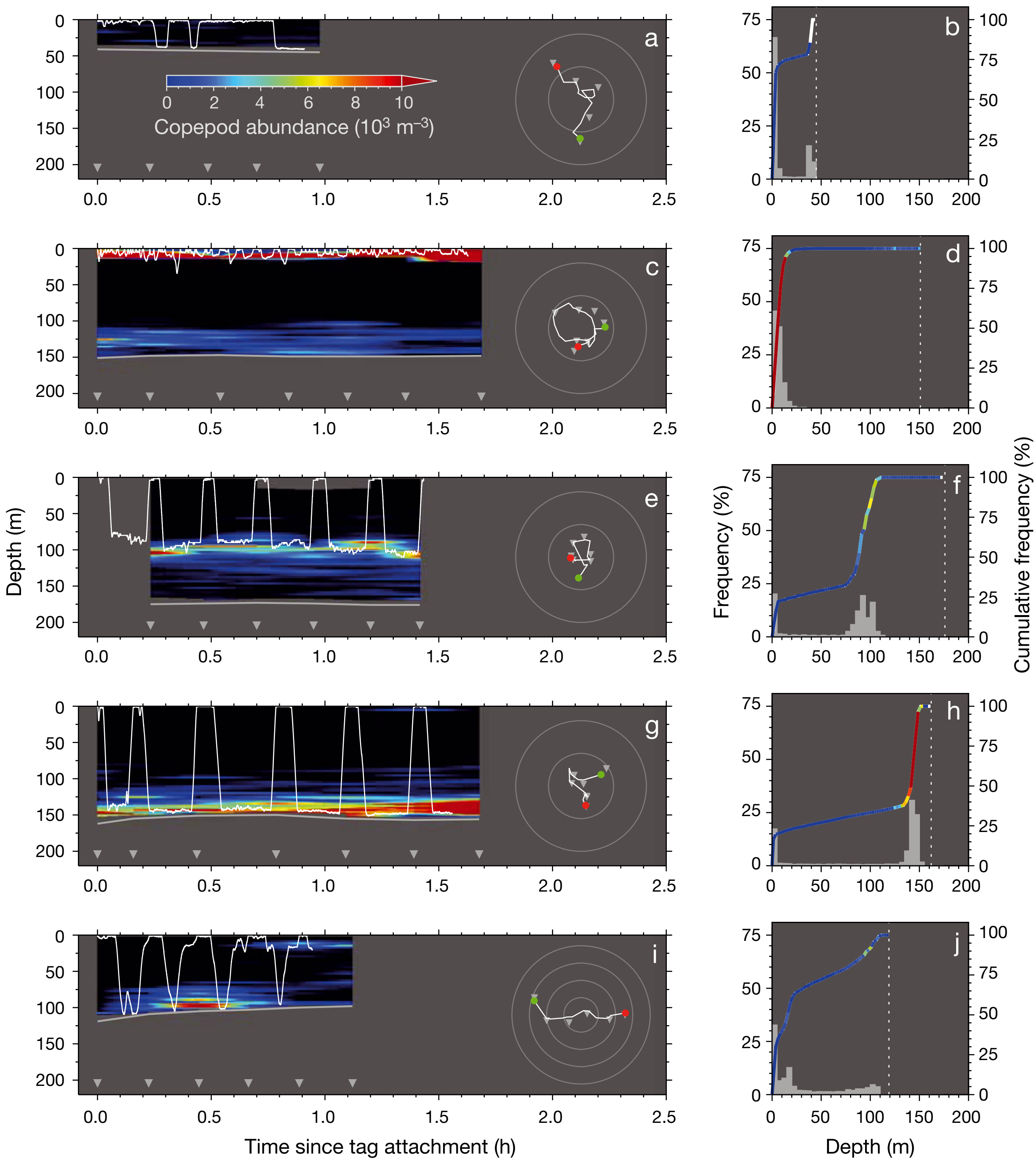

Fig. 2. (a,c,e,g,i) Dive data for tagged North Atlantic right whales *Eubalaena glacialis* (white line) with collocated late-stage *Calanus finmarchicus* abundance (colors). Sea floor (thick gray line) and times of casts with the vertical profiling instrument package (gray triangles) are shown. Inset indicates movements of the tagged whale, including start position (green circle), end position (red circle), and locations of casts (gray triangles). Concentric circles are 1 km apart. (b,d,f,h,j) Corresponding dive depth frequency (gray bars) and cumulative dive depth frequency (line) colored with average *C. finmarchicus* abundance. White portion of cumulative dive depth frequency in (b) indicates no *C. finmarchicus* abundance observations. Dotted line indicates the depth of the sea floor. Whales shown were tagged in (a,b) Cape Cod Bay, 13 March 2006, (c,d) Great South Channel, 30 May 2007, (e,f) Bay of Fundy, 29 August 2001, (g,h) Jeffreys Ledge, 11 December 2006, and (i,j) Great South Channel, 25 May 2006

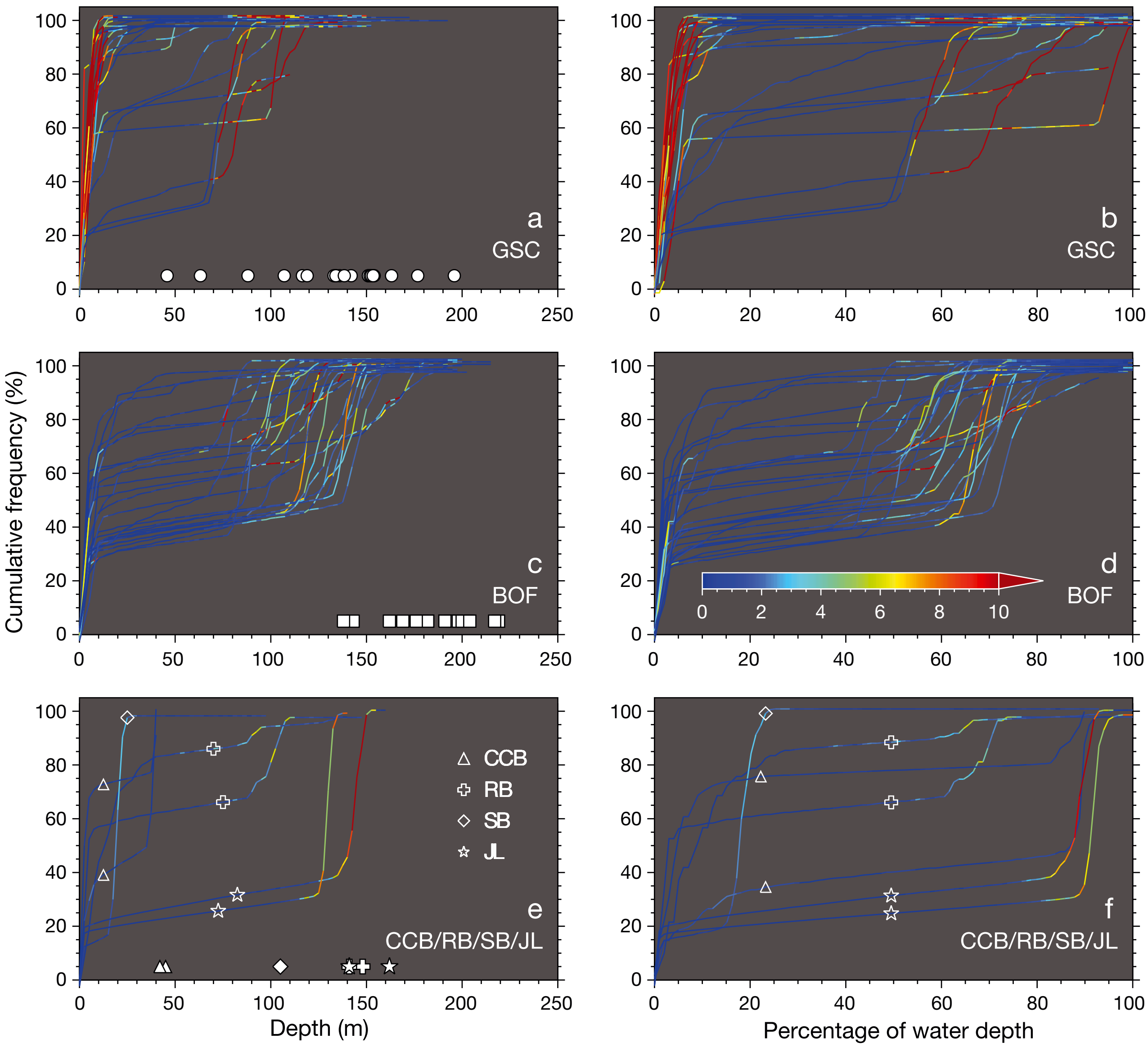

Fig. 3. Cumulative distributions of dive depth expressed (a,c,e) in meters and (b,d,f) as a percentage of water depth for tagged North Atlantic right whales *Eubalaena glacialis* in (a,b) the Great South Channel (GSC), (c,d) Bay of Fundy (BOF), and (e,f) Cape Cod Bay (CCB), Roseway Basin (RB), Stellwagen Bank (SB), and Jeffreys Ledge (JL). A random offset between ±2.5% was added to cumulative frequency to distinguish individual whales. Colors indicate abundance of late-stage *Calanus finmarchicus* measured in proximity to tagged whales; color bar in (d) indicates copepod abundance (10^3 copepods m^{-3}). Symbols above *x*-axis (in panels a,c,e) indicate water depth at tagging locations for each region, and symbols over each line in (e) and (f) indicate locations of tagging events. Symbols are as described in Fig. 1

(32%) dove to within 10 m of the sea floor during the period they were tagged (Fig. 4a, e.g. Fig. 2i), spending an average of 16% of their total tagged time in this depth stratum (range = 3–38%). While some of these dives were V-shaped, characterized by rapid descent and ascent with very little or no time spent in the 'at-depth' portion of the dive (e.g. Fig. 2i; hypothesized to be prospecting dives by Baumgartner & Mate 2003), many dives had similar characteristics to deep feeding dives (i.e. rapid descent, long durations within a narrow depth stratum, and rapid ascent) with the 'at-depth' portion of the dive spent near the sea floor where there were elevated concentrations of *C. finmarchicus* (Fig. 4b).

In contrast, right whale diving and foraging behavior in the Bay of Fundy was considerably less variable than in the Great South Channel (Fig. 3c). Right whales consistently dove to mid-water layers of *C.*

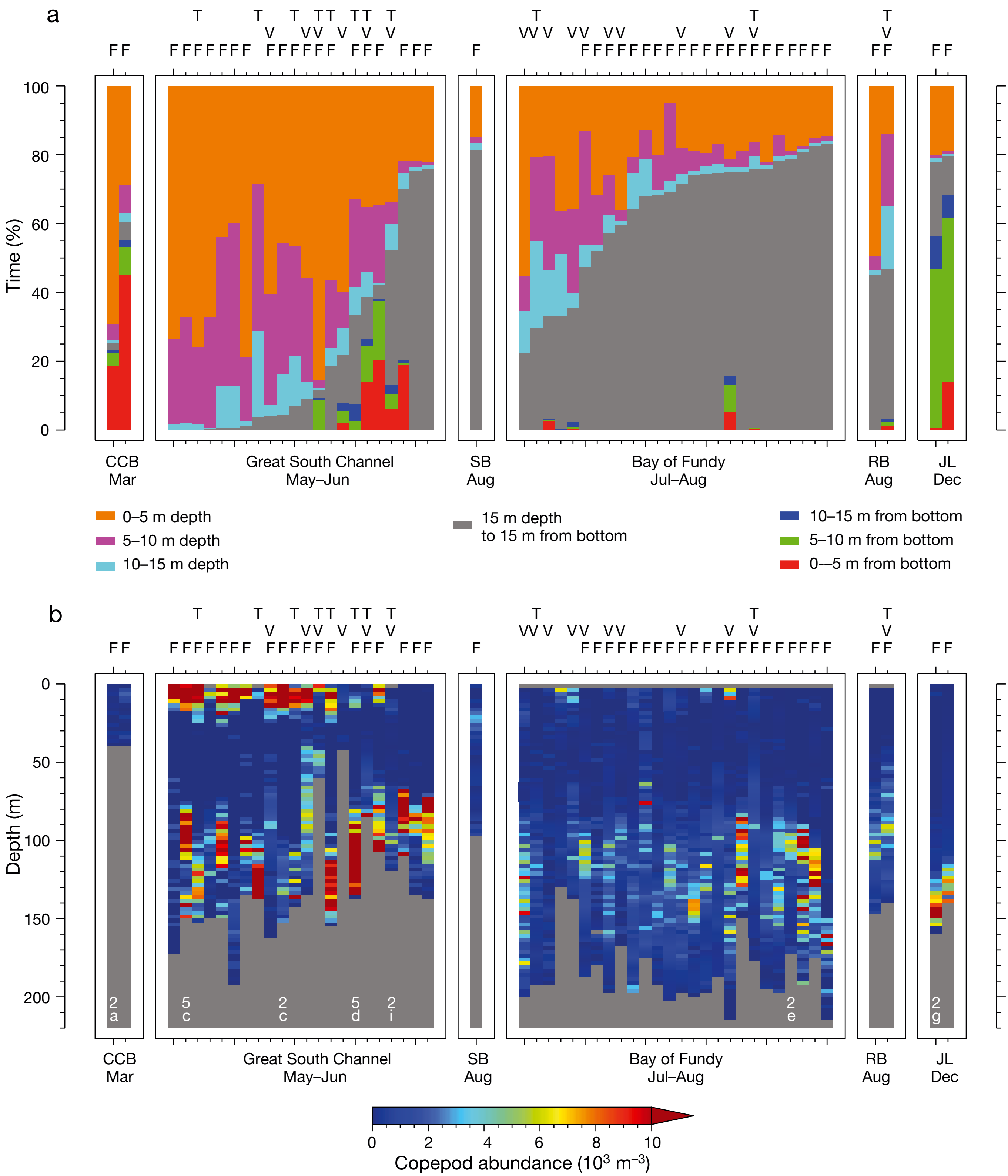

Fig. 4. (a) Percentage of time spent by North Atlantic right whales *Eubalaena glacialis* in various depth strata. There is 1 vertical bar for each tagged whale, and bars are ordered within each region for clarity by the percentage of time spent in the upper 15 m. Letters above the plots indicate observations of feeding (F), prospecting (V-shaped) dives (V), and traveling (T). (b) Average vertical distribution of *Calanus finmarchicus* measured in proximity to each tagged whale. Site abbreviations as in Fig. 3. Letters above plots as (a). Letters at bottom of plot indicate tagging events shown in Figs. 2 & 5

finmarchicus in the Bay of Fundy; on average, the at-depth portion of the dives in the Bay of Fundy occurred at 117.1 ± 22.9 m (n = 26, Table 2) and lasted 7.2 ± 3.5 min (n = 26, Table 2). In the Great South Channel, the at-depth portion of dives occurred at an average 19.7 ± 21.4 m (n = 22, Table 2) and lasted only 1.5 ± 1.7 min (n = 22, Table 2; note that this average depth is misleading, since dive depths were positively skewed in the Great South Channel; Figs. 3a & 4a). As reported by Baumgartner & Mate (2003), dives in the Bay of Fundy were to the top of the bottom mixed layer where layers of *C. finmarchicus* were consistently observed. Four of the 26 whales tagged in the Bay of Fundy (15%) dove to within 10 m of the sea floor during the period they were tagged (Fig. 4), spending an average of 4% of their total time in this depth stratum (range = 0.5–13%). Most of these dives were V-shaped.

Table 2. Characteristics of North Atlantic right whale *Eubalaena glacialis* dives by region, including average dive duration and average duration and depth during the at-depth portion of dives (i.e. excluding descent and ascent periods). Standard deviations are shown in parentheses. Dive statistics of all dives (not just feeding dives) were first averaged for each tagged whale; the reported values are grand averages of these individual averages

Region	n	Duration (min)	Duration at depth (min)	Depth (m)
Cape Cod Bay	2	3.4 (2.1)	1.9 (1.4)	18.1 (16.7)
Great South Channel (GSC)[a]	22	2.7 (2.2)	1.5 (1.7)	19.7 (21.4)
Stellwagen Bank	1	7.7	6.8	19.5
Bay of Fundy (BOF)[b]	26	10.9 (2.7)	7.2 (3.5)	117.1 (22.9)
Roseway Basin (RB)[b]	2	8.0 (1.0)	3.9 (2.3)	102.5 (2.3)
Jeffreys Ledge	2	13.4 (2.8)	10.3 (2.8)	125.5 (5.9)

[a]Distributions of dive characteristics in GSC are positively skewed, with some whales undertaking short shallow dives and others conducting longer deeper dives (see Fig. 4a)
[b]Baumgartner & Mate (2003; their Table 1) reported statistics of only feeding dives for whales tagged in the BOF and RB

The 2 right whales tagged in Cape Cod Bay during March 2006 spent time at both the surface and the bottom (Fig. 4a; e.g. Fig. 2a); the middle of the water column was used only for transiting between the surface and bottom. The at-depth portion of dives occurred at an average of 18.1 ± 16.7 m and lasted 1.9 ± 1.4 min (Table 2). OPC-derived *C. finmarchicus* abundance was extremely low throughout the water column (Figs. 3e & 4b; e.g. Fig. 2a). The single right whale tagged near Stellwagen Bank during August 2005 dove repeatedly to the base of the pycnocline where the subsurface chlorophyll maximum and a layer of *C. finmarchicus* (average maximum abundance of 5670 copepods m^{-3}) co-occurred; the at-depth portion of this whale's dives occurred at an average 19.5 m and lasted 6.8 min (Table 2). Like the whales tagged in the Bay of Fundy, the 2 right whales tagged in Roseway Basin during August 2001 dove to layers of *C. finmarchicus* located at mid-depth; at-depth portions of these 2 whales' dives occurred at an average 102.5 ± 2.3 m and lasted 3.9 ± 2.3 min (Table 2). Finally, the 2 right whales tagged near Jeffreys Ledge during December 2006 dove repeatedly to near the sea floor to forage on layers of *C. finmarchicus* concentrated there (e.g. Fig. 2g; OPC: 16 560 ± 1900 copepods m^{-3}). These 2 whales spent the most time of any of the tagged whales within 15 m of the sea floor (62 ± 8.4%). The at-depth portions of these 2 whales' dives occurred at an average 125.5 ± 5.9 m and lasted 10.3 ± 2.8 min (Table 2).

For the vast majority of cases when right whales exhibited feeding behavior and copepod data were available (n = 45), there was a strong correlation between dive depth and the depth of maximum *C. finmarchicus* concentration (Fig. 5a; $r^2 = 0.7073$, $p < 0.0001$). Variability in this relationship was caused by several cases (indicated by red filled circles in Fig. 5a) when 2 distinct layers of *C. finmarchicus* were present in the water column (e.g. Fig. 5c,d). In all but one of these cases, the abundance of *C. finmarchicus* was nearly the same or greater in the shallower layer than in the deeper layer (Fig. 5b), and the tagged right whales foraged at shallow depths (e.g. Fig. 5c). In the one case when *C. finmarchicus* abundance was greater in the deeper layer than the shallower layer, the tagged right whale actually moved between the 2 layers during the period it was tagged (Fig. 5d). When the 2-layer cases with depths of maximum copepod abundance greater than 50 m are excluded (the 4 cases above the 1:1 line in Fig. 5b), the correlation between dive depths and the depth of maximum copepod abundance increases substantially ($r^2 = 0.9370$, $p < 0.0001$) and the linear regression is 1-to-1 (Fig. 5a, dashed line).

For all right whales that exhibited feeding behavior (n = 47), the amount of time they spent at depth during each dive was strongly correlated with dive depth ($r^2 = 0.7939$, $p < 0.0001$; Fig. 6a). The slope of this relationship forced through the origin (the intercept of a simple linear regression was not significantly different from 0; p = 0.0589) was 0.0704 min

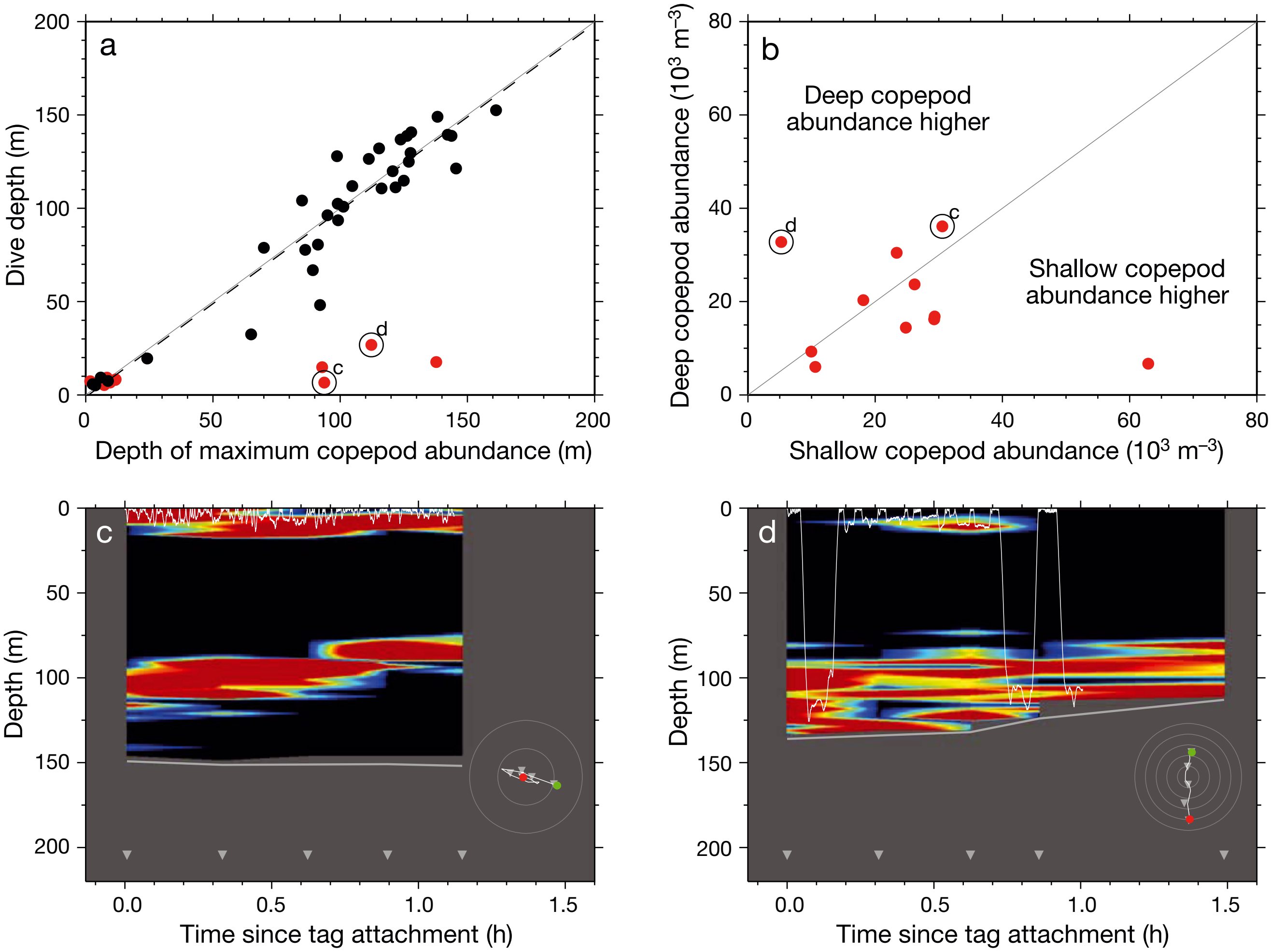

Fig. 5. (a) Average North Atlantic right whale *Eubalaena glacialis* dive depth versus the average depth of maximum copepod abundance. Color of filled circles indicates whether 2 distinct layers of *Calanus finmarchicus* were present (red) or absent (black). One-to-one line (gray) and linear regression line (dashed) are shown. Regression line excludes four 2-layer cases when the depth of maximum copepod abundance was greater than 50 m. Time series of circled 2-layer cases (in a and b) are shown in (c) and (d). (b) Average copepod abundance in deep versus shallow layers for all 2-layer cases. (c,d) Time series of dive data and collocated vertical distribution of *C. finmarchicus* in the same format as Fig. 2 shown for whales tagged in the Great South Channel on (c) 16 May 2010 and (d) 14 May 2007

m^{-1}, which corresponds to F_d = 59.6% according to Eq. (5). Total time at depth (calculated F_d) was not correlated with dive depth (r^2 = 0.0130, p = 0.4461; Fig. 6b), and averaged 51.3 ± 12.9%. The slight discrepancy between F_d estimated from the slope in Fig. 6a and the F_d estimated from the data in Fig. 6b is attributable to deviations from the ideal diving/foraging behavior represented by the model (e.g. Figs. 2a,i & 5d), as well as potential biases in α and *r*.

Despite spending roughly the same total amount of time at depth while foraging at shallow or deep depths, the frequency of diving (dives h^{-1}) changed significantly with foraging depth (Fig. 6c). According to the theoretical diving model (Eqs. 1 to 4), whales diving to shallow depths can achieve the same total time at depth (the same F_d) as whales diving to deep depths by increasing the frequency of their dives (*n*) to account for shorter commuting times (see contour lines and inset in Fig. 6c). Right whales appear to dive in accordance with the theoretical model, increasing the frequency of their dives as they forage at shallower depths to achieve roughly the same F_d as when foraging at deeper depths. However, if right whales employed similar dive durations and diving frequencies when foraging at shallow depths as they do when foraging at deep depths (i.e. long dive durations and only a few dives h^{-1}), they could actually increase their total time at depth (increased F_d). Our observations show that right whales clearly do not adopt this strategy (Fig. 6c), which suggests that they

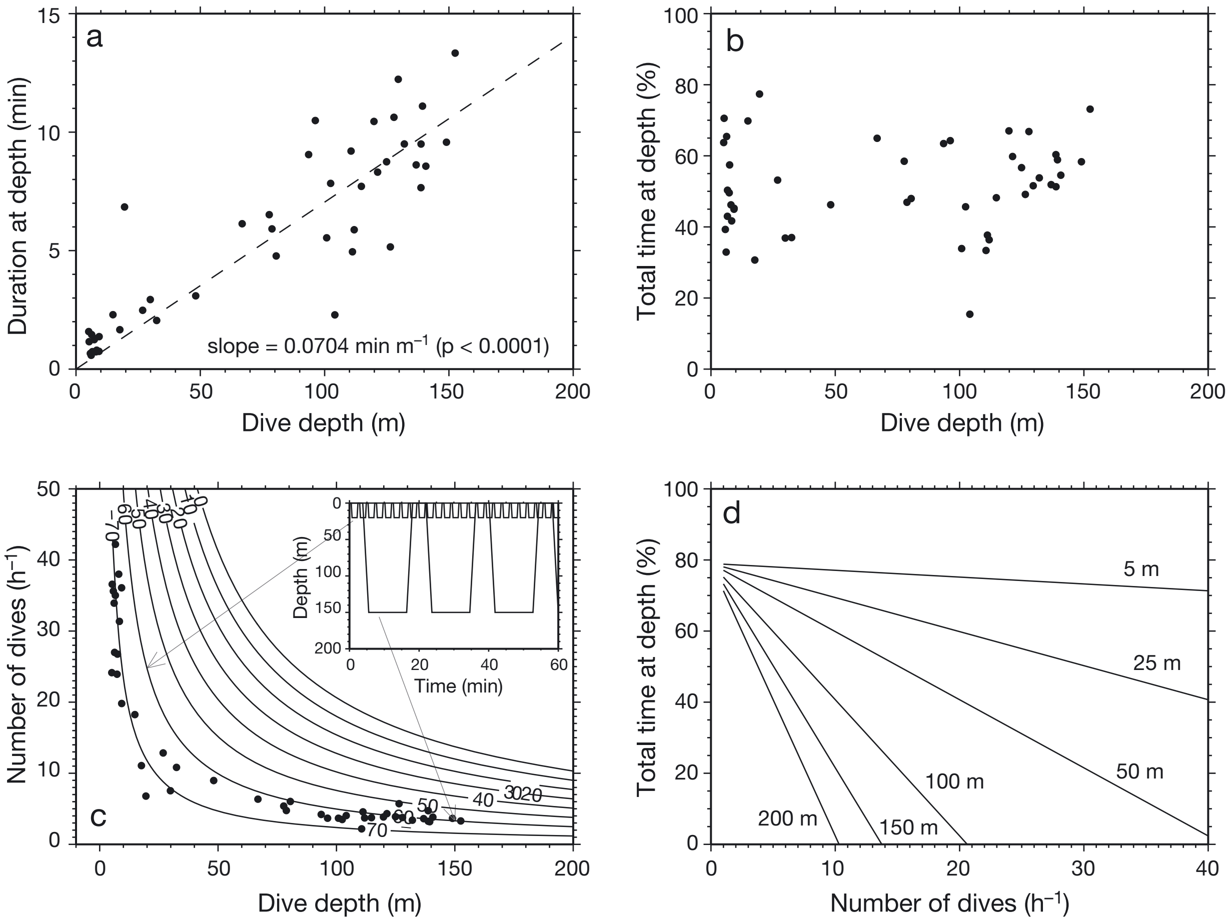

Fig. 6. (a) Average duration at depth for North Atlantic right whale *Eubalaena glacialis* dives versus average dive depth (n = 47). Linear regression forced through the origin is shown (dashed). (b) Total time at depth versus dive depth. (c) Number of dives h^{-1} versus dive depth (filled circles). Contour lines indicate theoretical fraction of time at depth (F_d) according to Eq. (4), expressed as a percentage. Inset shows theoretical dive behavior for F_d = 0.60 and dive depths of 20 and 150 m. (d) Theoretical relationship between total time at depth (F_d expressed as a percentage) and the number of dives (n) h^{-1} according to Eq. (4) for repeated dives to 5, 25, 50, 100, 150, and 200 m

do not maximize their time at depth, but instead optimize it based on factors not captured in the theoretical model (see 'Discussion' below).

The tagged whales spent on average 49 ± 28% (range = 16–99%, n = 55) of their time in the upper 10 m of the water column, which is within the draft of large commercial ships (e.g. tankers, container ships, bulk carriers; Rodrigue et al. 2017). Whales tagged in the spring spent an average 72 ± 25% (range = 23–99%, n = 22) of their time in the upper 10 m of the water column. Of all the tagged whales, 15 of 55 (27%) dove to within 5 m of the sea floor, and those 15 animals spent an average of 10 ± 12% (range = 0.1–45%) of their time within 5 m of the sea floor. Right whales dove near the sea floor in every habitat studied except the Stellwagen Bank region (where only 1 whale was tagged).

DISCUSSION

Diving behavior and copepod life history

While feeding, right whale diving behavior is governed by the vertical distribution of their prey. *Calanus finmarchicus* change their vertical distribution predictably throughout the year, and therefore right whale foraging behavior is, for the most part, also seasonally predictable. During mid- and late spring, the primarily herbivorous *C. finmarchicus* are actively feeding, growing, and reproducing in the euphotic zone (upper water column) where phytoplankton abundance is high (Durbin et al. 1995). Consequently, right whales were often observed feeding on *C. finmarchicus* near the surface during this time in the Great South Channel (e.g. Fig. 2c). During this same time, however, *C. finmarchicus* can undergo diel vertical migration (DVM), a strategy to avoid visual predators during the daytime by migrating to depth (i.e. to the dark refuge below the euphotic zone) before dawn, and migrating back into the surface layers at dusk to feed on phytoplankton (Baumgartner et al. 2011 and references therein). In addition to near-surface feeding, we observed right whales feeding at depth during the spring in the Great South Channel (Figs. 3a & 4). Baumgartner et al. (2011) observed a range of *C. finmarchicus* vertical migration behaviors in the Great South Channel, including strong DVM (all copepods occur at depth during the day and in the surface waters at night), weak DVM (only a portion of the copepod population migrates between the surface waters and depth), and no DVM (copepods remain in surface waters night and day), and they hypothesized based on patterns of occurrence that right whales were able to easily track these vertical migration behaviors to feed on *C. finmarchicus* throughout the water column during day or night. Our observations were collected only during the day, but they support the notion that right whales can feed on *C. finmarchicus* from surface to bottom over the continental shelf.

During summer, *C. finmarchicus* in the last juvenile stage arrest development, initiate an ontogenetic vertical migration to depth and enter a dormant state called diapause (Marshall & Orr 1955, Miller et al. 1991, Hirche 1996). *C. finmarchicus* remain at depth in diapause until early to mid-winter, surviving this long period of starvation by catabolizing the large lipid reserves built up for this purpose during spring (it is these same abundant lipid reserves that make *C. finmarchicus* so attractive to right whales). We observed right whales feeding at depth during the summer (Bay of Fundy, Roseway Basin; Figs. 2e, 3c, & 4) and late fall (Jeffreys Ledge; Figs. 2g, 3e, & 4) on discrete layers of copepods. Baumgartner et al. (2003b) found that the copepods upon which the tagged right whales fed at depth in the Bay of Fundy did not vertically migrate, suggesting that they were indeed in diapause. While summertime diapause is a general rule for *C. finmarchicus* in the Gulf of Maine and Scotian Shelf, there are sometimes exceptions. For example, we observed a right whale feeding on *C. finmarchicus* at the base of the thermocline in the subsurface chlorophyll maximum near Stellwagen Bank during August (Figs. 3e & 4); these copepods were clearly not in diapause at that time. Neritic populations of *C. finmarchicus* can take advantage of post-spring-bloom productivity over the continental shelf to extend development and reproduction (Durbin et al. 2000, McLaren et al. 2001), so *C. finmarchicus* can sometimes be available to right whales in surface waters during the summer and fall; however, the bulk of the population is in diapause at depth, so near surface feeding on *C. finmarchicus* during these seasons is uncommon.

Between early and mid-winter, *C. finmarchicus* emerge from diapause, molt into adults, and begin to reproduce (Miller et al. 1991). This first generation of the year develops slowly because of the cold water temperatures of winter, and does not attain a size that is catchable by right whale baleen until mid-spring (Mayo et al. 2001). Therefore, *C. finmarchicus* are unavailable to right whales during mid-winter to mid-spring, and they feed on other smaller and less nutritious species at this time (e.g. *Pseudocalanus* spp., *Centropages typicus*; Mayo & Marx 1990). We observed right whales in Cape Cod Bay during mid-March conducting feeding dives to the sea floor where we could detect no *C. finmarchicus* with the OPC (Figs. 2a, 3e, & 4); these whales were likely feeding on other copepods at the time (unfortunately, the VPR malfunctioned during these tagging events, so no other copepods were detectable). Right whales in Cape Cod Bay typically switch from smaller copepods to *C. finmarchicus* in April when *C. finmarchicus* enter the bay with a body size that is filterable by right whale baleen (Mayo & Marx 1990, Mayo et al. 2001).

Diving and foraging behavior

Right whales were observed to feed on highly aggregated layers of *C. finmarchicus* in nearly all parts of the water column between the surface and the sea floor, including at the surface, in the upper 15 m, at the base of the thermocline, at the top of the bottom mixed layer (Baumgartner & Mate 2003), near the sea floor (<15 m altitude), and within a few meters of the sea floor. Moreover, right whales visited the sea floor in every habitat studied except near Stellwagen Bank (where only 1 right whale was tagged), either to feed (e.g. Fig. 2a,g) or during an exploratory V-shaped dive (e.g. Fig. 2i). Because the sample sizes in Cape Cod Bay, Roseway Basin, and Jeffreys Ledge were very low, our observations of near-bottom diving in these habitats suggest that this is a common right whale behavior throughout their range. Even in habitats where surface skim feeding is often observed (Cape Cod Bay: Watkins & Schevill 1976, Mayo & Marx 1990, Parks et al. 2012; Great South Channel: Wishner et al. 1988, 1995, Kenney et al. 1995, Beardsley et al. 1996) or where right whales are known to feed at mid-water (Bay of Fundy and Roseway Basin: Baumgartner & Mate 2003), right whales visit the sea floor to either feed or presumably search for food (Fig. 4).

When feeding, right whales adhere to a simple model of diving that optimizes their time in the narrow stratum of maximum copepod abundance in the water column. Whales foraging at shallow depths dove much more frequently than whales foraging at deep depths, apparently in an effort to achieve a constant total time at depth (i.e. total feeding time) regardless of foraging depth. However, right whales foraging at shallow depths can actually spend more time at depth if they employ dive durations and dive frequencies similar to those used while foraging at deep depths. Why would a whale foraging at 5 m depth choose to limit its feeding time by conducting 20–40 short dives h^{-1} instead of maximizing its feeding time by conducting only a few long dives (like a whale foraging at 150 m)? Our observations indicate that right whales are clearly physiologically capable of both strategies. The theoretical model suggests that when foraging at 5 m, the total time spent at depth decreases by only a few percent when the frequency of dives increases from a few dives to 40 dives h^{-1} (Fig. 6d), whereas when foraging at 150 m, total time at depth decreases dramatically as dive frequency increases. Therefore, very little feeding time is actually lost when diving more frequently at shallower foraging depths. At the cost of a modest reduction in foraging time (Fig. 6d), right whales choose to dive more frequently for shorter periods of time when foraging on shallow aggregations of copepods. We suggest that they do this so that they can breathe more frequently and avoid the physiological stress of long-duration breath holding.

We did not observe resting behavior in any of the tagged right whales, likely because our tagging durations were short, but so-called 'logging' behavior (slow or no movement at the surface for periods of minutes to tens of minutes) is often observed in right whales. The tagged whales' dives were very likely within their aerobic dive limit, since surface times (measured as PCST) did not increase with dive duration or dive depth (see Baumgartner & Mate 2003); such a relationship would be expected if the aerobic dive limit is exceeded and the resulting oxygen debt incurred during anaerobic metabolism must be repaid during longer surfacings (Kooyman et al. 1980, 1983). Despite diving within their aerobic dive limit, it is conceivable that some period of rest at the surface is required after long periods (i.e. hours) of foraging on deep aggregations of copepods. Conversely, the higher dive (and surfacing/respiration) frequency observed for right whales feeding on shallow aggregations of copepods may allow continuous feeding without the need for rest. If this were true, continuous feeding may compensate for the modest reduction in foraging time associated with high dive frequency during shallow feeding; therefore, over longer time scales (tens of hours), this shallow-feeding behavior might allow the same or perhaps even more foraging time than deep-feeding behavior with low dive frequencies and occasional periods of rest. When 2 layers of copepods were available in the water column (Fig. 5), right whales chose to feed on the shallower layer (this choice assumes the whales were aware of both layers). The case shown in Fig. 5d illustrates both an awareness of the 2 layers (the whale visits both layers) and the choice to feed on the shallow layer despite the average maximum copepod abundance of the deep layer being over 6 times that of the shallow layer (Fig. 5b). While anecdotal (this is the only case where abundance in the deep layer was significantly higher than the shallow layer), this case suggests that right whales may prefer feeding at shallow depths whenever possible. We hypothesize that shallow feeding with high dive frequency (1) allows more frequent respiration, and (2) permits continuous feeding without the need for rest, which may ultimately increase foraging time. It is important to keep in mind, however, that shallow feeding on *C. finmarchicus* is usually only possible during spring; during summer, fall, and early winter, right whales feed on diapausing *C. finmarchicus* at mid-depth or near the sea floor, and by mid-winter, *C. finmarchicus* are unavailable to right whales (see 'Diving behavior and copepod life history' above).

Threats and management implications

Although the North Atlantic right whale population grew during the 2000s, the population size of fewer than 500 animals is still alarmingly low, and a combination of stressors could easily push the species to extinction (Kraus et al. 2016, Pace et al. 2017). In addition to anthropogenic threats, climate change is particularly worrisome for right whales because of their reliance on very few prey species. Environmental and ecosystem changes may displace *C. finmarchicus* from the Gulf of Maine and Scotian Shelf (Reygondeau & Beaugrand 2011) or fundamentally change its survivability in this region owing to significant changes in temperature-controlled diapause duration (Pierson et al. 2013, Wilson et al. 2016), but the highly specialized zooplanktivorous right whales do not have the luxury of switching to new prey species in these habitats. Right whales are dependent on the lipid-rich calanoid copepods of the Calanidae family (i.e. *C. finmarchicus*, *C. glacialis*, *C. hyperboreus*) and likely cannot survive year-round on the other smaller, less numerous, and lipid-deplete copepods of the North Atlantic (e.g. *Pseudocalanus* spp., *Centropages* spp., *Acartia* spp., *Metridia* spp.). Our foraging ecology observations presented here highlight this dependence. Even if *C. finmarchicus* remained abundant in the Gulf of Maine and Scotian Shelf, climate-induced changes in water column structure or *C. finmarchicus* behavior may disrupt the vertically compressed aggregations of copepods that right whales depend upon to feed.

In the face of these environmental changes, it is all the more critical to reduce human-caused mortality and serious injury in right whales. The present study indicates that industrial activities or conservation measures predicated on right whales avoiding a particular part of the water column are dangerous; right whales use the entire water column from surface to sea floor. While right whales are always at risk of ship strikes because they must spend time at the surface to breathe, right whales in springtime habitats are particularly vulnerable to ship strikes because they spend the vast majority of their time in the upper 10 m of the water column (i.e. within the draft of large commercial ships) (Parks et al. 2012, this study). Despite the regular occurrence of right whales in the western Gulf of Maine during the spring (e.g. Kenney et al. 1995, Mussoline et al. 2012), in all months but April less than 50 % of the length of the shipping lanes approaching Boston, Massachusetts, are subject to seasonal management area (SMA) rules that require vessels 19.8 m (65 feet) and over to travel no faster than 10 knots (Fig. 7). These speed restriction rules were implemented expressly to reduce right whale ship strikes (National Marine Fisheries Service 2008), but they are based on a static model of right whale distribution that assumes right whales reside in Cape Cod Bay during January, February, and March, transition to the Great South Channel during March and April, and then reside in the Great South Channel during May, June, and July. While that may be true on average, individual whales are highly mobile and likely do not remain within SMA boundaries at all times. Of 16 right whales outfitted with satellite tags during 1989–1991 and 2000 in the Bay of Fundy, a summertime habitat, half spent significant time (>50 % of satellite locations) outside of this habitat, and the area immediately adjacent to this habitat was heavily trafficked by the whales (Baumgartner & Mate 2005). There is no reason to think that right whales do not also travel through and possibly feed in the areas adjacent to Cape Cod Bay and the Great South Channel during the spring, and in particular between these 2 habitats during April and May. Taking into account their high mobility and the fact that the risk of ship strike is so acute during the spring owing to right whale diving behavior, it seems prudent to expand the current western Gulf of Maine seasonal management areas. In particular, we recommend that the end of the 'Off Race Point' SMA (Fig. 7 in blue) be extended from 1–31 May. Ironically, both Cape Cod Bay and the Great South Channel have SMAs in place during the first 2 wk of May, but the corridor between them does not.

We observed a relatively high incidence of near-sea-floor dives by right whales across habitats (1 in 4 tagged animals visited the sea floor), which is a serious cause for concern with respect to fixed fishing gear practices. Pot and trap gear typically have ground lines that connect multiple pots or traps at the sea floor, and end lines that connect the terminal pots/traps to a surface buoy. In 2009, buoyant ground lines that floated above the sea floor were eliminated by regulation in most US federal waters in the Gulf of Maine, but they remain in use in Maine coastal waters and in all Canadian waters (e.g. Brillant & Trippel 2010) despite evidence of their role in right whale entanglements (Johnson et al. 2005). Our observations suggest that right whales visit the sea floor far more often than previously thought, and that where used, floating ground lines are still a significant entanglement hazard for right whales. Some regulations allow the use of so-called 'neutrally buoyant' ground lines that supposedly hover just centimeters above the sea floor; however, all ground lines have a fixed density (specific gravity) and as such, will only be neutrally buoyant when the surrounding water has exactly the same density as the line. Because water density at the sea floor fluctuates over time and from region to region, 'neutrally buoyant' ground line will nearly always act as either floating or sinking ground line, and in cases where it acts as a floating ground line, it is just as hazardous as actual floating ground line.

Brillant & Trippel (2010) measured floating ground line heights for lobster pot gear set in the lower Bay of Fundy, and concluded that because 92 % of line elevations were at or below 3 m (the nominal body height of a right whale), floating ground lines in this habitat posed a small risk to right whales. Given the upwardly and posteriorly sloped shape of the ante-

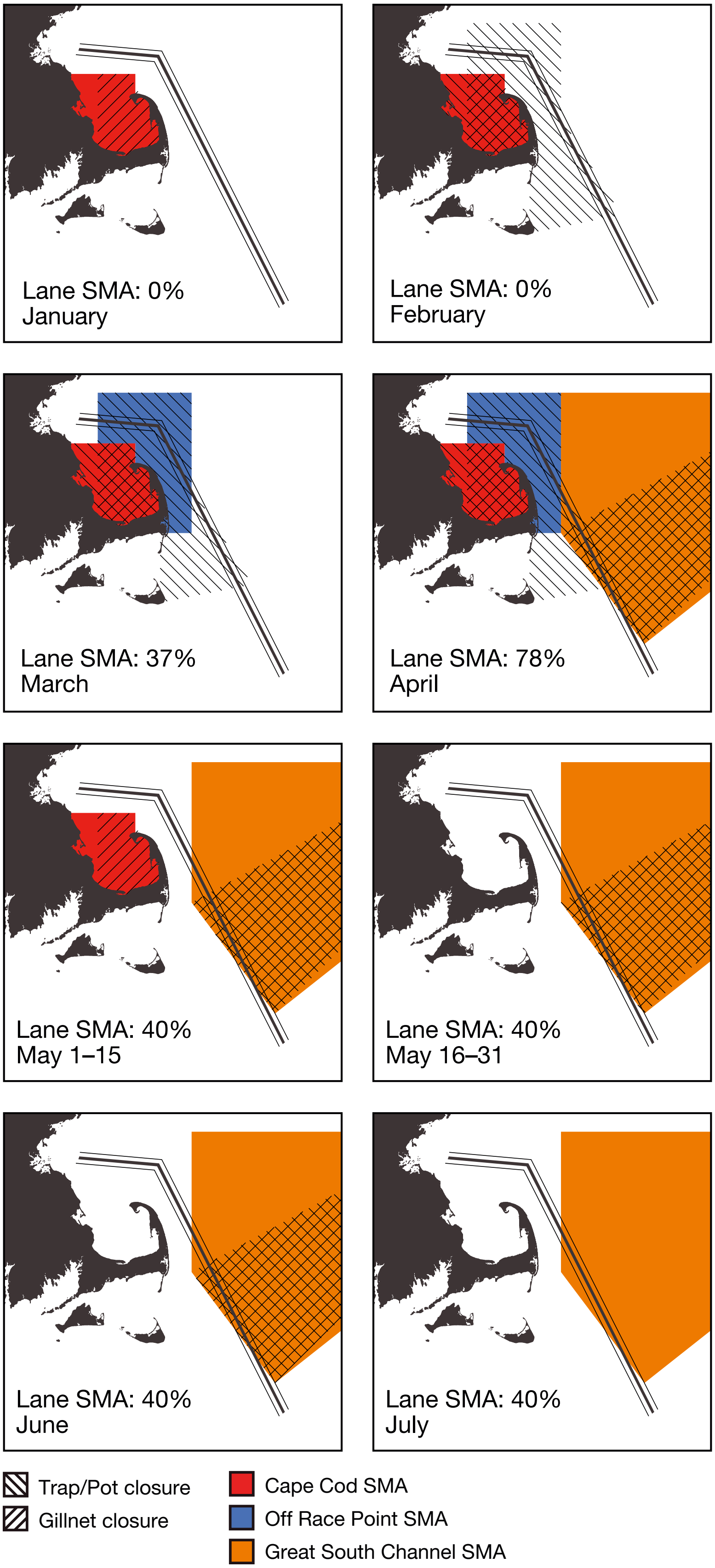

Fig. 7. Protections for North Atlantic right whales *Eubalaena glacialis* from January to July in the southwestern Gulf of Maine, including Cape Cod Bay seasonal management area (SMA, red), Off Race Point SMA (blue), Great South Channel SMA (orange), trap/pot closure areas (lines oriented from upper left to lower right), and gillnet closure areas (lines oriented from lower left to upper right); cross-hatched areas indicate simultaneous trap/pot and gillnet closures. Ships ≥19.8 m (65 feet) long must reduce speed to ≤10 knots in SMAs. Shipping lanes approaching Boston, Massachusetts, are shown, and the percentage of the length of the lanes subject to the 10 knot speed restriction (percentage of lanes in a SMA) is reported as 'Lane SMA'

rior tip of a right whale's lower jaw, lines suspended only a few tens of centimeters above the sea floor are at risk of getting entangled in a whale's mouth if it is foraging with the flattened ventral side of its lower jaw (chin) in contact with the sea floor (note that a tag on this same whale's back would be 3 m above the sea floor). Lines floating below 3 m height above the sea floor are still a significant threat. Although Baumgartner & Mate (2003) reported right whales foraging in the lower Bay of Fundy on *C. finmarchicus* at the top of the bottom mixed layer well above the sea floor, the tagging data reported by Goodyear (1996) provide evidence of right whales spending significant amounts of time at the sea floor in this same habitat, presumably feeding. Since monitoring began there in the 1980s, there have been hundreds of observations of right whales surfacing with mud on their heads in the lower Bay of Fundy (Mate et al. 1997, S. Kraus pers. comm.), and we even recovered 1 of our tags in this habitat with mud on it. These observations suggest that all floating ground lines pose a hazard to right whales.

The recent decline of right whales and their extremely low population size must be viewed as a crisis that demands immediate action in the US and Canada. Our study strongly suggests that right whales use the entire water column in all habitats, and that efforts to mitigate fishing gear entanglements and ship strikes should not assume otherwise. Although ship strikes have been reduced in recent years, additional protections are warranted based on movement patterns and foraging behavior, particularly in Massachusetts waters where ships have killed at least 2 right whales during 2016 and 2017. Mortality and serious injury from entanglements are at a historic high (currently twice the highest historical annual rate of mortality and serious injury from ship strikes), and new and bold approaches, such as reduced breaking strength line and rope-less fishing (Knowlton et al. 2016), are urgently needed. These new mitigation measures should be implemented as soon as possible to significantly reduce human-caused mortality and hopefully return right whales to the path of recovery.

Acknowledgements. We are indebted to Bruce Mate for his role in the work published in Baumgartner & Mate (2003). In addition to those acknowledged in Baumgartner & Mate (2003), we acknowledge the following people and organizations for work conducted between 2004 and 2010. We are grateful to the captains and crew of the NOAA ships 'Delaware II' and 'Albatross IV' and the RV 'Tioga' for their assistance, as well as to 2010 chief scientist Lisa Conger. Michael Moore, David Wiley, and Sarah Mussoline provided critical assistance in the field. Significant logistical, equipment, and personnel support was provided by the Northeast Fisheries Science Center, especially Richard Merrick, Peter Corkeron, Sofie Van Parijs, Maureen Taylor, and David Mountain. We are grateful to Peter Corkeron, Sean Hayes, Michael Simpkins, and 2 anonymous reviewers. for providing constructive criticism on earlier versions of this paper. Support for this research was provided by the NOAA Right Whale Grants Program, Northeast Consortium, Woods Hole Oceanographic Institution, NOAA Northeast Fisheries Science Center, and the Office of Naval Research. Tagging was conducted under Woods Hole Oceanographic Institution IACUC protocols and federal permits issued to Bruce Mate, NOAA Northeast Fisheries Science Center and M.F.B.

LITERATURE CITED

Baumgartner MF (2003) Comparisons of *Calanus finmarchicus* fifth copepodite abundance estimates from nets and an optical plankton counter. J Plankton Res 25:855–868

Baumgartner MF, Mate BR (2003) Summertime foraging ecology of North Atlantic right whales. Mar Ecol Prog Ser 264:123–135

Baumgartner MF, Mate BR (2005) Summer and fall habitat of North Atlantic right whales (*Eubalaena glacialis*) inferred from satellite telemetry. Can J Fish Aquat Sci 62: 527–543

Baumgartner MF, Cole TVN, Clapham PJ, Mate BR (2003a) North Atlantic right whale habitat in the lower Bay of Fundy and on the SW Scotian Shelf during 1999–2001. Mar Ecol Prog Ser 264:137–154

Baumgartner MF, Cole TVN, Campbell RG, Teegarden GJ, Durbin EG (2003b) Associations between North Atlantic right whales and their prey, *Calanus finmarchicus*, over diel and tidal time scales. Mar Ecol Prog Ser 264:155–166

Baumgartner MF, Mayo CA, Kenney RD (2007) Enormous carnivores, microscopic food, and a restaurant that's hard to find. In: Kraus SD, Rolland RM (eds) The urban whale: North Atlantic right whales at the crossroads. Harvard University Press, Cambridge, MA, p 138–171

Baumgartner MF, Freitag L, Partan J, Ball K, Prada K (2008) Tracking large marine predators in three dimensions: the real-time acoustic tracking system. IEEE J Oceanic Eng 33:146–157

Baumgartner MF, Lysiak NSJ, Schuman C, Urban-Rich J, Wenzel FW (2011) Diel vertical migration behavior of *Calanus finmarchicus* and its influence on right and sei whale occurrence. Mar Ecol Prog Ser 423:167–184

Beardsley RC, Epstein AW, Chen C, Wishner KF, Macaulay MC, Kenney RD (1996) Spatial variability in zooplankton abundance near feeding right whales in the Great South Channel. Deep Sea Res II 43:1601–1625

Brillant SW, Trippel EA (2010) Elevations of lobster fishery groundlines in relation to their potential to entangle endangered North Atlantic right whales in the Bay of Fundy, Canada. ICES J Mar Sci 67:355–364

Collett R (1909) A few notes on the whale *Balaena glacialis* and its capture in recent years in the North Atlantic by Norwegian whalers. Proc Zool Soc Lond 7:91–98

Davis CS, Gallager SM, Berman MS, Haury LR, Strickler JR (1992) The video plankton recorder (VPR): design and initial results. Arch Hydrobiol Beih Ergeb Limnol 36: 67–81

Davis CS, Gallager SM, Marra M, Stewart WK (1996) Rapid visualization of plankton abundance and taxonomic composition using the video plankton recorder. Deep Sea Res II 43:1947–1970

Dolphin WF (1987) Dive behavior and estimated energy expenditure of foraging humpback whales in southeast Alaska. Can J Zool 65:354–362

Durbin EG, Gilman SL, Campbell RG, Durbin AG (1995) Abundance, biomass, vertical migration and estimated development rate of the copepod *Calanus finmarchicus* in the southern Gulf of Maine during late spring. Cont Shelf Res 15:571–591

Durbin EG, Garrahan P, Casas M (2000) Abundance and distribution of *Calanus finmarchicus* on the Georges Bank during 1995 and 1996. ICES J Mar Sci 57: 1664–1685

Goodyear JD (1996) Significance of feeding habitats of North Atlantic right whales based on studies of diel behavior, diving, food ingestion rates, and prey. PhD dissertation, University of Guelph

Hayes SA, Josephson E, Maze-Foley K, Rosel PE (2017) U.S. Atlantic and Gulf of Mexico Marine Mammal Stock Assessments – 2016. NOAA Tech Memo NMFS-NE-241. NOAA, NMFS, Woods Hole, MA

Herman AW (1988) Simultaneous measurement of zooplankton and light attenuance with a new optical plankton counter. Cont Shelf Res 8:205–221

Herman AW (1992) Design and calibration of a new optical plankton counter capable of sizing small zooplankton. Deep-Sea Res 39:395–415

Hirche HJ (1996) Diapause in the marine copepod, *Calanus finmarchicus* — a review. Ophelia 44:129–143

Johnson A, Salvador G, Kenney J, Robbins J, Kraus S, Landry S, Clapham P (2005) Fishing gear involved in entanglements of right and humpback whales. Mar Mamm Sci 21:635–645

Kenney RD, Winn HE, Macaulay MC (1995) Cetaceans in the Great South Channel, 1979-1989: right whale (*Eubalaena glacialis*). Cont Shelf Res 15:385–414
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
Kooyman GL, Wahrenbrock EA, Castellini MA, Davis RW, Sinnett EE (1980) Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: evidence of preferred pathways from blood chemistry and behavior. J Comp Physiol B 138:335–346
Kooyman GL, Castellini MA, Davis RW, Maue RA (1983) Aerobic diving limits of immature Weddell seals. J Comp Physiol B 151:171–174
Kraus SD, Kenney RD, Mayo CA, McLellan WA, Moore MJ, Nowacek DP (2016) Recent scientific publications cast doubt on North Atlantic right whale future. Front Mar Sci 3:137
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
Marshall SM, Orr AP (1955) The biology of a marine copepod *Calanus finmarchicus* (Gunnerus). Oliver and Boyd, Edinburgh
Mate BR, Nieukirk SL, Kraus SD (1997) Satellite-monitored movements of the northern right whale. J Wildl Manage 61:1393–1405
Mayo CA, Marx MK (1990) Surface foraging behavior of the North Atlantic right whale, *Eubalaena glacialis*, and associated zooplankton characteristics. Can J Zool 68: 2214–2220
Mayo CA, Letcher BH, Scott S (2001) Zooplankton filtering efficiency of the baleen of a North Atlantic right whale, *Eubalaena glacialis.* J Cetacean Res Manag (Spec Issue) 2:225–229
McLaren IA, Head E, Sameoto DD (2001) Life cycles and seasonal distributions of *Calanus finmarchicus* on the central Scotian Shelf. Can J Fish Aquat Sci 58:659–670
Miller CB, Cowles TJ, Wiebe PH, Copley NJ, Grigg H (1991) Phenology in *Calanus finmarchicus*; hypotheses about control mechanisms. Mar Ecol Prog Ser 72:79–91
Murison LD, Gaskin DE (1989) The distribution of right whales and zooplankton in the Bay of Fundy, Canada. Can J Zool 67:1411–1420
Mussoline SE, Risch D, Hatch LT, Weinrich MT and others (2012) Seasonal and diel variation in North Atlantic right whale up-calls: implications for management and conservation in the northwestern Atlantic Ocean. Endang Species Res 17:17–26
National Marine Fisheries Service (2008) Final rule to implement speed restrictions to reduce the threat of ship collisions with North Atlantic right whales, rule 50 CFR Part 224. Fed Regist 73:60173–60191
Nowacek DP, Johnson MP, Tyack PL, Shorter KA, McLellan WA, Pabst DA (2001) Buoyant balaenids: the ups and downs of buoyancy in right whales. Proc Biol Sci 268: 1811–1816
Pace RM III, Cole TVN, Henry AG (2014) Incremental fishing gear modifications fail to significantly reduce large whale serious injury rates. Endang Species Res 26:115–126
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, doi 10.1002/ece3.3406
Parks SE, Warren JD, Stamieszkin K, Mayo CA, Wiley D (2012) Dangerous dining: surface foraging of North Atlantic right whales increases risk of vessel collisions. Biol Lett 8:57–60
Pierson JJ, Batchelder H, Saumweber W, Leising A, Runge J (2013) The impact of increasing temperatures on dormancy duration in *Calanus finmarchicus.* J Plankton Res 35:504–512
Reygondeau G, Beaugrand G (2011) Future climate-driven shifts in distribution of *Calanus finmarchicus.* Glob Change Biol 17:756–766
Rodrigue JP, Comtois C, Slack B (2017) The geography of transport systems, 4th edn. Routledge, London
Tucker MA, Rogers TL (2014) Examining predator–prey body size, trophic level and body mass across marine and terrestrial mammals. Proc Biol Sci 281:20142103
van der Hoop JM, Moore MJ, Barco SG, Cole TVN 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 (2015) Vessel strikes to large whales before and after the 2008 ship strike rule. Conserv Lett 8:24–32
Watkins WA, Schevill WE (1976) Right whale feeding and baleen rattle. J Mammal 57:58–66
Wilson RJ, Banas NS, Heath MR, Speirs DC (2016) Projected impacts of 21st century climate change on diapause in *Calanus finmarchicus.* Glob Change Biol 22:3332–3340
Winn HE, Goodyear JD, Kenney RD, Petricig RO (1995) Dive patterns of tagged right whales in the Great South Channel. Cont Shelf Res 15:593–611
Wishner KF, Durbin E, Durbin A, Macaulay M, Winn H, Kenney R (1988) Copepod patches and right whales in the Great South Channel off New England. Bull Mar Sci 43:825–844
Wishner KF, Schoenherr JR, Beardsley R, Chen C (1995) Abundance, distribution and population structure of the copepod *Calanus finmarchicus* in a springtime right whale feeding area in the southwestern Gulf of Maine. Cont Shelf Res 15:475–507

Editorial responsibility: Elliott Hazen, Pacific Grove, California, USA

Submitted: February 10, 2107; Accepted: August 22, 2017
Proofs received from author(s): September 28, 2017