

Associations between North Atlantic right whales and their prey, *Calanus finmarchicus*, over diel and tidal time scales

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ABSTRACT: Temporal variability in the distribution and abundance of North Atlantic right whales *Eubalaena glacialis* and their copepod prey, late-stage *Calanus finmarchicus*, was monitored at an oceanographic station in Grand Manan Basin of the lower Bay of Fundy for 29 h on 2 separate occasions. The vertical distribution of *C. finmarchicus* was measured at $1/2$ h intervals with an optical plankton counter (OPC) and at 6 or 12 h intervals with a MOCNESS. Right whale abundance was estimated from periodic point scans. Late-stage *C. finmarchicus* exhibited diel vertical migration in the upper 100 m of the water column, but the bulk of the population remained at depths below 100 m throughout both the day and night and was likely in diapause. Diel vertical migration is unlikely to be influenced by right whales, but may instead be motivated by abundant, near-surface food resources and avoidance of visual predators. Right whale sighting rate was correlated with OPC-detected *C. finmarchicus* fifth copepodite (C5) abundance at mid-depths (90–140 m); variability in both right whale sighting rate and *C. finmarchicus* C5 abundance in this depth stratum appeared to have similar periodicity to that of the tide. Energetic considerations suggest that right whales continue to feed on deep, diapausing layers of *C. finmarchicus* during the night, but the occasional presence of exploitable near-surface concentrations of *C. finmarchicus* suggests that nighttime near-surface feeding might sometimes occur.

KEY WORDS: Right whale · *Eubalaena glacialis* · *Calanus finmarchicus* · Diel vertical migration · Tides · Gulf of Maine · Bay of Fundy · Optical plankton counter

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INTRODUCTION

The North Atlantic right whale *Eubalaena glacialis* feeds primarily upon the calanoid copepod *Calanus finmarchicus*. It accomplishes this by filtering seawater through very fine baleen that can retain large copepods efficiently (Mayo et al. 2001). Because there are only roughly 300 individuals remaining in this endangered population (IWC 2001), right whale predation

probably has a negligible effect on *C. finmarchicus* population dynamics. However, right whale predation on older copepodite stages of *C. finmarchicus* must be intense in some regions where right whales aggregate annually, such as Cape Cod Bay in the late winter (Watkins & Schevill 1976, Mayo & Marx 1990), Great South Channel in the spring (Wishner et al. 1988, 1995, Beardsley et al. 1996) and the lower Bay of Fundy during the summer and early fall (Murison & Gaskin 1989,

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Woodley & Gaskin 1996, Baumgartner et al. 2003 this issue). The reliability of both right whale and *C. finmarchicus* aggregations in these regions provides an opportunity to study the unique trophic relationship between this predator and prey.

Studies that have employed net sampling near right whales in the lower Bay of Fundy suggest that right whales feed on *Calanus finmarchicus* fifth copepodites (C5) (Murison & Gaskin 1989, Woodley & Gaskin 1996, Baumgartner et al. 2003). Right whales forage during the day on *C. finmarchicus* C5 that aggregate in discrete layers deep in the water column just above a bottom mixed layer (Baumgartner & Mate 2003 this issue). Nighttime vertical migration to the surface by the copepods in these deep layers would have important implications for right whales. Surface feeding by the whales would be expected to have energetic benefits since transit time to shallower food resources is reduced. For a constant dive duration, reduced transit time increases feeding time, so comparatively more energy can potentially be acquired per dive when feeding near the surface than at depth.

Surface feeding may also be accompanied by costs to the whales, however. Right whale exposure to the natural toxins that cause paralytic shellfish poisoning (PSP) may be enhanced by feeding on near-surface aggregations of *Calanus finmarchicus* that have significantly higher PSP toxin levels than deeper copepods (Durbin et al. 2002). These toxins are produced by the dinoflagellate *Alexandrium fundyense*, which is present in the surface waters of the lower Bay of Fundy during the summer and early fall (Martin & White 1988, Townsend et al. 2001) and is consumed by *C. finmarchicus* (Turriff et al. 1995, Teegarden et al. 2001). Feeding on these contaminated *C. finmarchicus* may have detrimental effects on right whale respiratory capabilities (Geraci 1989). The North Atlantic right whale population also experiences significant mortality due to ship strikes (Kraus 1990, Kenney & Kraus 1993, Knowlton & Kraus 2001), and an increase in the time spent at the surface while feeding there would be expected to increase the risk of collision.

To better understand temporal variability in prey availability for right whales and the potential response of *Calanus finmarchicus* to right whale predation, we occupied oceanographic sta-

tions in the lower Bay of Fundy at which simultaneous diel vertical migration (DVM) studies and periodic point scans of right whales were conducted. The vertical distribution of *C. finmarchicus* C5 was monitored with a vertically profiled optical plankton counter (OPC) deployed every half hour and a multiple opening-closing net and environmental sensing system (MOCNESS) towed every 6 or 12 h. The vertical distributions of other late-stage *C. finmarchicus* (C4 and adults) were also monitored with the MOCNESS. These data were used to investigate vertical migration by *C. finmarchicus* and associated variability in right whale abundance over diel and tidal time scales.

MATERIALS AND METHODS

Two stations were occupied by NOAA ship 'Albatross IV' in Grand Manan Basin of the lower Bay of Fundy during the summer of 2001 (Fig. 1). The first

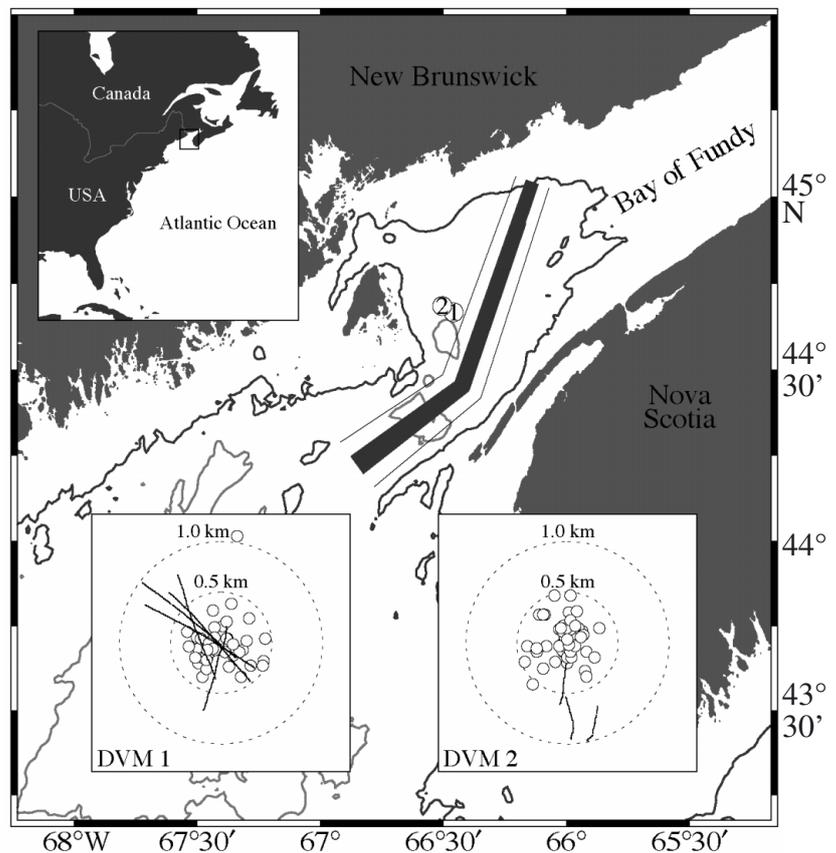


Fig. 1. Map of study area. ①, ②: Location of each station in the lower Bay of Fundy. Shipping lanes that passed through this region at the time of the study are also shown (they have since been changed). Location of the study area along the eastern seaboard of the United States and Canada shown in the upper left inset. Optical plankton counter (OPC) cast locations (○) and MOCNESS tow paths (lines) relative to each station (center of plot) shown in the lower insets. DVM: diel vertical migration

study (DVM 1) took place at 44° 40.0' N, 66° 27.5' W on 29 and 30 July. This location was selected because right whales had been consistently sighted there in the 2 previous summers. The second study (DVM 2) was conducted on 31 July and 1 August at a location (44° 41.1' N, 66° 30.3' W) where whales were initially present and abundant. The stations for DVM 1 and 2 were occupied for 29.2 and 28.7 h, respectively. A Focal Technologies model OPC-1T OPC (Herman 1988, 1992) was deployed in a vertical cast at a nominal descent speed of 1.0 m s⁻¹ every 30 min during each study. The OPC provided the vertical distribution of particles ranging in size from 0.25 to 20 mm. The abundance of particles between 1.5 and 2.0 mm equivalent circular diameter was computed over 5 m depth strata and converted to *Calanus finmarchicus* C5 abundance using the calibration equation of Baumgartner (2003). Vertical migration rates were determined when coherent changes in the distribution of *C. finmarchicus* C5 were observed in a portion of the water column. The depths of peak abundance during a migration period were regressed against time and the slope of the linear regression is reported as the migration rate. Only depths with peak abundances greater than 100 copepods m⁻³ were used in the regression. Day and night were defined as the periods bracketed by the times of sunset and sunrise as calculated from equations of solar elevation angle for each station (Kirk 1994). The beginning and end of nautical twilight were computed as the times when the solar elevation angle was -12° (i.e. 12° below the horizon) (Bowditch 1995).

At 6 (DVM 1) or 12 (DVM 2) h intervals, a MOCNESS (Wiebe et al. 1976, 1985) equipped with 150 µm mesh nets was towed through the station. The MOCNESS sampled 5 contiguous depth strata from approximately 10 m above the bottom to the surface. These strata were chosen after reviewing OPC data collected prior to the first MOCNESS tow in each DVM study. Samples were preserved in a 10% formalin-seawater solution and subsampled in the laboratory. All *Calanus finmarchicus* copepodite stages were enumerated in the subsamples, and the abundance of each stage was estimated from these counts, the subsample volume and the volume of seawater filtered by the net. The abundance data from the MOCNESS tows were not used to construct the OPC calibration equation of Baumgartner (2003).

Periodic visual surveys for right whales were conducted during each DVM study from the bow of NOAA Ship 'Albatross IV'. Observers searched for right whales using binoculars and the naked eye during several discrete, daytime survey periods that lasted an average of 34 min (range: 17–50 min). Scans of 3 to 4 min were conducted every 10 to 15 min during a survey period. Sighting rates were computed as the total

number of whales sighted within 2000 m of the ship during a survey period divided by the duration of the survey period. Repeat sightings of individual whales were undoubtedly made during successive scans within a survey period, so the sighting rate can only be considered a relative measure of abundance.

The relationship between right whale sighting rates and OPC-derived *Calanus finmarchicus* C5 abundance was examined using correlation analysis. Since *C. finmarchicus* C5 abundance could be computed over multiple depth strata and we had no formal hypothesis addressing in which depth stratum *C. finmarchicus* C5 abundance might influence right whale distribution, we examined correlations between right whale sighting rates and *C. finmarchicus* C5 abundance computed over all possible depth strata. The minimum depth for each depth stratum was systematically varied from 0 to 200 m in 5 m intervals. The maximum depth for each depth stratum was systematically varied from the minimum depth to 200 m in 5 m intervals. For each survey period and depth stratum, *C. finmarchicus* C5 abundance was averaged over the 3 OPC casts spanning the survey period.

Predictions of local tidal currents were acquired from Tides & Currents software (version 2.0) (Nautical Software 1996) based on U.S. National Oceanic and Atmospheric Administration and Canadian Hydrographic Service harmonic constants. The software provided estimates of current speeds and only 2 possible current directions (40° at flood and 235° at ebb) every 30 min at 44° 44' N, 66° 15' W. The tidal currents were integrated over time to estimate the displacement of a passive particle relative to this location. The phase of the tidal predictions was verified by comparing the tidal displacement to the temporal variability in water depth measured continuously by the NOAA Ship 'Albatross IV' scientific echo sounder (Simrad EK-500). The phases of the predictions and observations were in very good agreement such that, for instance, times of maximum tidal displacements coincided with observed periods of high and low water. The predicted times of high tide, low tide, maximum flood currents and maximum ebb currents were therefore considered accurate. The predicted current magnitude (and hence the absolute magnitude of the tidal displacement), however, was not considered accurate, since wind, baroclinic and residual barotropic effects are not included in the predictions.

RESULTS

DVM 1

The MOCNESS data suggested that the upper 20 m of the water column contained low abundances of

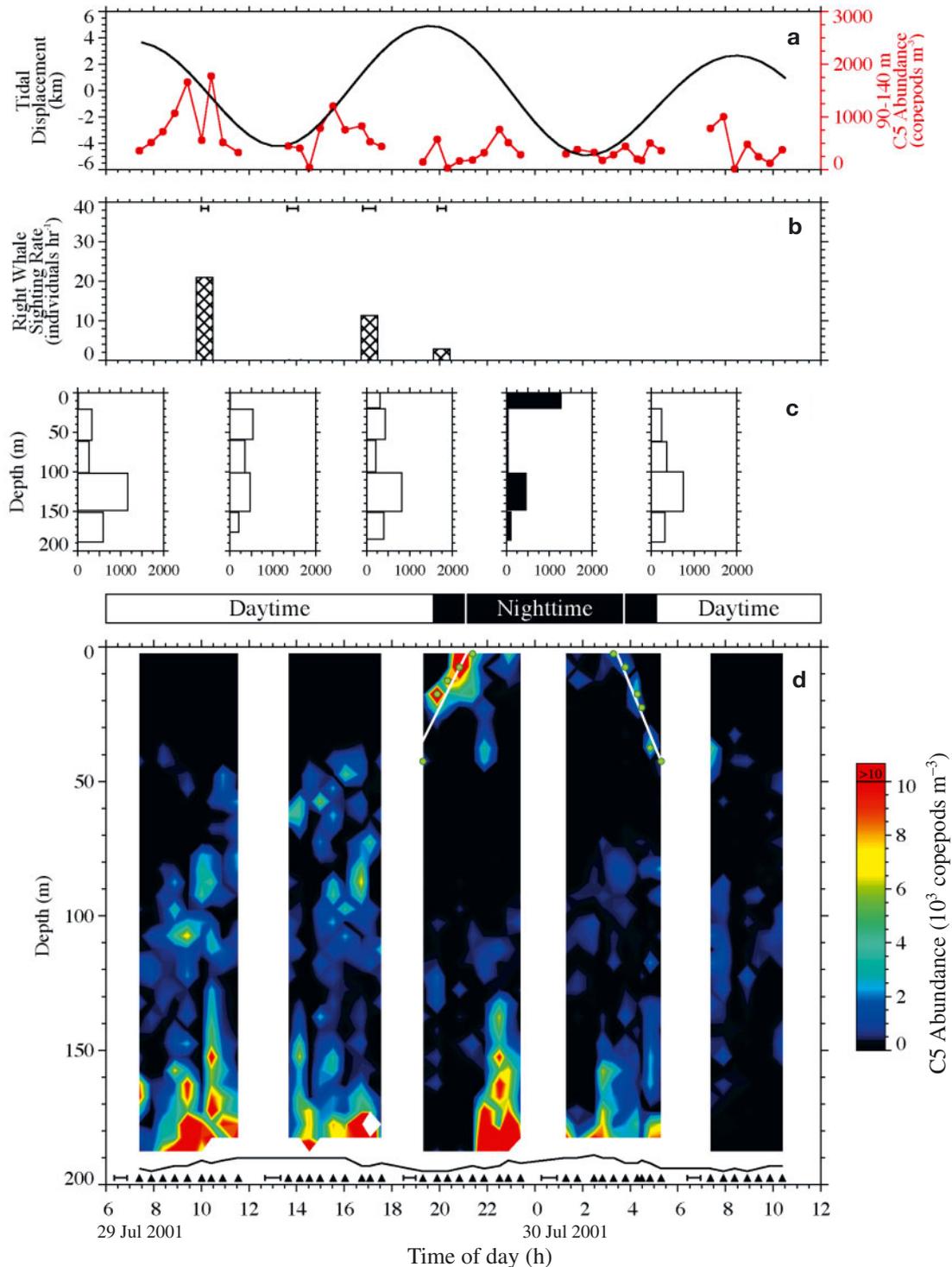


Fig. 2. *Eubalaena glacialis* and *Calanus finmarchicus*. (a) Tidal displacement during DVM 1 showing times of high tide (local maximums) and low tides (local minimums). OPC-detected *C. finmarchicus* C5 abundance between 90 and 140 m shown in red. (b) Right whale sighting rate within 2000 m of the ship. Bars just below top axis indicate survey periods. (c) Vertical distribution of *C. finmarchicus* C5 from the MOCNESS tows (copepods m⁻³). Individual plots are aligned over their respective tow periods in the accompanying plots. (d) Time evolution of OPC-detected *C. finmarchicus* C5 vertical distribution. Thick line at 190 to 195 m represents the bottom; (▲) and (▬) are times when respective OPC casts and MOCNESS tows were conducted. (●) Peaks in abundance in the upper 60 m at dusk and dawn. Linear regressions from which the migration rates were calculated are also shown (see 'Materials and methods'). Day/night periods and the start/end of nautical twilight (vertical white lines) are indicated above (d). Plots (a), (b) and (d) all have the same time axis (shown in d). Time axes are in Atlantic Standard Time

Calanus finmarchicus C5 for most of the daylight hours; however, the OPC data indicated that *C. finmarchicus* C5 abundance was low over the upper 40 m of the water column during this time (Fig. 2). OPC-detected *C. finmarchicus* C5 inhabiting depths of 40 to 100 m began migrating toward the surface within the half-hour prior to sunset at a rate of 0.50 cm s^{-1} ($n = 5$, $95\% \text{ CI} = 0.12 \text{ to } 0.87$). The data from the MOCNESS tow at 18:30 h suggested that some *C. finmarchicus* C5 appeared in the upper 20 m well before sunset (Fig. 2). The OPC-detected migrating layer reached the surface waters ($<5 \text{ m}$) at the beginning of nautical twilight. The dusk migration resulted in very low nighttime abundances in the depth stratum between 20 and 70–90 m. Within the half-hour before nautical twilight ended, *C. finmarchicus* C5 left the surface waters, migrated downward at 0.60 cm s^{-1} ($n = 6$, $95\% \text{ CI} = 0.42 \text{ to } 0.79$) and reoccupied depths at or below 40 m by sunrise. The MOCNESS data indicated that *C. finmarchicus* C4, C5 and adult females (C6F) all vertically migrated into and out of the surface waters: C4, C5 and C6F abundance in the upper 20 m averaged 213, 103 and 2 copepods m^{-3} during the daytime and 467, 1288 and 97 copepods m^{-3} during the nighttime, respectively (Fig. 3). A deeper population of *C. finmarchicus* C5 occupying depths between 100 and 150 m did not vertically migrate. The average OPC-derived observations above 150 m were corroborated by the MOCNESS results (Fig. 3c,d).

OPC-detected particle abundances in the size range overlapping that of *Calanus finmarchicus* C5 were very high at times near the bottom (Fig. 2); however, it is unclear if these particles were in fact *C. finmarchicus* C5. The MOCNESS tows did not indicate that large aggregations of *C. finmarchicus* C5 existed near the bottom (Fig. 3c,d). The particle size distribution near the bottom is also inconsistent with the presence of *C. finmarchicus* C5 (Fig. 4). In waters with high *C. finmarchicus* C5 abundance, the particle size distribution is expected to be modal at approximately 1.55 mm (Baumgartner 2003). This modal peak can be readily observed in the average particle size distributions in the surface at night (Fig. 4a), between 40 and 100 m during the day (Fig. 4b) and between 100 and 130 m at all hours (Fig. 4c). No modal peak is apparent in the waters near the bottom (Fig. 4d). Moreover, the times of high particle abundance coincide with the times of maximum flood and ebb currents, which suggests that the particles detected by the OPC near the bottom may be detritus or sediment that has been resuspended by strong tidal flow.

DVM 2

Diel vertical migration was also observed in the upper water column ($<80 \text{ m}$) during DVM 2. The OPC detected an aggregation of *Calanus finmarchicus* C5 residing at approximately 40 m depth during the daytime that migrated to the surface at night (Fig. 5, Fig. 6c,d). As was the case during DVM 1, upward

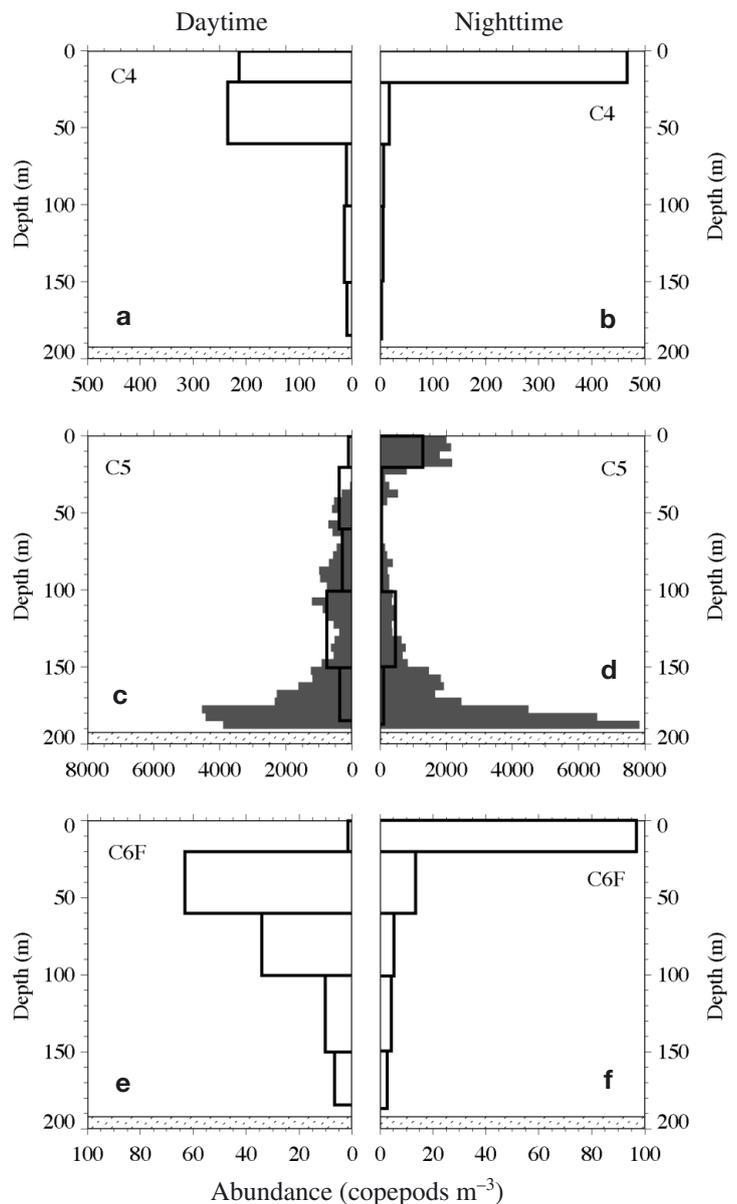


Fig. 3. *Calanus finmarchicus*. Vertical distribution of (a,b) C4, (c,d) C5 and (e,f) adult females (C6F) averaged over all daytime (a,c,e) and nighttime (b,d,f) MOCNESS tows during DVM 1. (c,d) Average OPC-derived, daytime and nighttime vertical distributions of *C. finmarchicus* C5 shown as gray bars. Bottom indicated by the hatched area. Note that the apparent high abundance of *C. finmarchicus* C5 detected near the bottom by the OPC is likely due to resuspended sediments or detritus (see 'Results: DVM 1')

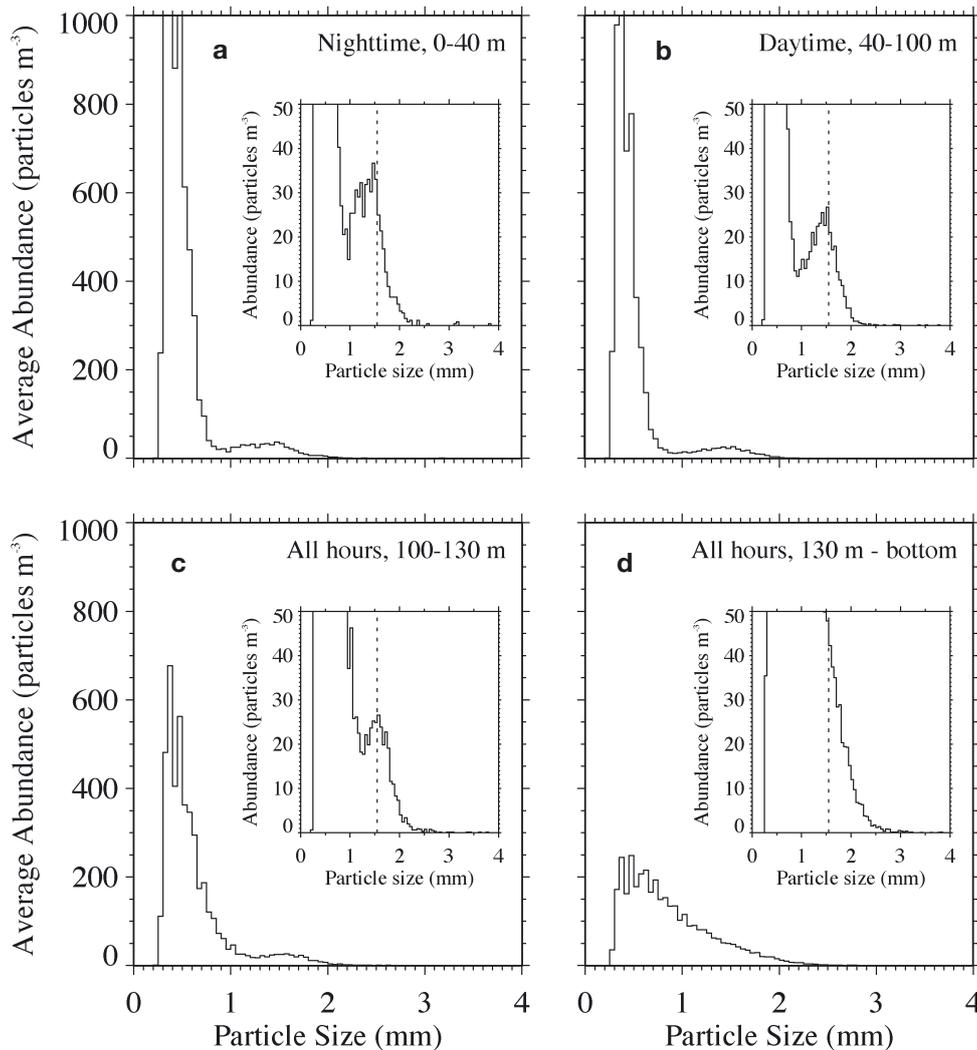


Fig. 4. Average particle size distributions for OPC data collected during DVM 1 (a) between 0 and 40 m at night, (b) between 40 and 100 m during the day, (c) between 100 and 130 m during all hours and (d) between 130 m and the bottom during all hours. Insets show details of average particle distributions between 0 and 50 particles m^{-3} . Dotted line in each inset indicates the expected mode for *Calanus finmarchicus* C5 (1.55 mm) from Baumgartner (2003)

migration began in the half-hour prior to sunset and the migrating layer reached the surface (<5 m) at the beginning of nautical twilight. The upward migration rate of OPC-detected *C. finmarchicus* C5 (0.67 $cm\ s^{-1}$, $n = 5$, 95% CI = 0.46 to 0.89) was not significantly different from that observed during DVM 1. There were too few resolvable local peaks in abundance to adequately determine the timing or rate of the downward migration at dawn. A substantial portion of the *C. finmarchicus* C5 population resided below 80 m during both the daytime and nighttime. Local peaks in this depth stratum were observed well above the bottom with the exception of a single cast that occurred soon after dawn. The data from this cast had characteristics similar to those observed near the bottom during DVM 1 (e.g. a size distribution similar to Fig. 4d, occurrence at the bottom during maximum tidal currents), so this cast may have also captured a resuspension event. The MOCNESS data corroborated the diel vertical migra-

tion in the upper water column and the presence of the more abundant deep layer of *C. finmarchicus* C5 (Fig. 6c,d). These data also indicated vertical migration into and out of the surface waters by *C. finmarchicus* C4 and C6F as well: C4, C5 and C6F abundance in the upper 20 m averaged 0.3 , 1.1 and 0.3 copepods m^{-3} during the daytime and 34 , 135 and 28 copepods m^{-3} during the nighttime, respectively (Fig. 6). Agreement between the average OPC-derived *C. finmarchicus* C5 abundance estimates and those of the MOCNESS for all sampled depths was very good (Fig. 6c,d).

Right whale abundance

Significant correlations ($p < 0.05$) occurred between right whale sighting rates and OPC-derived *Calanus finmarchicus* C5 abundance computed over depth strata having minimum depths of 65 to 110 m and max-

imum depths of 115 to 160 m. The maximum correlation occurred when OPC-derived *C. finmarchicus* C5 abundance was computed between 90 and 140 m ($n = 10$, $r = 0.731$, $p = 0.016$; Fig. 7). There appears to be a single outlier from DVM 2 (survey effort on 31 July,

18:10 to 18:53 h AST) that is characterized by a high sighting rate and a low *C. finmarchicus* C5 abundance (Fig. 7). The *C. finmarchicus* C5 abundance from 90 to 140 m was quite variable around the time of this survey, which may be the result of spatial heterogeneity

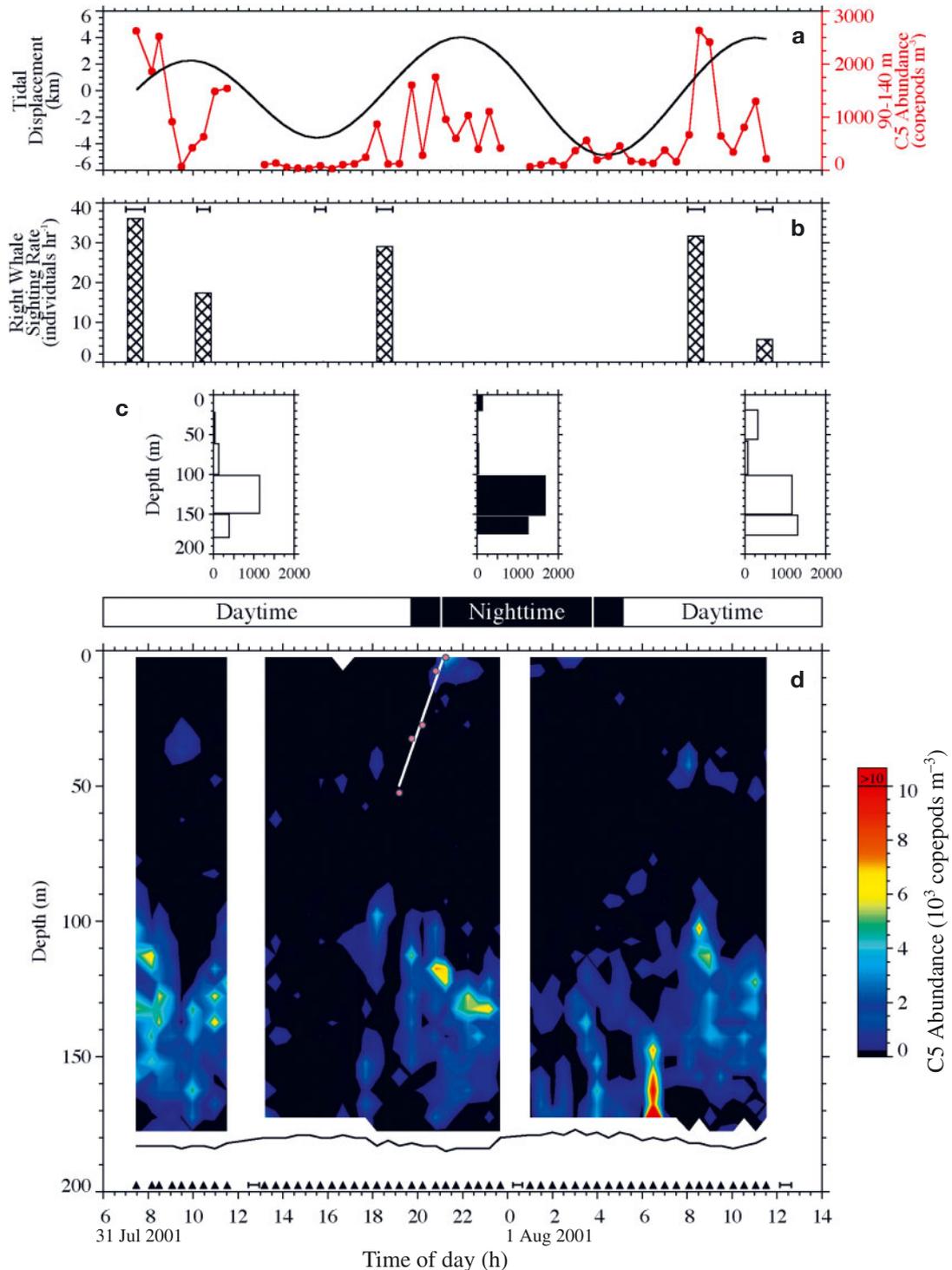


Fig. 5. *Eubalaena glacialis* and *Calanus finmarchicus*. Results from DVM 2. Axes and labels as in Fig. 2. Rate of downward migration at dawn was not estimated (see 'Results: DVM 2')

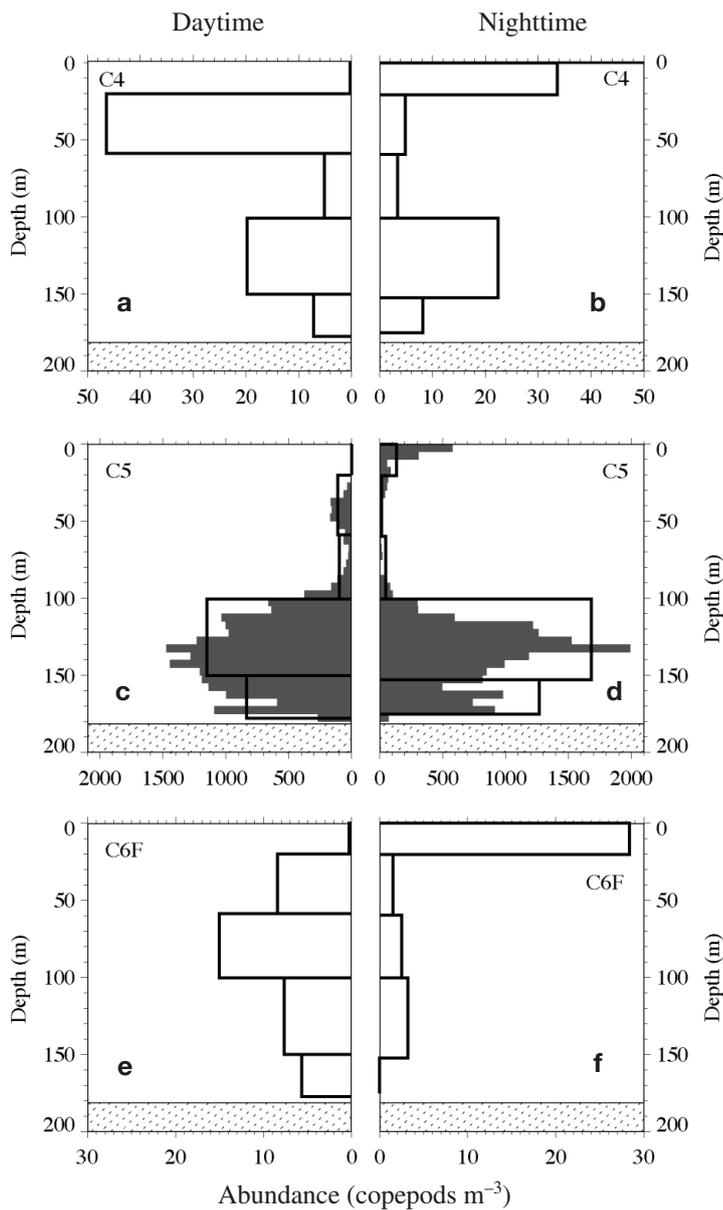


Fig. 6. *Calanus finmarchicus*. Vertical distribution of (a,b) C4, (c,d) C5 and (e,f) adult females (C6F) averaged over all daytime (a,c,e) and nighttime (b,d,f) MOCNESS tows during DVM 2. (c,d) Average OPC-derived, daytime and nighttime vertical distributions of *C. finmarchicus* C5 shown as gray bars. Bottom indicated by the hatched area

(patchiness) in *C. finmarchicus* C5 distribution (Fig. 5). When this outlier is removed, the correlation between right whale sighting rate and 90 to 140 m *C. finmarchicus* C5 abundance becomes remarkably strong and highly significant ($n = 9$, $r = 0.969$, $p < 0.0001$). No significant correlations were detected between right whale sighting rate and *C. finmarchicus* C5 abundance computed in depth strata near the surface, the bottom or spanning the entire water column. Temporal vari-

ability in right whale sighting rates at each fixed oceanographic station appeared to have similar periodicity to that of the tide. This was particularly apparent during DVM 2, when peaks in sighting rates occurred when patches of *C. finmarchicus* C5 at mid-water were advected past the station just before high tide (Fig. 5a,b).

DISCUSSION

A large portion of the *Calanus finmarchicus* C5 population in each DVM study did not migrate, but instead remained below 100 m throughout both day and night. Examination of the MOCNESS samples immediately after collection indicated that these non-migrating copepods had empty guts, well-developed oil sacs and were less active than individuals collected in the migrating layer. These observations indicate that the deep layer was composed of copepods in diapause. Diapause is a resting state employed by *C. finmarchicus* to survive the long period of low food availability during the summer and fall (Hirche 1996). *C. finmarchicus* C5 enter diapause after arresting their development and undertaking an ontogenetic vertical migration to depths where predation may be minimized (Kaartvedt 1996, Dale et al. 1999) and temperatures are low enough to ensure low rates of metabolism and oil reserve depletion (Ingvarsdóttir et al. 1999). In contrast to the diapausing *C. finmarchicus* C5, the copepods that composed the migrating layer had smaller oil sacs (ca. 33% smaller than deep animals) and food in their guts, females had mature oocytes (an indication of active spawning) and surface net and bucket samples revealed the presence of all developmental stages (nauplii, copepodites and adults). These observations indicate an actively feeding and growing population in the upper water column.

The upward vertical migration by copepods at dusk is thought to be motivated by the presence of food in the surface waters (e.g. Dagg et al. 1989, Dagg 1997). DVM may be arrested, however, when surface food resources become depleted (Dagg 1985, Durbin et al. 1995). Campbell et al. (2001) found evidence of food limitation in *Calanus finmarchicus* in surface waters with chlorophyll a concentrations less than $1 \mu\text{g l}^{-1}$, whereas *C. finmarchicus* were in much better condition and had higher egg production rates in waters with chlorophyll a concentrations of between

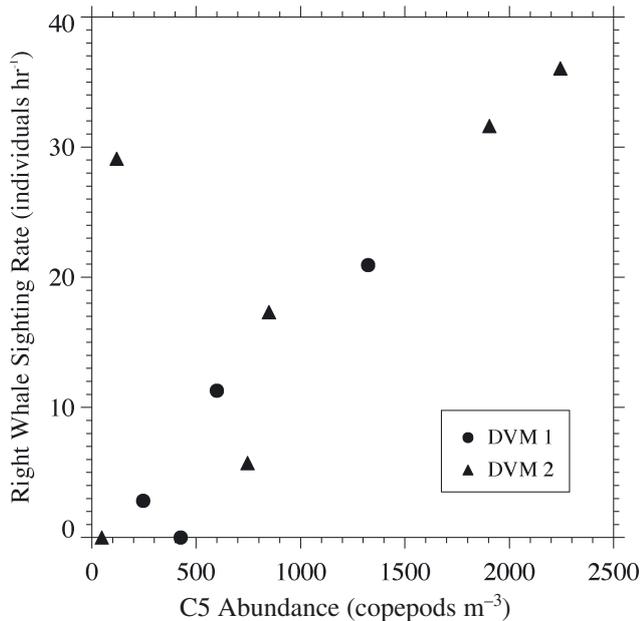


Fig. 7. *Eubalaena glacialis* and *Calanus finmarchicus*. Right whale sighting rate within 2000 m of the ship versus *C. finmarchicus* C5 abundance between 90 and 140 m. (●) Observations from DVM 1; (▲) observations from DVM 2

1.5 and 1.8 $\mu\text{g l}^{-1}$. During the present study, maximum, *in situ* chlorophyll *a* concentrations in the upper 15 m were greater than 2 $\mu\text{g l}^{-1}$. Moreover, the presence of all development stages, spawning females and individuals with food in their guts indicate that *C. finmarchicus* in the migrating layer were not food limited to any great extent. Migration to the surface layer at dusk by *C. finmarchicus* is therefore likely due to the presence of abundant, exploitable food resources.

Migration out of the surface layers near dawn is widely considered to be a strategy employed by copepods to evade visual predators by seeking refuge below the euphotic zone (e.g. Bollens & Frost 1989, Bollens et al. 1992). Several visual predators of *Calanus finmarchicus* occur in the lower Bay of Fundy, including euphausiids (Kulka et al. 1982), planktivorous fish (Sinclair & Iles 1985) and seabirds (Mercier & Gaskin 1985, Brown & Gaskin 1988). It is possible that right whales could also utilize vision while preying on *C. finmarchicus* in the euphotic zone (Kenney et al. 2001). Despite their high, individual ingestion rates, however, predation pressure from right whales is relatively low and unlikely to influence *C. finmarchicus* DVM behavior. To illustrate this, consider the euphausiid *Meganyctiphanes norvegica* or northern krill, an effective visual predator of copepods (Torgersen 2001). *M. norvegica* is abundant in Grand Manan Basin (Kulka et al. 1982) and has a catholic diet that includes *C. finmarchicus* (McClatchie 1985, Båmstedt & Karlson

1998, Lass et al. 2001, Torgersen 2001). Based on an ingestion rate of $12.5 \times 10^4 \text{ W ind.}^{-1}$ (Baumgartner & Mate 2003) or $1.6 \times 10^9 \text{ copepods ind.}^{-1} \text{ d}^{-1}$, 150 right whales (half of the population) would have an estimated predation rate on *C. finmarchicus* of $0.24 \times 10^{12} \text{ copepods d}^{-1}$. By comparison, *M. norvegica* would have an estimated predation rate 7.5 times that, or $1.8 \times 10^{12} \text{ copepods d}^{-1}$, based on an average abundance of 100 ind. m^{-2} (Kulka et al. 1982), an ingestion rate of $1 \text{ copepod ind.}^{-1} \text{ h}^{-1}$ (Båmstedt & Karlson 1998) and an approximate surface area for Grand Manan Basin of 750 km^2 . (The numbers upon which these predation rates are based were chosen from the maximum of their range for right whales and the minimum of their range for *M. norvegica* to provide a conservative estimate of the relative importance of right whale predation relative to that of *M. norvegica*.) Thus, visual predation by more abundant species, such as *M. norvegica* or herring *Clupea harengus*, is expected to have much greater influence over *C. finmarchicus* DVM than predation by right whales.

The selection of daytime depths by the migrating layer of *Calanus finmarchicus* may also be driven by predator avoidance. *C. finmarchicus* C5 and C6F migrated to depths between 40 and 100 m at dawn while *C. finmarchicus* C4 appeared to migrate to shallower depths of between 20 and 60 m. Kulka et al. (1982) and Hurley et al. (1983) described the respective vertical distributions of euphausiids (*Meganyctiphanes norvegica*, *Thysanoessa inermis* and *T. longicaudata*) and chaetognaths (*Sagiitta elegans*) during a DVM study in Grand Manan Basin. They reported that nearly all of the euphausiids and chaetognaths occurred below 100 m during net sampling at noon. Although the *in situ* vertical distribution of predators during the present study is unknown (the net sampling was not designed to quantitatively assess invertebrate predator abundance), *C. finmarchicus* may select a daytime depth stratum that is deep and dark enough to minimize visual predation, yet is shallow enough to avoid mortality caused by euphausiids and chaetognaths that are capable of raptorial predation via mechanical detection (Newbury 1972, Torgersen 2001). The daytime vertical distribution of the migrating *C. finmarchicus* also separates them from the deeper diaupasing layers of *C. finmarchicus* C5 upon which right whales feed during the day (Baumgartner & Mate 2003). However, the selection of a daytime depth that minimizes right whale predation is probably only an incidental benefit of avoidance of other, more abundant predators (see above).

Right whale daytime abundance was correlated with OPC-detected *Calanus finmarchicus* C5 abundance at mid-depths (90 to 140 m) and Baumgartner & Mate (2003) demonstrated that tagged right whales in the

lower Bay of Fundy concentrated their foraging effort on deep layers of *C. finmarchicus* C5 below 90 m during the daytime. These results indicate that right whales bypass the migrating layer to feed on the deeper, diapausing *C. finmarchicus* during the day. From the perspective of an optimally foraging whale, feeding in the deeper layer has a higher energetic cost than feeding in the shallower layer because transit time to the depth of feeding is increased and thus feeding time at that depth is decreased. For example, ingestion rates would be reduced by 8 to 19% when feeding on a layer between 90 and 140 m (transit time of 2.1 to 3.3 min) relative to feeding on an identical layer at 50 m (transit time of 1.2 min) based on an average descent speed of 1.40 m s^{-1} , average ascent speed of 1.47 m s^{-1} and average dive duration of 12.2 min (Baumgartner & Mate 2003). However, when compared to the copepods in the migrating layer, the individuals that comprised the deeper diapausing layer were much more abundant, had a higher caloric content (owing to their larger oil sacs) and were less active (i.e. less able to avoid capture). Competition for these deeper *C. finmarchicus* from visual predators would likely be negligible as well. Thus, the energetic benefits of feeding on this deep layer probably far outweigh the relative costs.

During the night, the energetic cost of feeding on the migrating layer would be even further reduced relative to the cost of feeding on the diapausing *Calanus finmarchicus* because near-surface feeding entails almost no transit time at all. The low abundance of migrating animals observed near the surface during the later nighttime hours of DVM 1 and during all of the nighttime hours of DVM 2 suggests that, like during the daytime, feeding on the diapausing *C. finmarchicus* would provide the most energetic benefit. During DVM 1, however, surface concentrations of *C. finmarchicus* C5 in the early nighttime hours exceeded those found in the deeper layer (Figs. 2 & 3d) and were augmented by high *C. finmarchicus* C4 concentrations (Fig. 3b). This high surface abundance may have formed from the concentration of *C. finmarchicus* spread over 40 to 100 m by day into a 10 to 15 m layer at the surface at night. Furthermore, the *C. finmarchicus* C5 abundance in the surface waters at this time exceeded the minimum concentrations upon which right whales have been observed feeding during the day (ca. 3000 copepods m^{-3} ; Baumgartner & Mate 2003). Although these surface *C. finmarchicus* were of lower caloric content and were more likely to avoid capture, the decreased energetic cost of foraging at the surface and the relatively high abundance of *C. finmarchicus* suggests that this patch could have provided more energetic benefit than the deep diapausing layer. The right whale sighting rate observed just before this surface patch was

encountered, however, was low (Fig. 2), which suggests that the patch may have been ephemeral or too small in size to be readily detected by the whales.

Dolphin movements and abundance have been correlated with tidal currents (e.g. Shane 1980, Parsons 1998, Mendes et al. 2002), but many of these studies document near-shore situations where small-scale tidal fronts can presumably concentrate prey and attract the dolphins (Mendes et al. 2002). In the middle of Grand Manan Basin, the tides do not produce fronts, but should instead advect passive particles in the familiar tidal ellipse (if lower frequency currents are neglected). We therefore had no expectation that temporal variability in right whale abundance around an arbitrary location would be associated with any particular phase of the tide. The observed correlations among right whale sighting rate, mid-water *Calanus finmarchicus* C5 abundance and within-study tidal state are likely the result of (1) advection of both predator and prey by the tides and (2) small scale (100s of m or less) movements by the right whales to keep them within or near prey patches. From our perspective at a fixed geographic location, the tidal currents carried the whales and the patches of *C. finmarchicus* upon which they were feeding near the station, and thus right whale and mid-water *C. finmarchicus* abundance increased. Then, as the tide turned and tidal currents advected both the whales and the patches away from the station, right whale and *C. finmarchicus* abundance decreased. During DVM 2, it appears that the same mid-water patch of *C. finmarchicus* C5 was sampled just before (and possibly just after) each high tide, and right whale abundance was high whenever the patch was present. If this was indeed a single patch observed on 3 separate occasions, then our data suggest that right whales may remain with a patch for up to a day and over spatial scales of several kilometers. Moreover, these data suggest that a patch can persist at these same temporal and spatial scales despite predation by the whales.

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