

Summertime foraging ecology of North Atlantic right whales

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ABSTRACT: North Atlantic right whales were instrumented with suction-cup mounted, time-depth recorders (TDR) during the summers of 2000 and 2001 to examine their diving and foraging behavior. Simultaneous observations of temperature, salinity and the vertical distribution of their principal prey, *Calanus finmarchicus* stage 5 copepodites (C5), were obtained along each whale's track with a conductivity-temperature-depth instrument (CTD) and an optical plankton counter (OPC). Right whale feeding dives were characterized by rapid descent from the surface to a particular depth between 80 and 175 m, remarkable fidelity to that depth for 5 to 14 min and then rapid ascent back to the surface. The average depth of dive was strongly and positively correlated with both the average depth of peak *C. finmarchicus* C5 abundance and the average depth of the bottom mixed layer's upper surface. Significantly longer surface intervals were observed for reproductively active females and their calves when compared to other individuals, indicating that this critical segment of the population may be at increased risk of ship strikes owing to their diving behavior. Ingestion rates calculated from TDR and OPC data exceeded estimated daily metabolic requirements for most of the tagged right whales; however, short deployment durations and uncertainty in metabolic rates make it impossible to judge whether individual right whales were obtaining sufficient energy to meet the metabolic costs of reproduction. Improvements in attachment durations and the development of novel methods to estimate the metabolic rates of large whales *in situ* are required to determine whether right whale reproduction is limited by insufficient food resources.

KEY WORDS: Right whale · *Eubalaena glacialis* · *Calanus finmarchicus* · Diving behavior · Energetics · Aggregation

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INTRODUCTION

The foraging behavior of marine mammals is difficult to observe directly, because it often occurs below the sea surface. The miniaturization of sensors and data loggers in recent decades has facilitated the development of time-depth recorders (TDR) to study the diving behavior of marine mammals (Kooyman 1989, Costa 1993), but obtaining information about prey distribution and abundance at the same temporal and spatial scales of the TDR is rarely feasible. The North Atlantic

right whale *Eubalaena glacialis* occupies a unique trophic position in the marine ecosystem; it is one of the world's largest predators (up to 17 m), yet it feeds primarily on one of the smallest marine animals, the 2 to 3 mm long calanoid copepod *Calanus finmarchicus*. Assessing the abundance of this copepod at spatial scales that are relevant to a right whale (10s of cm to m in the vertical, 10s to 100s of m in the horizontal) is nearly impossible with conventional net sampling methods. Targeted net sampling is only feasible when right whales are feeding at or very near the surface

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and copepod patches can be visually identified (Watkins & Schevill 1976, Wishner et al. 1988, 1995, Mayo & Marx 1990, Beardsley et al. 1996). With the advent of instrumentation to estimate the abundance of zooplankton, however, the distribution of *C. finmarchicus* can now be adequately and rapidly sampled at spatial scales much closer to those utilized by the whales.

North Atlantic right whales are one of the most endangered large whales, and despite international protection from whaling since the 1930s, this species has failed to recover to its pre-exploitation population levels (Clapham et al. 1999). Recent estimates suggest that only around 300 individuals remain (Knowlton et al. 1994, IWC 2001, Kraus et al. 2001), and the current, unacceptably high mortality rates (due, in part, to ship strikes and fishing gear entanglements) are projected to cause extinction within a few centuries (Caswell et al. 1999, Fujiwara & Caswell 2001). Consequently, there is an urgent need for information about the habitat and habitat use of right whales to improve conservation efforts. There is also a need to improve our understanding of food availability and foraging success as determinants of reproductive success. One of the hypotheses to explain the lack of recovery in this population states that centuries of depressed abundance due to whaling has allowed other predators of *Calanus finmarchicus* to flourish (e.g. planktivorous fish, see Payne et al. 1990), so sufficient food resources to support substantial population growth no longer exist (IWC 2001). Recent results linking temporal variability in both crude right whale survival probability (Fujiwara & Caswell 2001) and right whale reproductive success (Kenney et al. 2001) to the North Atlantic Oscillation, which, in turn, affects *C. finmarchicus* abundance (Fromentin & Planque 1996, Greene & Pershing 2000, Conversi et al. 2001), seem consistent with this hypothesis.

Right whales have been observed feeding on older copepodite stages of *Calanus finmarchicus* in Cape Cod Bay (Watkins & Schevill 1976, Mayo & Marx 1990) and in the Great South Channel (Wishner et al. 1988, 1995, Beardsley et al. 1996) in the late winter and spring. Surface feeding occurs occasionally, but subsurface feeding is much more common (Watkins & Schevill 1976, Mayo & Marx 1990, Kenney et al. 1995). During the summer, right whales can be found in the lower Bay of Fundy and on the SW Scotian Shelf, where they continue to feed on older stages of *C. finmarchicus* (Stone et al. 1988, Murison & Gaskin 1989, Woodley & Gaskin 1996). At this time of year, the bulk of the *C. finmarchicus* population consists of stage 5 copepodites (C5) that are in a resting state deep in the water column (Sameoto & Herman 1990, Miller et al. 1991). Net sampling by Murison & Gaskin (1989) in the

lower Bay of Fundy indicated that *C. finmarchicus* C5 was the dominant zooplankton near right whales and that these copepods occurred at depths below 100 m. Both Murison & Gaskin (1989) and Goodyear (1993) observed right whales diving to depths below 100 m in the lower Bay of Fundy.

We report here on a study of right whale diving and foraging behavior in the lower Bay of Fundy and on the southwestern Scotian Shelf. Right whale diving behavior was monitored via suction-cup mounted TDRs, and observations of *Calanus finmarchicus* C5 vertical distribution were obtained near the tagged whales with an optical plankton counter (OPC). These measurements were used to investigate the hypothesis that right whales exploit high abundances of *C. finmarchicus* C5 concentrated in discrete layers. Kenney et al. (1986) suggested that foraging must occur on discrete layers of zooplankton for right whales to satisfy their energetic demands. We used the OPC to sample these discrete layers at temporal and spatial scales similar to those of the foraging whales. Simultaneous observations of temperature and salinity obtained with a conductivity-temperature-depth instrument (CTD) also allowed an investigation of the hydrographic features that promote the formation or persistence of these layers. To address the hypothesis of insufficient food resources, right whale ingestion rates were estimated from the TDR and OPC data and compared to daily metabolic requirements.

MATERIALS AND METHODS

The tag used during the 2000 summer field season consisted of a modified Wildlife Computers model MK7 TDR that recorded pressure (converted to depth at a resolution of 2 m), temperature and relative light intensity every second. The tag needed to be recovered for access to these data. The TDR also included a slot in which a Telonics model CHP-1P, 149 MHz radio transmitter was placed. Syntactic foam floatation was molded around one end of the TDR to make the entire tag positively buoyant. The tag was attached to a whale via a silicone suction cup and detachment was uncontrolled. In 2001, a Vemco model V22P acoustic transmitter was included in the tag to allow tracking while a whale was submerged. The acoustic transmitter emitted 36 kHz pulses at 165 dB (re 1 μ Pa at 1 m) at intervals proportional to the depth of the tag (e.g. every 1.03 s at 10 m and 0.76 s at 200 m). A corrosive release mechanism was also incorporated in the tag in 2001 that was designed to provide reliable attachment durations of between 1 and 2 h. The suction cup was changed in 2001 to a more robust, rubber material. In both 2000 and 2001, the tag was attached with a 9 m

telescoping pole from an elevated platform in the bow of a 7.5 m rigid-hulled inflatable boat (RHIB).

Visual observations were used to assess the reaction of whales to close boat approaches. However, the value of these observations in gauging the overall effects of tagging is unclear. It is important to consider the effect of tagging on biologically meaningful activities (e.g. feeding, breeding) and to use objective data when doing so. Toward that end, the diving behavior of the tagged whales was also investigated for reactions to close boat approach and tagging. The tagged right whales engaged primarily in feeding behavior (see 'Results'), so only whales tagged for over 1 h with 2 or more feeding dives were examined. The characteristics of the first feeding dive (duration, average dive depth, descent speed, ascent speed) were compared to those of the second, third, fourth and last observed feeding dives to document any significant changes in diving behavior as a result of the tag attachment process. This first feeding dive occurred up to 7.5 min after tag deployment. In addition, the characteristics of the second feeding dive were compared to those of the third, fourth and last dives, and the characteristics of the third feeding dive were compared to those of the fourth and last dives.

Following deployment, the whale was tracked at the surface via the radio transmitter, and in 2001, via the acoustic transmitter when the whale was submerged. Recovery of the tag after detachment was facilitated with these same systems. Right whales were tagged and tracked only during daylight hours. Radio tracking was accomplished with a 4-element Yagi antenna and a receiver. Bearing alone was estimated from the received signal intensity, and the range of the system was over 1 km. Acoustic tracking was accomplished with a directional hydrophone and a receiver. Bearing and horizontal distance to the animal were estimated from the received acoustic signal intensity and, with some experience, these could be judged to within 15° and 50 to 100 m, respectively. The pulse interval was measured, converted to depth and displayed by the acoustic receiver, so an estimate of the depth of the whale was also available in real time. To test the range of the acoustic system, a transmitter was suspended in the lower Bay of Fundy at 75 m and detectability was tested at various distances. The maximum distance tested was 1 km before weather forced an end to the experiment, but the signal was easily detected at this maximum distance.

Upon each resurfacing of a tagged whale after a long dive, the resurfacing position was obtained by parking a RHIB on the exact location and obtaining a global positioning system (GPS) measurement. Shortly thereafter, NOAA Ship 'Delaware II' would occupy this same position and deploy an instrument package consisting of a Seabird model SBE19 CTD and a Focal Technologies model OPC-1T. These instruments were housed in a rosette cage and deployed in a vertical cast at a nominal 0.5 m s⁻¹ (2000) or 1.0 m s⁻¹ (2001) descent rate. The CTD provided the vertical distribution of temperature and salinity and the OPC provided the vertical distribution of particle abundance in sizes ranging from 0.25 to 20 mm (Herman 1988, 1992). The abundance of *Calanus finmarchicus* C5 was estimated from the OPC data using a calibration equation developed from comparisons between OPC measurements and net samples collected in this same region (Baumgartner 2003). During tracking, behavioral observations and social interactions were noted and when possible photographs were taken for comparison with the New England right whale catalog (Hamilton & Martin 1999) to identify tagged individuals.

Dives were defined as any vertical excursion below 50 m. The period between these dives was typically spent at or just below the surface. Vertical excursions between the surface and 50 m typically occurred during traveling or associations with other right whales. Dives were considered to be initiated when the vertical descent speed exceeded 0.5 m s⁻¹ and the descent portion of the dive was terminated when the vertical descent speed dropped below 0.5 m s⁻¹ (Fig. 1).

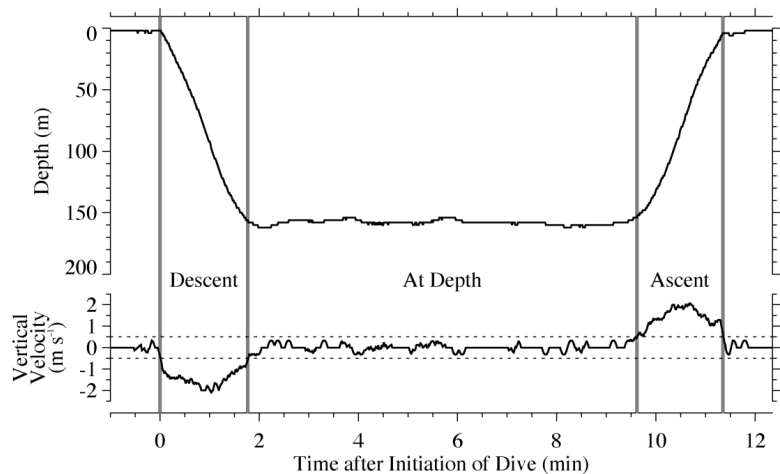


Fig. 1. *Eubalaena glacialis*. Typical right whale feeding dive with descent, at depth and ascent portions shown. By convention, the descent portion begins when the downward velocity exceeds 0.5 m s⁻¹ and ends when the downward velocity drops below 0.5 m s⁻¹. Likewise, the ascent portion begins when the upward velocity exceeds 0.5 m s⁻¹ and ends when the upward velocity drops below 0.5 m s⁻¹.

Ascent was initiated when the vertical ascent speed exceeded 0.5 m s^{-1} and the dive was terminated when the vertical ascent speed dropped below 0.5 m s^{-1} . The dive duration was defined as the time between the initiation of the descent and the termination of the ascent. The duration at depth was defined as the time between the termination of the descent and the initiation of the ascent. The mean and SD of the dive depth were computed during the at-depth portion of the dive (i.e. between the termination of the descent and the initiation of the ascent). Classification of dives was facilitated by a Ward's minimum-variance cluster analysis and visualization with multivariate star plots (Johnson 1998). The cluster analysis and visualization were conducted on the dive duration, duration at depth, descent speed, ascent speed and SD of the dive depth. Dives were classified into 3 types: feeding, V-shaped and 'other'. Surface intervals were measured after feeding dives only when the successive dive was also a feeding dive and no social activity was observed. Surface intervals were also expressed as a percentage of the total dive cycle time (PCST: after Dolphin 1987). The total dive cycle time was computed as the sum of the dive duration and the succeeding surface interval.

The vertical distribution of *Calanus finmarchicus* C5 was estimated from the calibrated OPC data in 4 m depth strata below 50 m. The depth of the peak *C. finmarchicus* C5 abundance was chosen as the midpoint of the depth stratum containing the maximum *C. finmarchicus* C5 concentration. The lower Bay of Fundy is characterized by strong tidal flow that interacts with the sea floor to create a turbulent, well-mixed bottom layer. To examine the potential relationships among this bottom mixed layer, the vertical distribution of *C. finmarchicus* C5 and the diving behavior of the tagged right whales, the depth of the top of this layer was determined from the CTD data. The top of this boundary layer was defined as the deepest depth at which the density differed from the bottom density by at least 0.05 kg m^{-3} .

Each tagged whale was considered an independent observation. Therefore, individual dive characteristics (e.g. mean dive depth, dive duration, duration at depth) and associated environmental conditions (peak *Calanus finmarchicus* C5 abundance, depth of peak abundance and bottom mixed layer depth) were averaged to provide a single observation of each variable for each whale. For comparisons between dive characteristics and environmental conditions, only data for dives with accompanying CTD/OPC casts were averaged. Dive characteristics and associated environmental conditions were compared using correlation analysis.

Total ingestion of *Calanus finmarchicus* C5 (I_d) was estimated for each feeding dive as

$$I_d = A_g S T_d E_{C5} C \quad (1)$$

where A_g is the area of the whale's gape (the opening through which water enters the mouth), S is the swimming speed, T_d is the duration at depth, E_{C5} is the energy (calorific) content of a single *C. finmarchicus* C5 and C is the estimated *C. finmarchicus* C5 concentration available to the whale. The total ingestion rate (I') during the period when the whale was tagged was estimated as follows:

$$I' = \frac{T_f \sum I_d}{T_t \sum T_d} \quad (2)$$

where T_f is the total time spent at depth during feeding dives, T_t is the total time the tag was attached to the whale and the summation of I_d and T_d occurred over all dives that had accompanying CTD/OPC casts. The ratio of T_f to T_t is considered the fraction of time spent feeding. The gape area was assumed to be 1.21 m^2 (Mayo et al. 2001) and the energy content of a single *C. finmarchicus* C5 was fixed at $1.62 \times 10^{-3} \text{ kcal copepod}^{-1}$ (Comita 1966) or $6.78 \text{ J copepod}^{-1}$ ($1 \text{ kcal} = 4186.8 \text{ J}$). In 2001, improved tracking with the acoustic transmitter allowed accurate measurements of both diving and resurfacing locations. The distance between the diving and resurfacing locations divided by the dive duration was used as an estimate of the swimming speed during feeding (S in Eq. 1). These speeds must be considered minimum speeds, however, since we do not know whether the whales foraged along straight-line paths between the diving and resurfacing positions. To account for this, swimming speeds were increased to 1.5 m s^{-1} whenever the observed minimum speed was less than 1.5 m s^{-1} . Speeds were assumed to be 1.5 m s^{-1} for all dives in 2000. In Cape Cod Bay, Mayo et al. (2001) observed average swimming speeds during surface feeding of 1.34 m s^{-1} and Watkins & Shevill (1976) report speeds of 'up to 3 knots' or 1.54 m s^{-1} . Minimum swimming speeds in the present study averaged nearly 1 m s^{-1} (see Table 3 in 'Results'); however, subsurface foraging paths in the Bay of Fundy are not necessarily straight (D. P. Nowacek pers. comm.). Therefore, 1.5 m s^{-1} is assumed to be a reasonable estimate of true speed during feeding.

To investigate whether sufficient food was available to the tagged whales, the rate of ingestion was compared to the estimated rate needed to meet the daily metabolic requirements for maintenance in right whales. For simplicity, a right whale's day was divided into 2 activities: foraging and resting. The metabolic rate during foraging was assumed to be equal to the diving metabolic rate (DMR). Assuming that the

tagged right whales were able to continue to feed at I' for T h each day, the fraction of the daily metabolic requirement met by each whale is

$$\frac{\text{daily assimilation}}{\text{daily requirement}} = \frac{AI'T}{\text{DMR}(T) + \text{RMR}(24 - T)} \quad (3)$$

where A is the assimilation efficiency and RMR is the resting metabolic rate. The time required to meet the daily metabolic requirement (T_{req}) is then

$$T_{\text{req}} = \frac{24 \text{ RMR}}{AI' + \text{RMR} - \text{DMR}} \quad (4)$$

Both DMR and RMR were assumed to be multiples of the basal metabolic rate (BMR), which was estimated as

$$\text{BMR} = \frac{4186.8}{86400} [70M^{0.75}] \quad (5)$$

where M is the mass of a right whale in kg. The term in brackets is after Kleiber (1975) and the first term converts Kleiber's expression from kcal d^{-1} to W (or J s^{-1}). The assimilation efficiency and body mass are assumed to be 0.80 (Lockyer 1981) and 40 000 kg (Kenney & Winn 1986), respectively; therefore, $\text{BMR} = 0.96 \times 10^4 \text{ W}$. The magnitude of DMR is unknown for right whales, but for other species, DMR is $1.5 - 2 \times \text{BMR}$ in Weddell seals (Kooyman et al. 1973, Castellini et al. 1992), $2 - 3 \times \text{BMR}$ in northern elephant seals (Costa & Williams 1999) and nearly $6 \times \text{BMR}$ in the bottlenose dolphin and otariids (sea lions and fur seals) (Costa & Gentry 1986, Costa et al. 1989, Costa & Williams 1999). When compared to other marine mammals, the DMR for right whales is probably low since the energetic costs associated with continuous filter feeding do not appear particularly expensive (relative to lunge feeding in rorquals, for instance; Croll et al. 2001) and their insulating blubber layer is thick. Recent energetic investigations of bowhead whales, a closely related species to the right whale, suggest these whales have very low metabolic rates due, in part, to a very thick blubber layer and a low core temperature (J. C. George pers. comm.). We assume here that $\text{DMR} = 2 \times \text{BMR}$ and $\text{RMR} = 1 \times \text{BMR}$. For consistency with the literature, we also present ingestion rate as a fraction of the ingestion rate required to meet basal metabolic requirements. This latter rate (I'_{BMR}) is estimated as

$$I'_{\text{BMR}} = \frac{1}{A} \text{BMR} \quad (6)$$

or $1.20 \times 10^4 \text{ W}$.

RESULTS

A total of 28 right whales were tagged in the lower Bay of Fundy between 11 July and 28 August 2000 (Fig. 2). All but 2 of the tags were recovered. The

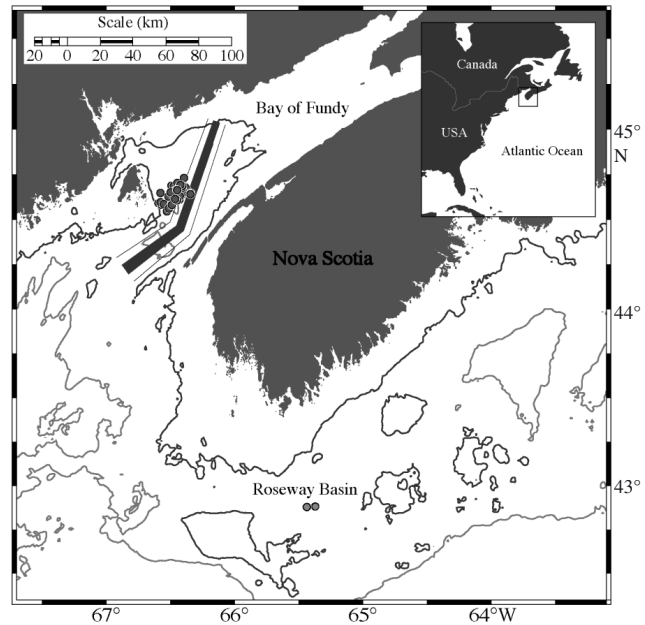


Fig. 2. Map of study area. (●) Tagging locations in the lower Bay of Fundy and Roseway Basin. Shipping lanes through the lower Bay of Fundy at the time of this study and the 91 m (50 fathom) and 200 m isobaths are also shown

median duration of attachment was 28 min and 23.1% ($n = 6$) of the tagging events exceeded 1 h. During a single event in 2000, a rubber suction cup was used instead of the silicone cup and the resulting attachment duration was 7 h. A total of 63 complete dives was recorded of which 93.7% ($n = 59$) were feeding dives, 4.8% ($n = 3$) were V-shaped and 1.6% ($n = 1$) were classified as 'other.' From 11 to 29 August 2001, 25 right whales were tagged and all of the tags were recovered. Of these 25 whales, 6 adults (presumably female) with calves, 2 calves and 1 pregnant (R. M. Rolland pers. comm.) female were tagged. Two of the whales were tagged in Roseway Basin on the southwestern Scotian Shelf and the remaining 23 were tagged in the lower Bay of Fundy (Fig. 2). The median duration of attachment was 86 min and 64.0% ($n = 16$) of the tagging events exceeded 1 h. A total of 86 complete dives was recorded of which 88.4% ($n = 76$) were feeding dives, 5.8% ($n = 5$) were V-shaped and 5.8% ($n = 5$) were classified as 'other.' Of the 149 total dives recorded in both 2000 and 2001, 86.6% ($n = 129$) had an accompanying CTD/OPC cast which, on average, was conducted 21.5 min after and 158 m away from the whale's resurfacing location.

Strong reaction to tagging or the close approach of the RHIB was uncommon. In 2000, 71% of the 42 whales that were closely approached by the RHIB

(within 10 m) showed no observable reaction (22 of 28 successfully tagged individuals and 8 of 14 unsuccessfully tagged individuals). Of the remaining whales, reactions included lifting the head or flukes, arching the back, rolling to one side, rolling to one side and beating the flukes (on 1 occasion), or performing a head lunge (on 1 occasion). Observations during close boat approaches in 2001 were qualitatively similar to those collected in 2000. The characteristics of the first, second, third, fourth and last feeding dives were compared for the 18 whales that were tagged for over 1 h and had 2 or more feeding dives. The duration of the first feeding dive was, on average, 13% ($n = 18$, $p = 0.0061$), 15% ($n = 17$, $p = 0.0039$), 17% ($n = 16$, $p = 0.0010$) and 14% ($n = 12$, $p = 0.045$) shorter than the second, third, fourth and last dives, respectively. In contrast, no significant differences in dive duration ($p > 0.05$) were detected in comparisons of the second and successive dives or the third and successive dives. Differences in dive duration between the first and successive dives did not depend on the time between tag attachment and the first feeding dive (correlation analysis, $p > 0.5$). No significant differences in descent speed, ascent speed or dive depth ($p > 0.05$) were detected in comparisons between the first dive and successive dives.

Based on these results, the effect of the tag attachment process on diving behavior is considered to be small and short-lived; hence, none of the subsequent analyses take this effect into account. Only the duration of the first feeding dive was affected by the tagging process, and the difference between this first dive and successive dives was small (~15% shorter). Reduction in dive duration during the first dive is likely caused by inadequate ventilation during the surfacing interval in which the tag was deployed which, in turn, may be due to evasion of the boat by premature diving, longer submergence times between breaths or increased swim speeds.

Feeding dives were characterized by a rapid descent from the surface to a particular depth, remarkable fidelity to that depth for an average of just over 9 min and then a rapid ascent back to the surface (Fig. 1, Table 1). Ascent speed averaged 0.07 m s^{-1} (95% CI: $0.01 - 0.13 \text{ m s}^{-1}$) faster than the corresponding descent speed during feeding dives (one-sample t -test, $p = 0.026$). Excluding the tagged calves, females with calves and the pregnant female, there was no evidence to suggest that PCST was correlated with either depth ($r = 0.119$, $p = 0.73$) or dive duration ($r = 0.029$, $p = 0.93$). For these indi-

viduals, PCST averaged 21.2% ($n = 11$, $SD = 4.1\%$, range = 15.8 – 30.1%) whereas for the tagged calves and females with calves, PCST averaged 34.2% ($n = 4$, $SD = 9.2\%$, range = 24.3 – 44.3%). The PCST for the pregnant female (shown in Fig. 4c) was 51.1%, which was the highest observed. Excluding the pregnant female, dive durations for calves and females with calves were similar to the other whales (2-sample t -test, $p = 0.78$: however, note low sample size and thus low power of test), but surface intervals were significantly higher (2-sample t -test, $p = 0.0011$). Surface intervals for calves and females with calves averaged 5.69 min ($n = 4$, $SD = 1.22 \text{ min}$, range = 4.54 – 6.97 min) whereas surface intervals for all other individuals excluding the pregnant female averaged 3.13 min ($n = 11$, $SD = 0.99 \text{ min}$, range = 1.65 – 5.06 min). The pregnant female had the highest average surface interval of 11.08 min.

Traveling (e.g. Fig. 3b) and social activity (e.g. Fig. 3c) were also observed and it was during these times that dives classified as V-shaped and 'other' often occurred. Of the 8 dives classified as V-shaped, 5 were to within 10 m of the bottom mixed layer (e.g. Fig. 4c,d). Of the 6 dives classified as 'other', 2 of the dives were to within 10 m of the bottom mixed layer (Fig. 3b,c) and 4 were to the sea floor (e.g. Fig. 3b). In all, 5 brief excursions to the bottom were observed (e.g. Fig. 3b,d), but none of these individuals remained at or near the bottom. Feeding dives did not occur near the bottom.

We observed increases in dive duration, descent speed and ascent speed with dive depth during feeding dives which contributed to a positive correlation between duration at depth and dive depth (Table 2). These dive characteristics were also strongly and positively correlated with the depth of the peak *Calanus finmarchicus* C5 abundance. There was suggestive, but inconclusive evidence that both dive duration and

Table 1. *Eubalaena glacialis* and *Calanus finmarchicus*. Summary of feeding dive characteristics for whales that engaged in at least 1 feeding dive while tagged. Dive characteristics were initially averaged to provide a single observation for each whale. Distance and minimum speed were computed from the consecutive diving and resurfacing positions obtained in 2001 only. Prey abundance refers to the peak abundance of *C. finmarchicus* C5 in the water column

Dive characteristics	n	Median	Mean	SD	95% CI	Range
Dive duration (min)	34	12.65	12.17	2.22	11.39–12.94	7.83–16.32
Duration at depth (min)	34	9.50	9.39	2.29	8.59–10.18	4.72–13.55
Descent speed (m s^{-1})	34	1.38	1.40	0.30	1.29–1.50	0.81–2.00
Ascent speed (m s^{-1})	34	1.54	1.47	0.26	1.38–1.56	0.93–2.05
Dive depth (m)	34	119.9	121.2	24.2	112.8–129.7	78.7–174.0
Distance (km)	18	0.59	0.59	0.20	0.49–0.70	0.21–0.94
Minimum speed (km h^{-1})	18	0.85	0.93	0.44	0.71–1.15	0.38–1.94
Prey abundance (copepods m^{-3})	31	6219	7481	4581	5800–9161	2059–20610

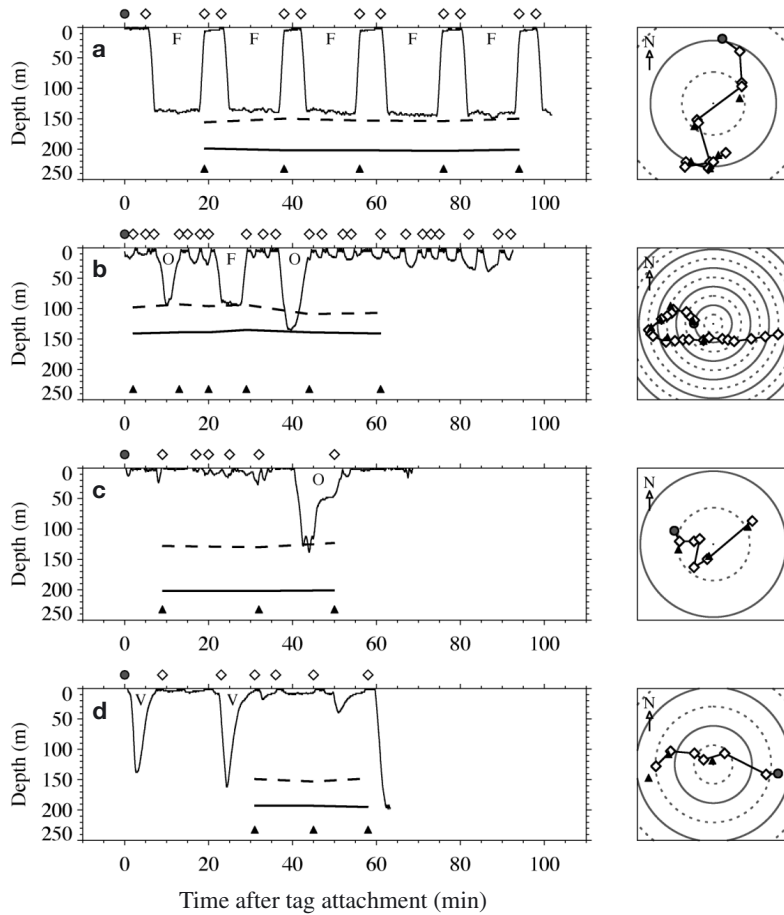


Fig. 3. *Eubalaena glacialis*. Diving and tracking observations illustrating (a) feeding, (b) traveling, (c) socializing and (d) presumed searching behaviors. Individual dives were classified and labeled as feeding (F), V-shaped (V) or 'other' (O). (● ◇) Times (on the time series) and locations (on the accompanying map) of visual contacts. (▲) Times and locations at which a resurfacing occurred and a conductivity-temperature-depth/optical plankton counter (CTD/OPC) cast was conducted. Solid and dashed lines indicate the sea floor and the top of the bottom mixed layer, respectively, measured at the location of each CTD/OPC cast. Concentric lines on the accompanying maps are separated by 0.5 km. Tags detached at depth in (a) and at the bottom in (d)

duration at depth were correlated with peak *C. finmarchicus* C5 abundance ($r = 0.339$, $p = 0.062$ for dive duration; $r = 0.353$, $p = 0.051$ for duration at depth; Table 2). *C. finmarchicus* C5 were very often aggregated in discrete layers near foraging right whales and the at-depth portion of the whales' dives were spent in or near these layers (Fig. 4). The average depth of dive was strongly correlated with the average depth of peak *C. finmarchicus* C5 abundance ($r = 0.902$, $p < 0.0001$, Table 2, Fig. 5a). There was no evidence to suggest that the relationship between the average depth of dive and the average depth of maximum *C. finmarchicus* C5 abundance was different from one-to-one (H_0 : intercept = 0, $p = 0.93$; H_0 : slope = 1, $p = 0.76$). The discrete layers of *C. finmarchicus* C5 upon which the whales presumably fed were often observed near the bottom mixed layer (Fig. 4). Consequently, the whales' average dive depth was strongly correlated with the average depth of the bottom mixed layer ($r = 0.865$, $p < 0.0001$, Fig. 5b). Average dive depths were shallower than the bottom mixed layer by an average of 7 m, however, which indicates that *C. finmarchicus* C5 typically aggregated just above the bottom mixed layer.

Since right whales were observed foraging at the depth of maximum *Calanus finmarchicus* C5 abundance, total ingestion (I_d from Eq. 1) was computed for every feeding dive using the estimate of the peak *C. finmarchicus* C5 abundance from the accompanying OPC cast. Ingestion rates (I' from Eq. 2)

Table 2. *Eubalaena glacialis* and *Calanus finmarchicus*. Correlation matrix of feeding dive characteristics for tagged individuals that engaged in at least 1 feeding dive for which an accompanying CTD/OPC cast was conducted. $n = 31$ for each correlation coefficient. Prey abundance refers to the peak abundance of *C. finmarchicus* C5 in the water column

	Dive duration	Duration at depth	Descent speed	Ascent speed	Prey abundance	Depth of peak prey abundance
Dive depth	0.586***	0.447*	0.470**	0.533**	0.093	0.902***
Dive duration		0.974***	0.558**	0.728***	0.339 [†]	0.569***
Duration at depth			0.635***	0.778***	0.353 [†]	0.469**
Descent speed				0.766***	0.234	0.538**
Ascent speed					0.234	0.604***
Prey abundance						0.031

*** $p < 0.001$, ** $0.001 \leq p < 0.01$, * $0.01 \leq p < 0.05$, [†] $0.05 \leq p < 0.10$

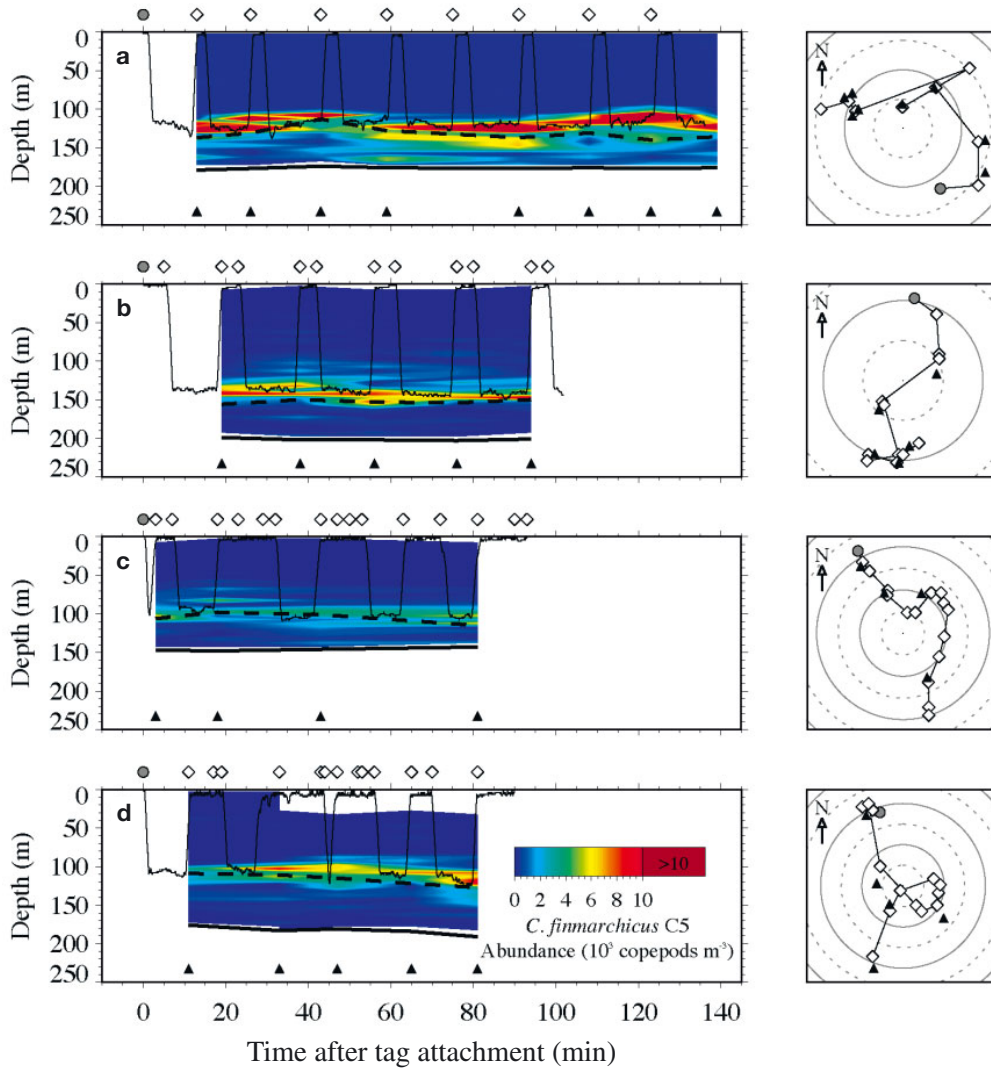


Fig. 4. *Eubalaena glacialis* and *Calanus finmarchicus*. (a–d) Examples of diving and tracking observations during feeding behavior. Contoured *C. finmarchicus* C5 abundance estimated from the OPC casts is shown. Color scale shown in (d) applies to all plots. Symbols and lines are the same as in Fig. 3

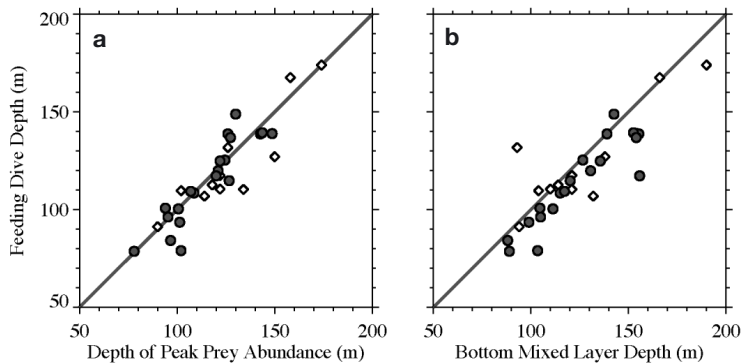


Fig. 5. *Eubalaena glacialis* and *Calanus finmarchicus*. Average depth of feeding dive versus (a) average depth of peak *C. finmarchicus* C5 abundance and (b) average depth of the bottom mixed layer. (●) Tagged whales that had 2 or more feeding dives with accompanying CTD/OPC casts. (◊) Tagged whales that had only 1 feeding dive with an accompanying CTD/OPC cast

Table 3. *Eubalaena glacialis* and *Calanus finmarchicus*. Number of feeding dives, duration of tag attachment, percent time feeding, average minimum speed between diving and resurfacing positions, average peak *C. finmarchicus* C5 abundance below 50 m, ingestion rate (I'), ingestion rate as a fraction of the ingestion rate required to meet estimated basal metabolic requirements (I'_{BMR}), and time required to meet daily metabolic requirement (T_{req}) from Eq. (4). Data are from deployments lasting over 1 h. The first column contains the label used for each whale in Fig. 6. Fig. numbers are also provided for those deployments shown in Figs. 3 and 4. Minimum speeds were not calculated for individuals tagged in 2000 (see 'Materials and methods' for explanation). Missing values for T_{req} indicate $T_{\text{req}} > 24$ h

Label in Fig. 6	No. feeding dives	Attachment duration (min)	% time feeding	Speed (m s ⁻¹)	Prey abundance (copepods m ⁻³)	I' (10 ⁴ W)	I' ($\times I'_{\text{BMR}}$)	T_{req} (h)	Fig.
1 ^a	0	69	0.0	–	–	0.00	0.00	–	3c
2 ^a	0	63	0.0	–	–	0.00	0.00	–	3d
3	0	92	0.0	–	–	0.00	0.00	–	
4 ^b	1	93	5.1	1.94	5592	0.45	0.38	–	3b
5	2	102	13.5	0.38	3500	0.53	0.44	–	
6	6	98	48.7	0.75	3124	1.89	1.57	–	
7 ^{b,c}	4	93	30.7	1.01	5124	1.89	1.57	–	4c
8	6	101	63.3	0.95	3020	2.37	1.98	–	
9	4	66	54.5	0.52	3677	2.48	2.07	22.5	
10	7	96	45.9	1.87	3087	2.49	2.08	22.3	
11 ^a	9	198	40.6	–	6331	3.23	2.69	14.2	
12	6	112	52.0	0.84	5332	3.31	2.76	13.6	
13	5	87	57.1	0.61	4673	3.39	2.83	13.1	
14	4	82	43.7	0.92	6602	3.53	2.94	12.4	
15	7	118	53.2	0.85	5440	3.55	2.96	12.3	
16 ^d	3	66	54.7	0.99	5759	3.73	3.11	11.4	
17 ^a	23	422	54.2	–	6233	4.19	3.50	9.6	
18 ^e	4	90	33.7	1.54	8672	4.64	3.87	8.4	4d
19	6	86	64.2	0.61	9871	7.69	6.41	4.4	
20 ^a	6	68	48.0	–	12867	7.78	6.49	4.4	
21 ^d	5	102	57.7	0.68	11893	8.47	7.06	4.0	3a,4b
22 ^a	8	136	68.0	–	14945	12.48	10.41	2.6	4a
Average			40.4	0.96	6618	3.55	2.96		

^aWhales tagged in 2000. All other whales tagged in 2001; ^bwhales tagged in Roseway Basin on southwestern Scotian Shelf. All other whales tagged in Grand Manan Basin of the lower Bay of Fundy; ^cpregnant female; ^dadult (presumably female) with calf; ^ecalf

were estimated only for those whales tracked over 1 h (Table 3). Of the 22 tagged individuals examined, 14 had ingestion rates that were high enough to meet estimated daily metabolic requirements. However, 2 of these 14 would have needed to feed for nearly 24 h at the observed ingestion rates to meet this requirement, whereas 4 would have needed less than 5 h. The concentration of *C. finmarchicus* C5 explained 94% of the variation in the estimated ingestion rates when assessed with a regression model forced through the origin (Fig. 6). The resulting regression equation, i.e. $I' = (6.58 \text{ m}^3 \text{ W}) \times C$, suggests that the minimum *C. finmarchicus* C5 concentration required to meet daily metabolic requirements is 3600 copepods m⁻³ (foraging would need to continue for 24 h d⁻¹ to meet this requirement). The minimum peak concentration observed near whales that were tagged for over 1 h and that engaged in feeding dives was ca. 3000 copepods m⁻³ (Table 3), which is in good agreement with the minimum concentration required to meet daily metabolic requirements. One of the tagged whales engaged in behavior that we interpret as searching (Fig. 3d) and peak concentrations of *C. finmarchicus* C5 near this individual averaged ca. 1300 copepods m⁻³. A whale

feeding continuously on this concentration (i.e. 24 h d⁻¹) would ingest only 35% of its daily requirement on average, whereas feeding on a concentration of 3000 copepods m⁻³ would yield 83% of the daily requirement. The evidence from this single individual suggests that right whales may ignore *C. finmarchicus* C5 concentrations as low as 1300 copepods m⁻³ because foraging would not come close to meeting the daily requirement, yet peak concentrations over 3000 copepods m⁻³ that nearly provide the daily requirement may be more acceptable.

DISCUSSION

The stereotypical shape of feeding dives in North Atlantic right whales is optimized for exploiting zooplankton aggregated in discrete layers. Rapid descents and ascents reduce transit time to foraging depths, and these transit times are even further reduced when diving to deeper depths by increasing both descent and ascent rates. Thus, duration at the depth where feeding occurs is maximized. The significantly faster ascents relative to descents are due to the right whale's

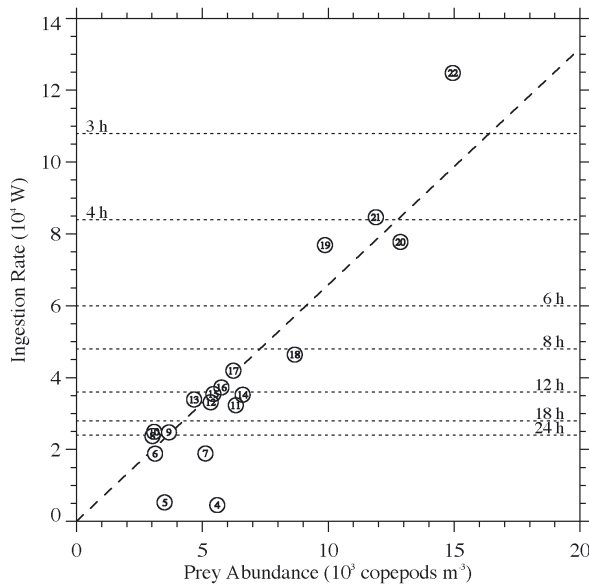


Fig. 6. *Eubalaena glacialis* and *Calanus finmarchicus*. Estimated ingestion rate versus average peak *C. finmarchicus* C5 abundance. (4) to (22): Labels for whales reference data in Table 3. A linear regression forced through the origin was fitted to the data and is shown as the dashed line. Horizontal, dotted lines indicate the ingestion rates and times spent foraging required to meet daily metabolic needs (e.g. ingestion for 8 h d⁻¹ at a rate of 4.8×10^4 W would be sufficient to meet daily metabolic requirements)

positive buoyancy, which the whale must overcome by fluke stroking on descent, but is exploited to reduce energy expenditure by gliding on ascent (Nowacek et al. 2001). The low variability in dive depth during the at-depth portion of the feeding dive is in marked contrast to the high variability in dive depth exhibited by blue and fin whales (Croll et al. 2001). These differences are presumably related to feeding ecology. Right whales feed on zooplankton aggregated in discrete layers by continuously swimming with their mouths agape, but blue and fin whales are gulp feeders that engulf euphausiids or fish along with vast quantities of seawater in a single mouthful. The variability in dive depths during the at-depth portion of these rorquals' dives, therefore, has been interpreted as lunge feeding (Croll et al. 2001). The duration of the tagged right whales' dives (average 12.2 min) were much longer than fin (5.5 min; Croll et al. 2001), blue (6.6 min; Croll et al. 2001) and humpback whales (2.8 min; Dolphin 1987). Croll et al. (2001) have suggested that increased dive durations in the Balaenidae (right and bowhead whales) are a result of lower metabolic costs associated with continuous filter feeding. Conversely, decreased dive durations in rorquals are a consequence of the higher metabolic costs associated with lunge feeding.

When dive durations exceed the capacity for aerobic metabolism, anaerobic metabolism causes lactate to build in the blood which must be cleared during the succeeding surfacing interval. Dives that exceed this aerobic dive limit (ADL), therefore, are associated with disproportionately longer surfacing intervals (Kooyman et al. 1980, 1983). Dolphin (1987) reported increasing PCST for humpback whale dives that exceeded 60 m in depth and suggested that this increased time at the surface was required to repay the oxygen debt incurred during anaerobic metabolism. In the present study, there was no evidence that PCST was correlated with either dive depth or duration for the tagged right whales. We observed average PCST values of 21.2% (excluding calves, females with calves and the pregnant female), which is in good agreement with PCST values for presumed aerobic dives by Weddell seals (21%; Kooyman et al. 1980) and humpback whales (21.4%; Dolphin 1987). These results suggest that the tagged right whales were diving within their ADL. Although the dive durations for calves and females with calves were similar to the other whales, surface intervals were significantly higher, which resulted in a higher PCST for calves and females with calves. The calves were seldom more than a body's length away from their presumed mothers and they often surfaced and dove simultaneously with the adult as well. The extended surface intervals and higher PCST values for the tagged females with calves, then, are interpreted as being governed by the calf's diving capabilities. Theoretical ADL is computed as the total oxygen stores divided by DMR and while total oxygen stores increase linearly with body mass (M), DMR increases with $M^{0.75}$ (Costa & Williams 1999). ADL is therefore proportional to $M^{0.25}$, so a calf's ADL will be lower than that of an adult simply due to its reduced body size. In addition to the effect of body size on ADL, calves must also have higher metabolic rates to fuel growth which will further reduce their ADL. Croll et al. (2001) estimated total O₂ stores for blue and fin whales to be an average 55.6 ml O₂ kg⁻¹. Assuming right whales have similar total O₂ stores and that a calf's DMR = 4 × BMR (i.e. DMR = $4 \times [70M^{0.75} \text{ kcal d}^{-1}] / [4.8 \text{ kcal (l O}_2\text{)}^{-1}] / [1440 \text{ min d}^{-1}]$), a 5000 kg calf (New England Aquarium unpubl. data cited in Brown et al. 2001) would have a theoretical ADL of 11.5 min. Observed dive durations for calves and females with calves averaged 11.60 min (n = 5, SD = 2.04 min, range = 8.84 to 14.09 min). The prolonged surface intervals, elevated PCST values and these ADL calculations suggest that right whale calves may dive for durations close to their ADL, but caution is warranted when interpreting these results because of the low sample size and the uncertainty in estimating both total O₂ stores and diving metabolic rate for right whales.

The significantly longer surface intervals observed for calves, females with calves and the pregnant female may indicate that reproductively active females and their calves are at comparatively greater risk for collisions with ships than other animals in the population. Fujiwara & Caswell (2001) estimated that the survivorship of right whale mothers declined from 1980 to 1995, while the survivorship of mature males and (non-calving) females remained unchanged over the same period. Higher rates of mortality among right whale mothers may be due to their use of the calving grounds off the southeast United States, where the volume of shipping traffic is high (Fujiwara & Caswell 2001). However, our results suggest that the diving behavior of reproductively active females and their calves may also place them at greater risk of ship strikes on the feeding grounds as well.

The strong correlation between dive depths and the depth of maximum *Calanus finmarchicus* C5 abundance indicate that right whales are adept at locating and exploiting discrete layers of highly concentrated prey. The accuracy with which they target these layers would seem to rule out the possibility that right whales sample the water column mouthful by mouthful until they reach a suitable prey concentration. Instead, the transition from the descent phase to the at-depth portion of the dive occurs very quickly and the fidelity to the depth initially targeted is often remarkable. These observations suggest that right whales can detect layers of *C. finmarchicus* C5 without opening their mouths. The sensory mechanisms by which the whales accomplish this are unknown, but may include vision or sensory hairs (Kenney et al. 2001). Rowntree (1996) even suggests that the cyamid amphipods that inhabit right whale callosities may aid in locating prey. As is typical for turbid coastal environments, light levels at mid-depth in Grand Manan Basin are probably very low and vision would only be useful during daylight hours. *C. finmarchicus* do not bioluminesce as do some other copepods (e.g. *Metridia* spp.), so direct visual detection of prey in the absence of ambient light is probably not possible. Regardless of the sensory mechanisms employed, right whales may be able to restrict their search for suitable prey concentrations using cues from the physical environment. The tagged right whales rarely ventured into the bottom mixed layer proper and when they did so, it was typically during an excursion to the sea floor that seemed exploratory in nature. There are a variety of cues with which right whales can detect the presence of this mixed layer, including shear at the top of the layer (i.e. rapid velocity changes with depth), turbulence within the layer itself or particular temperature or salinity properties. With foraging experience, right whales may learn that suitable prey concentrations of *C. finmarchicus* are

uncommon in the bottom mixed layer, so only occasional forays into this layer are necessary. Moreover, searching may be further restricted to only a few 10s of m around the top of this boundary layer since *C. finmarchicus* C5 aggregate just above the bottom mixed layer at this time of year.

Our calculations suggest that many of the tagged right whales ingest *Calanus finmarchicus* C5 at rates sufficient to meet daily metabolic requirements. It is very important to bear in mind, however, that the selection of $DMR = 2 \times BMR$, though based on sound reasoning, is truthfully only a guess. Metabolic rates have only been directly measured in species that can be captured and manipulated. Current methods of measuring metabolic rates cannot be applied to adult mysticetes. Croll et al. (2001) observed dive durations in blue and fin whales that were much shorter than calculated ADL values using $DMR = 4 \times BMR$. They inferred from these data that the metabolic costs of lunge feeding were well in excess of $4 \times BMR$. The number of right whales deemed to be successfully foraging is quite sensitive to the choice of DMR (Fig. 7). If DMR values for right whales also exceed $4 \times BMR$, then only 4 of the 22 individuals with tag attachments lasting over 1 h would have been ingesting *C. finmarchicus* C5 at a rate sufficient to meet their daily metabolic requirement (Fig. 7). Uncertainties in estimating metabolic rates inhibit our ability to accurately determine whether right whales are able to forage successfully. The development and application of new methods to directly measure either absolute or relative (i.e. diving vs. resting) metabolic rates for large cetaceans is sorely needed.

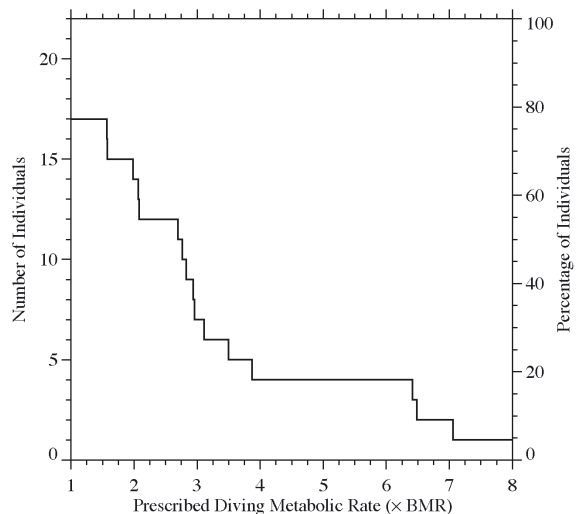


Fig. 7. *Eubalaena glacialis*. Number (and percentage) of whales shown in Table 3 that ingested prey at a rate sufficient to meet daily metabolic requirements for different choices of the diving metabolic rate (DMR). DMR shown as a multiple of the estimated basal metabolic rate (BMR)

Despite the uncertainties in DMR, it is clear that some of the tagged whales were easily ingesting *Calanus finmarchicus* C5 at a rate sufficient to meet their daily metabolic requirements. These whales were able to identify and exploit very dense aggregations of *C. finmarchicus* C5, which indicates that food resources upon which individual right whales can survive seem to exist. Since no emaciated right whales were observed in the field and some tagged whales chose socializing with conspecifics over foraging, this result is in no way surprising. It seems clear that sufficient food resources exist for individual right whales to survive, but the benchmark for successful foraging in a viable population is not simply meeting daily or even annual maintenance requirements. Ingestion must also be sufficient to fuel reproduction, including the metabolic costs of social behavior (a rather energetic activity in right whales), growth of a fetus and support of a newborn calf via lactation. Of the 22 individuals examined, 15 ingested *C. finmarchicus* C5 at rates that would require more than half of the day to be dedicated to foraging just to meet daily metabolic requirements (Table 3). These results might suggest that sufficient food resources do not exist to support the elevated metabolic demands associated with reproduction for most of the population. However, a few caveats must be recalled before such a claim could be made.

The deployment durations during this study were short; most successful deployments were between 0.5 and 2 h. Therefore, the ingestion rates estimated here may not accurately reflect daily ingestion rates. Since we observed a few whales foraging on abundances of *Calanus finmarchicus* C5 in excess of 10 000 copepods m^{-3} , we know that very dense concentrations are occasionally encountered. For those whales that had low ingestion rates during the period they were tagged, it is possible that they might also encounter similarly high abundances after several more hours of foraging effort. Accurate daily ingestion rates can only be obtained with deployments that last at least 24 h. Ingestion rates can further be improved with direct swim speed measurements (relative to the water, not the ground), although we believe the error in the estimated ingestion rates attributable to a fixed swim speed ($1.5 m s^{-1}$) is relatively small. In light of these considerations, we cannot judge whether sufficient food resources exist to support right whale population growth with our data. However, clear directions for future work are indicated. Day-long deployments with concurrent zooplankton sampling are necessary to obtain accurate daily ingestion rates. Day-long deployments would also yield data on the amount of time devoted to foraging (T in Eq. 3), resting and social activities. As mentioned before, innovative methods to measure metabolic rates in large cetaceans are also needed. Finally, it is important to obtain simi-

lar measurements outside the lower Bay of Fundy throughout the spring-summer-fall feeding season. Since right whales are capable of storing fat, it is possible that feeding conditions elsewhere may provide the bulk of the energy required to meet reproductive metabolic costs (e.g. Beardsley et al. 1996). Focusing only on 1 feeding habitat, then, might provide a distorted view of whether sufficient food resources exist to support right whale population growth.

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