

AN ABSTRACT OF THE DISSERTATION OF

Mark F. Baumgartner for the degree of Doctor of Philosophy in Oceanography
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Title: Right Whale Ecology in the Northwest Atlantic Ocean.

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Bruce R. Mate

The ecology of the North Atlantic right whale (*Eubalaena glacialis*) was examined at three spatial scales during the summer and early fall on their northern feeding grounds. The diving and foraging behavior of right whales was investigated at spatial scales of hundreds to thousands of meters by tagging right whales with time-depth recorders to document their diving behavior. The vertical distributions of temperature, salinity and copepods were measured along the tagged whale's track with a conductivity-temperature-depth instrument (CTD) and an optical plankton counter (OPC). Right whales were observed diving to and presumably feeding on discrete layers of their primary prey, older stages of the calanoid copepod *Calanus finmarchicus*, aggregated just above the bottom mixed layer. Simultaneous visual and oceanographic surveys conducted in the lower Bay of Fundy and Roseway Basin were used to examine right whale distribution at spatial scales of tens of kilometers. Right whale occurrence was associated with greater depths and thicker bottom mixed layers in these regions. There was additional evidence of an association between right whales and ocean fronts in Roseway Basin. Right whale distribution was also examined on spatial scales of hundreds of kilometers by outfitting whales with satellite-monitored radio tags. Movements of the tagged

whales were compared to climatological and remotely-sensed environmental datasets to elucidate habitat preferences. The tagged whales moved extensively throughout the Gulf of Maine and western Scotian Shelf, where they frequented shallow basins with cold bottom waters, but avoided deep, comparatively warmer basins. Two of the right whale ecology studies described here depended on the OPC for measures of right whale prey distribution and abundance. A final study was conducted to investigate the response of the OPC to *C. finmarchicus* copepodite stage 5 (C5). Comparisons between collocated OPC casts and zooplankton net samples indicated that the OPC was adept at detecting *C. finmarchicus* C5. A calibration equation was developed to predict *C. finmarchicus* C5 abundance from OPC-derived particle abundance.

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Right Whale Ecology in the Northwest Atlantic Ocean

by

Mark F. Baumgartner

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Mark F. Baumgartner, Author

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Tim Cole and Phil Clapham (National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, Massachusetts) collected the visual sighting data used in Chapter 3.

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DEDICATION

To my father

Edward M. Baumgartner

1931 – 2002

Whose parental concern about me getting paid to study whales
was surpassed only by his pride in me for doing what I love

RIGHT WHALE ECOLOGY IN THE NORTHWEST ATLANTIC OCEAN

1. INTRODUCTION

1.1. STATUS

The right whale genus contains three species: the North Atlantic right whale (*Eubalaena glacialis*), the North Pacific right whale (*Eubalaena japonica*) and the southern right whale (*Eubalaena australis*). Each of these whales are similar in appearance with a rotund dark body, large head, no dorsal fin and roughened patches of skin called callosities on the top of the head, around the mouth and above the eyes. Only recently has genetic evidence confirmed these three distinct species (Rosenbaum et al., 2000). Previous classifications included *E. glacialis* and *E. japonica* as a single species, *E. glacialis* (Leatherwood and Reeves, 1983), and *E. glacialis*, *E. japonica* and *E. australis* as a single species, *Balaena glacialis* (Rice, 1998). Rice (1998) also argued that all right whales not only belong in the same species, but they also belong in the same genus as the bowhead whale (*B. mysticetus*). Rosenbaum et al. (2000) provided evidence to refute this taxonomic classification.

Right whales were the first large whales to be harvested commercially. They were the “right” whale to hunt because they were a coastal species that swam slowly and floated after being killed. Whaling began in the Bay of Biscay off the coasts of France and Spain in the 12th century (Brownell et al., 1986; Aguilar, 1986). The history of right whaling grimly foreshadowed the fate of other large whale species such as the sperm and blue whales: an intense, unmanaged, continuous harvest ended only when extremely low abundance made hunting

unprofitable. International protection was afforded to the right whale only in 1935 (Brownell et al., 1986), after many centuries of commercial whaling. Despite this protection, illegal Soviet whaling in the 1960's nearly extirpated the eastern North Pacific right whale population (Brownell et al., 2001).

The number of southern right whales off Australia, Argentina and South Africa is estimated to be 7,000 and annual population growth rates in these areas are between 7 and 8% (IWC, 2001a). Although recovery has not been documented in other areas that were historically occupied (IWC, 2001a), these high population growth rates suggest that *E. australis* may be recovering from exploitation. The North Pacific right whale population may be split into eastern and western stocks, and, while the western stock is estimated to be quite low (in the low hundreds of animals), sightings of *E. japonica* in the eastern North Pacific are exceedingly rare. The population size of the eastern stock is likely on the order of tens of animals (Brownell et al., 2001). Similarly, the North Atlantic right whale population may have been separated into eastern and western stocks, but the eastern stock is thought to be nearly, if not completely, extirpated (Brown, 1986). Modern population estimates for the surviving western stock indicate that about 300 individuals remain (IWC, 2001b). In contrast, the eastern North Pacific stock of gray whales (*Eschrichtius robustus*), which was also reduced to a very low abundance by whaling (c.a. 1,000-2,000; Rice and Wolman, 1971) and acquired international protection in the 1930's, has rebounded to an estimated population size of over 26,000 (Rugh et al., 1999) and was recently removed from the U.S. endangered species list.

The causes for lack of recovery in the North Atlantic right whale population are unknown. When compared to the southern right whale, the North Atlantic right whale has lower calving rates and longer calving intervals (IWC, 2001b) as well as thinner blubber thickness (Miller et al., 2001). In such a small population, inbreeding is very likely, however kinship analyses suggest that this may not be the

case for North Atlantic right whale (IWC, 2001b). The thinner blubber layer of *E. glacialis* suggests that environmental factors, such as nutritional deficiency or toxin exposure, may also contribute to its lack of recovery. Emaciated whales are neither seen at sea nor wash ashore, so it is likely that these environmental factors may affect reproductive success instead of causing outright mortality. Ship strikes and fishing gear entanglements do, however, account for a substantial proportion of known mortalities in this population (Kraus, 1990; Kenney and Kraus, 1993; Knowlton and Kraus, 2001). Knowlton and Kraus (2001) reported that 59% (19 of 32) of known, non-neonate mortalities from 1970-1999 were caused by ship strikes ($n = 16$) and fishing gear entanglements ($n = 3$). These human-caused mortalities are a source of much concern because they hinder population growth that may already be suppressed due to reproductive failure.

1.2. SEASONAL DISTRIBUTION

Winn et al. (1986) described a model of seasonal distribution for the North Atlantic right whale along the eastern seaboard of the United States and Canada based on sightings from surveys and reliable historical sources (Figure 1.1). Right whales are found in the Cape Cod and Massachusetts Bay region in the late winter and early to middle spring. During the late spring and early summer, right whales frequent the Great South Channel between Cape Cod and Georges Bank. By late summer, right whales are typically found in the lower Bay of Fundy or in Roseway Basin on the southwestern Scotian Shelf. Right whales frequent those areas until late into the fall. A small percentage of animals, primarily pregnant females, move to the coasts of Florida and Georgia in the southeastern United States. This region is the only known calving grounds for the North Atlantic right whale. The whereabouts of the rest of the population during the winter are unknown. Winn et

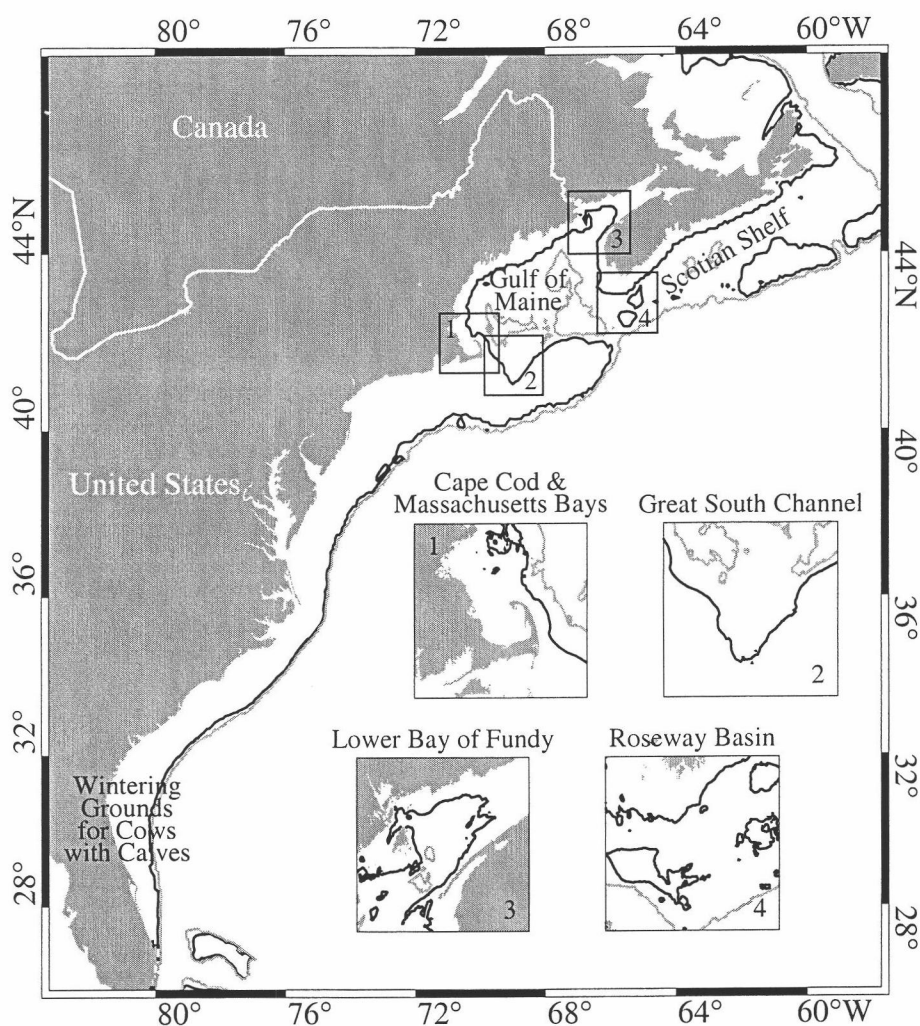


Figure 1.1. Right whale high-use areas. Seasonal distribution described in the text. Insets depict major feeding grounds and have identical map scales. The 91 m (50 fathom, dark line) and 200 m isobaths (gray line) are shown.

al. (1986) hypothesized that animals that do not visit the calving grounds during the winter may scatter along the continental shelf waters of the eastern United States.

The seasonal distributional pattern of Winn et al. (1986) indicates an orderly migration between regions, but recent evidence suggests that inter-regional movements occur on much shorter time scales. Mate et al. (1997) equipped whales with satellite-monitored radio tags in the lower Bay of Fundy during the late summer and early fall. These animals were tracked throughout the Gulf of Maine, Scotian Shelf and the northern mid-Atlantic Bight. Many of the tagged animals returned to the lower Bay of Fundy after short excursions (tens of days) out of the Bay. Distribution at a population level may be well-defined by the Winn et al. (1986) model, but movements of individual right whales are likely more variable than it suggests.

There are also interesting exceptions to this model. Callosity and scarring patterns in right whales make it possible to identify individual whales, and a catalog of animals has been developed for the North Atlantic population (Kraus et al., 1986; Crone and Kraus, 1990; Hamilton and Martin, 1999). Knowlton et al. (1992) describe photographic documentation of animals in the Labrador Basin and on the Cape Farewell Grounds between Greenland and Iceland that were identified within the bounds of the Winn et al. (1986) model at other times. Whaling records suggest that these regions were once populated with right whales (Aguilar, 1986; Reeves and Mitchell, 1986), but recent sightings are rare (IWC, 2001b). M. K. Marx (personal communication) has also documented the photo-identification of the same right whale during May 1999 in the Great South Channel and during September 1999 in Kvaenangen fjord in northern Norway. Very few reliable sightings of North Atlantic right whales have been documented in the eastern North Atlantic during the 20th century (Brown, 1986).

Interannual variability in the relative use of certain regions within the Winn et al. (1986) model has also been documented. Payne et al. (1990) described a

significant increase in abundance of right whales near Stellwagen Bank (the eastern boundary of Massachusetts Bay) in 1986, presumably in response to an observed increase in the abundance of their primary prey, the calanoid copepod *Calanus finmarchicus* (see below). This increase in right whale and *C. finmarchicus* abundance was accompanied by a decrease in species that typically inhabit these waters, humpback (*Megaptera novaeangliae*) and fin (*Balaenoptera physalus*) whales and their primary prey, sand lance (*Ammodytes* spp.). Kenney (2001) described the results of spring surveys in the Great South Channel during 1992 when right whales were uncharacteristically absent. He attributed these anomalous conditions to a zooplankton community dominated by pteropods instead of the typically dominant copepod, *C. finmarchicus*.

There may also be other areas, either within or outside the Winn et al. (1986) model, that may be of great importance to right whales. The lower Bay of Fundy is considered a “nursery” area because many females bring their calves to this region in the summer. However, one-third of reproductively active females never bring their calves to the lower Bay of Fundy (Schaeff et al., 1993). Schaeff et al. (1993) and Malik et al. (1999) found significant genetic differences between these two groups of females and both suggested that a second, as yet undiscovered, nursery area may exist. Also, Weinrich et al. (2000) examined historical sightings of right whales around Jefferys Ledge off the coast of New Hampshire and southern Maine and suggested that this area may be used by right whales in the summer and fall.

1.3. PREY

Direct examination of North Atlantic right whale stomachs have suggested that calanoid copepods and euphausiids are eaten (Collett, 1909; Allen, 1916). In

the northwestern Atlantic, the inferred primary prey is *C. finmarchicus*. Zooplankton tows near right whales have consistently been dominated by older stages of *C. finmarchicus* in Cape Cod Bay (Watkins and Schevill, 1976; Mayo and Marx, 1990), the Great South Channel (Wishner et al, 1988, 1995; Beardsley, 1996) and the lower Bay of Fundy (Murison and Gaskin, 1989; Woodley and Gaskin, 1996). Moreover, Stone et al. (1988) found mandibles of *C. finmarchicus* in right whale feces collected in Roseway Basin of the southwestern Scotian Shelf. Right whales have very fine baleen which is well-adapted to filtering *C. finmarchicus*. Mayo et al. (2001) demonstrated that right whale baleen filters a size fraction of Cape Cod zooplankton containing greater than 95% of the available energetic content, and that this size fraction corresponded to that caught by a 0.333 mm mesh net. Since older stages of *C. finmarchicus* are retained on 0.333 mm mesh net at 100% efficiency, the results of Mayo et al. (2001) suggest that the capture efficiency of older stages of *C. finmarchicus* by right whale baleen is very high. Watkins and Schevill (1976) and Mayo and Marx (1990) also documented dominance by juvenile euphausiids, *Centropages* spp., *Pseudocalanus* spp. and barnacle larvae near right whales in Cape Cod Bay, which suggests that other prey may be exploited in this region.

1.4. FORAGING BEHAVIOR

Right whales have no known capacity to aggregate zooplankton on their own, so they depend upon the behavior of their prey and the physical environment to aggregate prey for them. Profitable filter feeding requires high abundances of prey aggregated at spatial scales matching the animal's foraging capabilities. For instance, the right whale gape (the area of the mouth through which seawater enters to be filtered) is only approximately 1.2 m^2 (Mayo et al., 2001), thus right whales

require prey to be strongly aggregated in the vertical dimension. Suitable conditions occasionally occur within tens of centimeters of the sea surface in Cape Cod Bay and the Great South Channel, where right whales can be observed "skim feeding" on discrete patches of zooplankton. Both Watkins and Schevill (1976) and Mayo and Marx (1990) described these bouts of skim feeding in Cape Cod Bay, while Kenney et al. (1995) and Beardsley et al. (1996) described similar behavior in the Great South Channel. Each of these accounts described right whales concentrating their foraging effort on a visible patch of zooplankton at the surface by swimming through the patch with the mouth agape and turning back into the patch at the periphery. Subsurface feeding is more common than skim feeding in these areas (Watkins and Schevill, 1976; Kenney et al., 1995) as well as in the lower Bay of Fundy (Murison and Gaskin, 1989; Goodyear, 1993). Diving behavior has been examined in Cape Cod Bay (Watkins and Schevill, 1976), the Great South Channel (Winn et al., 1995) and the lower Bay of Fundy (Goodyear et al., 1993), but few data have been presented on dive depths and no data have been presented on dive depths relative to the vertical distribution of prey. However, Watkins and Schevill (1976) inferred that right whales may feed on discrete layers of zooplankton in Cape Cod Bay from their observations of right whale sound production at constant depths from a three-dimensional hydrophone array.

1.5. RIGHT WHALES AND OCEANOGRAPHY

The most exhaustive investigation of right whales and oceanography occurred in 1988 and 1989 in the Great South Channel during the South Channel Ocean Productivity Experiment (SCOPEX; Kenney and Wishner, 1995). Various aspects of the ecosystem were studied to document associations between the distribution of right whales and *C. finmarchicus* and to determine why dense

aggregations of *C. finmarchicus* occurred in the region. These aspects included hydrography, currents, phytoplankton abundance and growth, zooplankton community composition, *C. finmarchicus* abundance, vertical migration and growth and right whale abundance, distribution and diving behavior. The distribution of right whales was suggested to be influenced by a low-salinity plume extending to the east from Cape Cod. The highest *C. finmarchicus* abundances were found in the leading edge of this plume. Cooler temperatures and lower food availability in the region during 1989 may have delayed *C. finmarchicus* development so that the appearance of older-stage copepodites occurred downstream (i.e., toward the eastern side of the Great South Channel) and thus the distribution of the right whales was also moved downstream with the low-salinity plume when compared to 1988.

Earlier work in the Great South Channel by Brown and Winn (1989) examined right whale distribution with respect to thermal fronts detected in remotely-sensed infrared imagery. A persistent front bisects the Great South Channel at about the 60-70 m isobath and separates shallower, tidally mixed waters to the south from deeper, stratified waters to the north. Brown and Winn (1989) found evidence to suggest that right whales were not randomly distributed about this front although their statistical methods were somewhat dubious. They did not observe right whales in proximity to the front, but instead found the whales a median distance of 11.4 km away. Brown and Winn (1989) provided much stronger evidence that right whales remain on the warmer, stratified side of the front in what Miller et al. (1998) describe as the SCOPEX gyre. Chen et al. (1995) observed cyclonic circulation in the stratified region north of the front and provided some evidence for a closed gyre. The modeling results of Miller et al. (1998) suggest that this gyre is indeed closed and may accumulate *C. finmarchicus* stage 5 copepodites entering diapause.

Woodley and Gaskin (1996) compared a variety of oceanographic measurements collected both in the presence and absence of whales in the lower Bay of Fundy. They found right whales in areas characterized by warmer surface temperatures, greater water depths, lower topographic variations or higher *C. finmarchicus* abundances when compared to areas without right whales. Like Murison and Gaskin (1989), they suggested that right whales could be found in areas with high surface stratification. Woodley and Gaskin (1996) also suggested that right whales were present in the deep basin of the lower Bay of Fundy (Grand Manan Basin) because a gyre concentrated *C. finmarchicus* there.

1.6. DOCTORAL RESEARCH

This dissertation describes three studies of right whale ecology at multiple spatial scales. I have examined the relationships between the behavior, occurrence and movements of right whales and observed environmental features, conditions or processes during the summer and early fall. Specific attention was paid to the linkages among the physical environment, the most lipid-rich stage of *C. finmarchicus* (copepodite stage 5 or C5) and right whales.

The first study (Chapter 2) examined right whale foraging behavior at small spatial scales (hundreds to thousands of meters) in the lower Bay of Fundy and Roseway Basin on the southwestern Scotian Shelf. Relationships among right whale diving behavior, *C. finmarchicus* C5 distribution and hydrographic features were investigated by tracking right whales tagged with suction-cup mounted, time-depth recorders and simultaneously measuring the vertical distributions of temperature, salinity and *C. finmarchicus* C5. The energetic implications of the observed foraging behavior were also examined.

The second study (Chapter 3) investigated regional-scale (tens of kilometers) variability in right whale occurrence with respect to a number of environmental factors, including surface stratification, *C. finmarchicus* C5 abundance, hydrographic properties and remotely-sensed sea surface temperature, surface chlorophyll and their horizontal gradients. These gradients were used as proxies for the presence of ocean fronts. Data for this study were collected over 3 years in the lower Bay of Fundy and Roseway Basin, so in addition to examining spatial variability in right whale occurrence, a tentative investigation of interannual variability was also possible.

The third study (Chapter 4) examined the movements of right whales over large spatial scales (hundreds of kilometers) and weekly time scales. Satellite-monitored radio tags were attached to right whales in the lower Bay of Fundy in 2000 to track their summer and fall movements. These data were combined with the results of Mate et al. (1997) in a novel analysis of right whale movements with respect to geographic areas and oceanographic conditions.

Traditional net sampling to assess the vertical distribution of *C. finmarchicus* C5 in the studies described in Chapters 2 and 3 would have been far too slow and laborious and would not have provided adequate vertical resolution. Therefore, an optical plankton counter (OPC; Herman, 1988, 1992) was used as a means to rapidly obtain *C. finmarchicus* C5 abundance estimates. This instrument counts and sizes particles in the water column between 0.25 and 20 mm, but cannot identify the particle (e.g., as *C. finmarchicus*, as a copepod, as a gelatinous organism or even as an inanimate particle such as marine snow or suspended sediment). To “ground-truth” or calibrate the OPC measurements, then, a final study (Chapter 5) compares *C. finmarchicus* C5 estimates obtained with the OPC to collocated net samples. This study seeks the optimum size range in which *C. finmarchicus* C5 can be detected by the OPC and a calibration equation relating

particle abundance in that optimum size range with *C. finmarchicus* C5 abundance observed in the net samples.

Chapter 6 of this dissertation provides an integrated summary of the results, speculates on their meaning and implications and offers some directions for future research.

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2. SUMMERTIME FORAGING ECOLOGY OF NORTH ATLANTIC RIGHT WHALES

2.1. ABSTRACT

North Atlantic right whales were instrumented with suction-cup mounted, time-depth recorders (TDR) during the summers of 2000 and 2001 in the lower Bay of Fundy and in Roseway Basin of the southwestern Scotian Shelf. 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 79 and 174 m, remarkable fidelity to that depth for 7.8 to 16.3 min and then rapid ascent back to the surface. The duration of surface intervals between feeding dives suggest that adult right whales dive aerobically, but longer surface intervals and theoretical aerobic dive limit calculations suggest that this may not be true of right whale calves. 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. These results indicate that right whales are adept at locating and exploiting very discrete, dense concentrations of *C. finmarchicus* C5 that typically occur just above the bottom mixed layer at this time of year. Most tagged right whales ingested *C. finmarchicus* C5 at estimated rates sufficient to meet daily metabolic requirements, however many of these animals would require over 12 hours of feeding at observed ingestion rates to do so. Short deployments and uncertainty in metabolic rates during different activities and life history events (e.g., foraging, resting, socializing, pregnancy, lactation) make it difficult to judge whether individual right whales were obtaining sufficient energy to meet the

metabolic costs of reproduction. However, our results demonstrate that it is possible to estimate ingestion rates for right whales with TDR and OPC measurements, and with longer attachment durations and additional measurements, it may be possible to more accurately estimate and compare the daily assimilation and metabolic requirements of right whales.

2.2. INTRODUCTION

The predatory 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 2-3 mm long calanoid copepod *Calanus finmarchicus*. Assessing the abundance of this copepod at spatial scales that are relevant to a right whale (meters in the vertical, tens to hundreds of meters 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 and copepod patches can be visually identified (Watkins and Schevill, 1976; Wishner et al., 1988, 1995; Mayo and 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 1930's, 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 and Caswell, 2001). Consequently, there is an urgent need for information about the habitat and habitat use of right whales to inform 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 suggests that centuries of depressed abundance due to whaling has allowed other predators of *C. 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 crude right whale survival probability to the North Atlantic Oscillation (Fujiwara and Caswell, 2001) which, in turn, affects *C. finmarchicus* abundance (Fromentin and Planque, 1996; Conversi et al., 2001), seem consistent with this hypothesis.

Right whales have been observed feeding on older copepodite stages of *C. finmarchicus* in Cape Cod Bay (Watkins and Schevill, 1976; Mayo and 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 and Schevill, 1976; Mayo and Marx, 1990; Kenney et al., 1995). During the summer, right whales can be found in the lower Bay of Fundy and on the southwestern Scotian Shelf where they continue to feed on older stages of *C. finmarchicus* (Stone et al., 1988; Murison and Gaskin, 1989; Woodley and 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 and Herman, 1990; Miller et al., 1991). Net sampling by Murison and Gaskin (1989) in the lower Bay of Fundy indicated that *C. finmarchicus* C5 was the dominant zooplankton near right whales and that indeed, these copepods occurred at depths below 100 m. Both Murison and 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, time-depth recorders (TDR) and observations of *C. 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.

2.3. METHODS

The tag used during the 2000 summer field season consisted of a modified Wildlife Computers model MK7 time-depth recorder (TDR) equipped with a light-emitting diode at the end of a stalk. The TDR recorded pressure (converted to

depth at a resolution of 2 m), temperature and relative light intensity every second and required recovery 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 Pascal 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 approximately 90 min. 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).

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 50-100 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 conductivity-temperature-depth instrument (CTD) and a Focal Technologies model OPC-1T optical plankton counter (OPC). 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 (Chapter 5). During tracking, behavioral observations and social interactions were noted and photographs were taken for comparison with the New England right whale catalog (Hamilton and 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 animals. 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} (Figure 2.1). 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

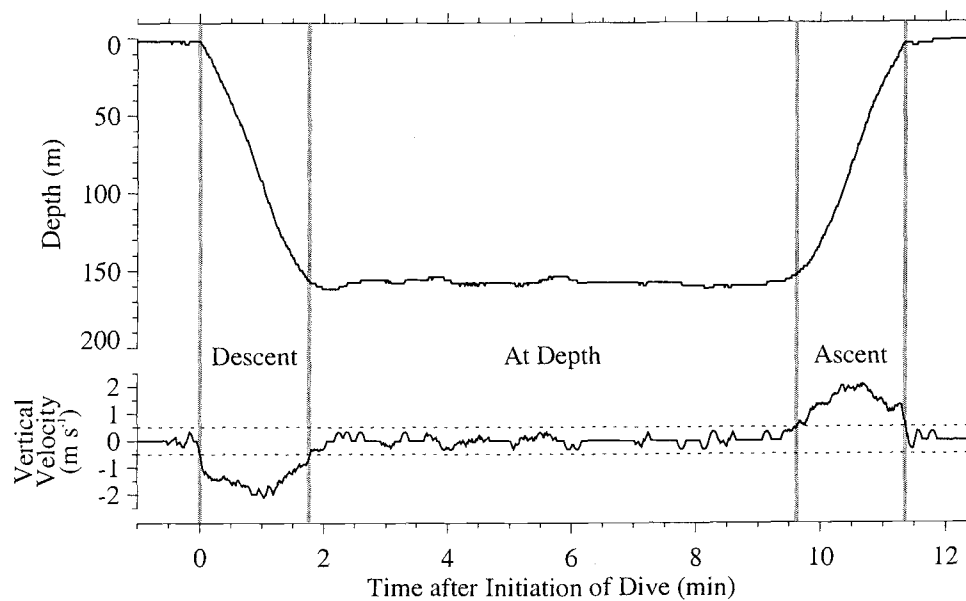


Figure 2.1. Typical right whale feeding dive with descent, at-depth and ascent portions shown. By convention, the descent portion begins when the downward velocity exceeds 0.5 m s^{-1} and ends when the downward velocity drops below 0.5 m s^{-1} . Likewise, the ascent portion begins when the upward velocity exceeds 0.5 m s^{-1} and ends when the upward velocity drops below 0.5 m s^{-1} .

the termination of the descent and the initiation of the ascent. The mean and standard deviation 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 the standard deviation of the dive depth. Dives were classified into three 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 *C. 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 strata 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 between 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 *C. 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 *C. finmarchicus* C5 (I_d) was estimated for each feeding dive as

$$I_d = A_g S T_d E_{C5} C \quad (2.1)$$

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 animal was tagged was estimated as follows:

$$I' = \frac{T_f \sum I_d}{T_t \sum T_d} \quad (2.2)$$

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 fixed at 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 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 equation 2.1). These

swim speeds must be considered minimum speeds, however, since we do not know if the whales foraged along straight-line paths between the diving and resurfacing positions. To account for this, swim speeds were increased to 1.5 m s^{-1} whenever the observed minimum swim speed was less than 1.5 m s^{-1} . Swim 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 swim speeds during surface feeding of 1.34 m s^{-1} and Watkins and Shevill (1976) report swim speeds of “up to 3 knots” or 1.54 m s^{-1} . Minimum swim speeds in the present study averaged nearly 1 m s^{-1} (see Table 2.3 in Results), however subsurface foraging paths in the Bay of Fundy are rarely straight (D. Nowacek, personal communication). Therefore, 1.5 m s^{-1} is assumed to be a reasonable estimate of true swim speeds 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 two 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 hours each day, the fraction of the daily metabolic requirement met by each whale is

$$\frac{\text{daily assimilation}}{\text{daily requirement}} = \frac{A I' T}{DMR(T) + RMR(24 - T)} \quad (2.3)$$

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

$$T_{req} = \frac{24 RMR}{A I' + RMR - DMR} \quad (2.4)$$

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

$$BMR = \frac{4186.8}{86400} [70 M^{0.75}] \quad (2.5)$$

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 day^{-1} to watts (W or J s^{-1}). The assimilation efficiency and body mass are assumed to be 0.80 (Lockyer, 1981) and 40,000 kg (Kenney and Winn, 1986), respectively, therefore $BMR = 0.96 \times 10^4 \text{ W}$. The magnitude of DMR is unknown for right whales, but for other species, DMR ranges from $1.5 - 2 \times BMR$ in Weddell seals (Kooyman et al., 1973; Castellini et al., 1992), $2 - 3 \times BMR$ in northern elephant seals (Costa and Williams, 1999, p. 200) and nearly $6 \times BMR$ in the bottlenose dolphin and otariids (sea lions and fur seals) (Costa and Gentry, 1986; Costa et al., 1989; Costa and Williams, 1999, p. 199). 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 fairly 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 (George et al., 2001). We assume here that $DMR = 2 \times BMR$ and $RMR = 1 \times BMR$. 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

$$I'_{BMR} = \frac{1}{A} BMR \quad (2.6)$$

or 1.20×10^4 W.

2.4. RESULTS

Twenty eight right whales were tagged in the lower Bay of Fundy between 11 July and 28 August, 2000 (Figure 2.2). Of these 28, all but 2 of the tags were recovered. The median duration was 28 min and 23.1% ($n = 6$) of the tagging events exceeded 1 hour. During a single event in 2000, a rubber suction cup was used instead of the silicone cup and the resulting attachment duration was 7 hours. A total of 63 complete dives were 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 11-29 August, 2001, 25 right whales were tagged and all of the tags were successfully recovered. Of these 25 whales, 6 adults (presumably female) with calves, two calves and a single, known pregnant female (R. Rolland, personal communication) 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 (Figure 2.2). The median duration was 86 min and 64.0% ($n = 16$) of the tagging events exceeded 1 hour. A total of 86 complete dives were 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.

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

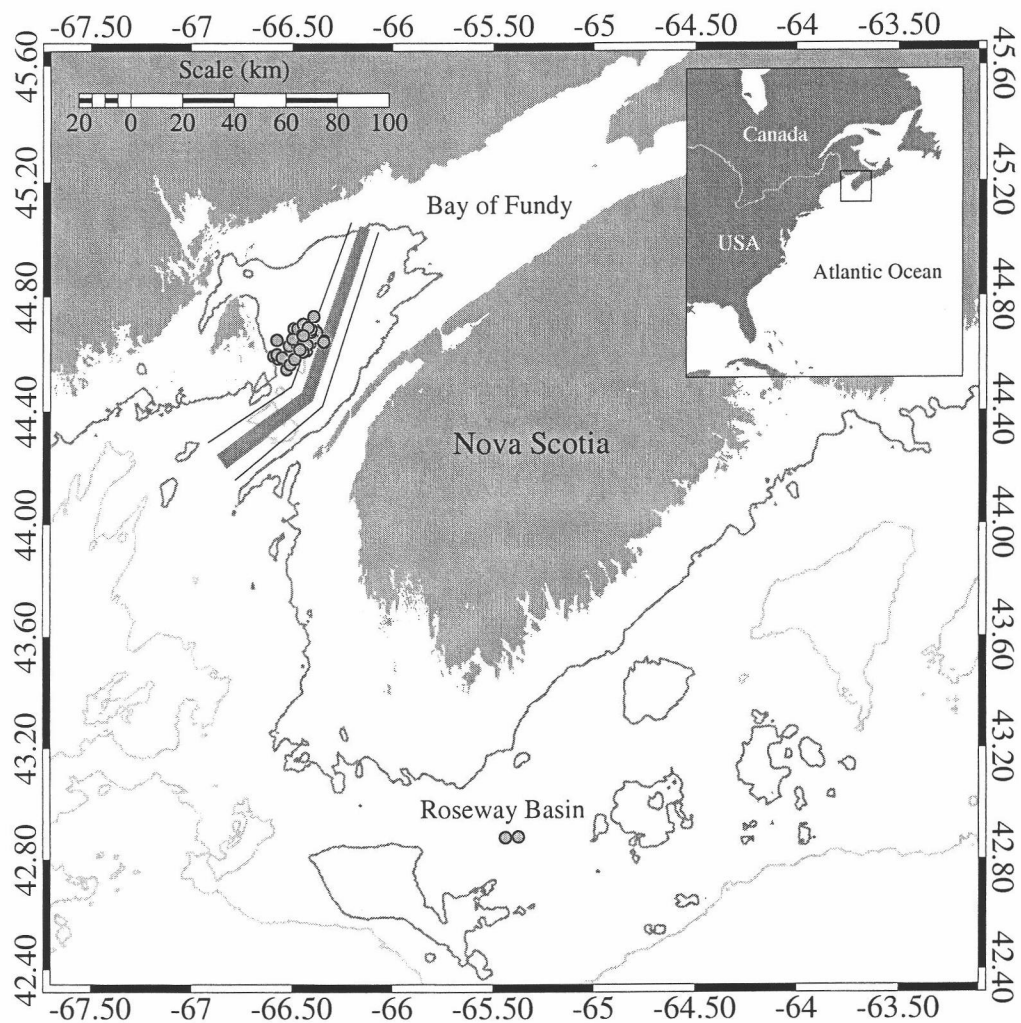


Figure 2.2. Map of study area. Tagging locations in the lower Bay of Fundy and Roseway Basin are shown as filled circles. Shipping lanes through the lower Bay of Fundy and the 91 m (50 fathom) and 200 m isobaths are also shown.

and then a rapid ascent back to the surface (Figure 2.1, Table 2.1). Ascent speed was an average 0.07 m s^{-1} (95% CI: $0.01 - 0.13 \text{ m s}^{-1}$) faster than the corresponding

Table 2.1. Summary of feeding dive characteristics for animals that engaged in at least one 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.

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 hr^{-1})	18	0.85	0.93	0.44	0.71 – 1.15	0.38 – 1.94
Peak abundance (copepods m^{-3})	31	6219	7481	4581	5800 – 9161	2059 – 20610

descent speed during feeding dives (one sample t-test, $p = 0.026$). Excluding the tagged calves, females with calves and the single, known 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 animals, PCST averaged 21.2% ($n = 11$, $\text{SD} = 4.1\%$, range = 15.8 – 30.1%) whereas for the tagged calves and females with calves, PCST averaged 34.2% ($n = 4$, $\text{SD} = 9.2\%$, range = 24.3 – 44.3%). The PCST for the known pregnant female (shown in Figure 2.4c) 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 animals (two sample t-test, $p = 0.78$), but surface intervals were significantly higher (two sample t-test, $p = 0.0011$). Surface intervals for calves and females with calves averaged

5.69 min ($n = 4$, $SD = 1.22$ min, range = 4.54 – 6.97 min) whereas surface intervals for all other animals excluding the pregnant female averaged 3.13 min ($n = 11$, $SD = 0.99$ min, range = 1.65 – 5.06 min). The pregnant female had the highest average surface interval of 11.08 min.

Traveling (e.g., Figure 2.3b) and social activity (e.g., Figure 2.3c) 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., Figures 2.4c and 2.4d). Of the 6 dives classified as “other”, 2 of the dives were to within 10 m of the bottom mixed layer (Figure 2.3b and 2.3c) and 4 were to the sea floor (e.g., Figure 2.3b). In all, 5 brief excursions to the bottom were observed (e.g., Figures 2.3b and 2.3d), but none of these animals 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 2.2). These dive characteristics were also strongly and positively correlated with the depth of the peak *C. finmarchicus* C5 abundance. There was suggestive, but inconclusive evidence that both dive duration and 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 2.2). *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 (Figure 2.4). 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 2.2, Figure 2.5a). 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.*

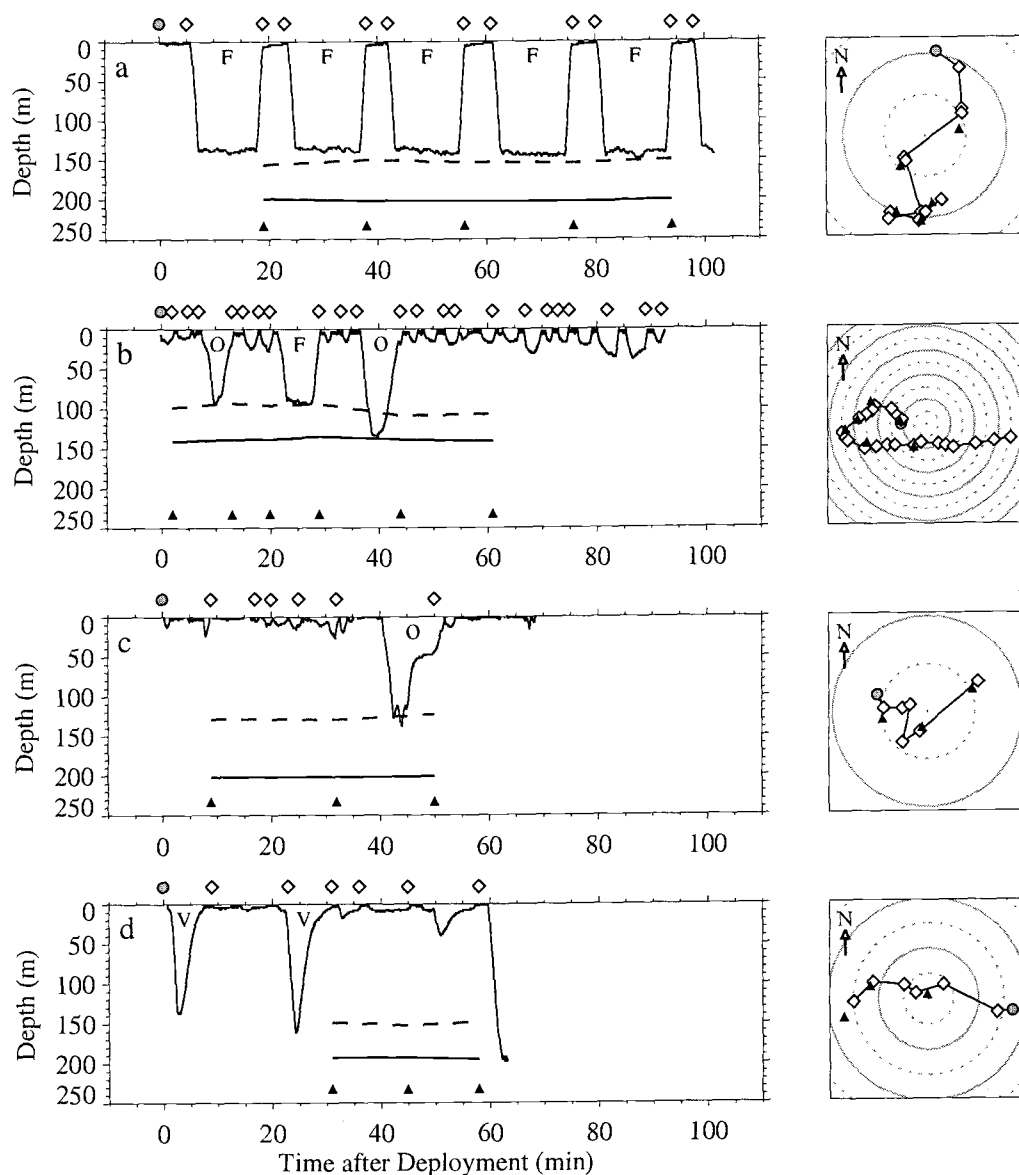


Figure 2.3. Diving and tracking observations illustrating (a) feeding, (b) traveling, (c) socializing and (d) presumed searching behaviors. Individual dives were classified and labeled as feeding (F), V-shaped (V) or "other" (O). Diamonds and the filled circle indicate the times (on the time series) and locations (on the accompanying map) of visual contacts. Triangles indicate the times and locations at which a resurfacing occurred and a 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 the CTD/OPC cast. Alternating dotted and solid gray lines on the accompanying maps are separated by 0.5 km. Tags detached at depth in (a) and at the bottom in (d).

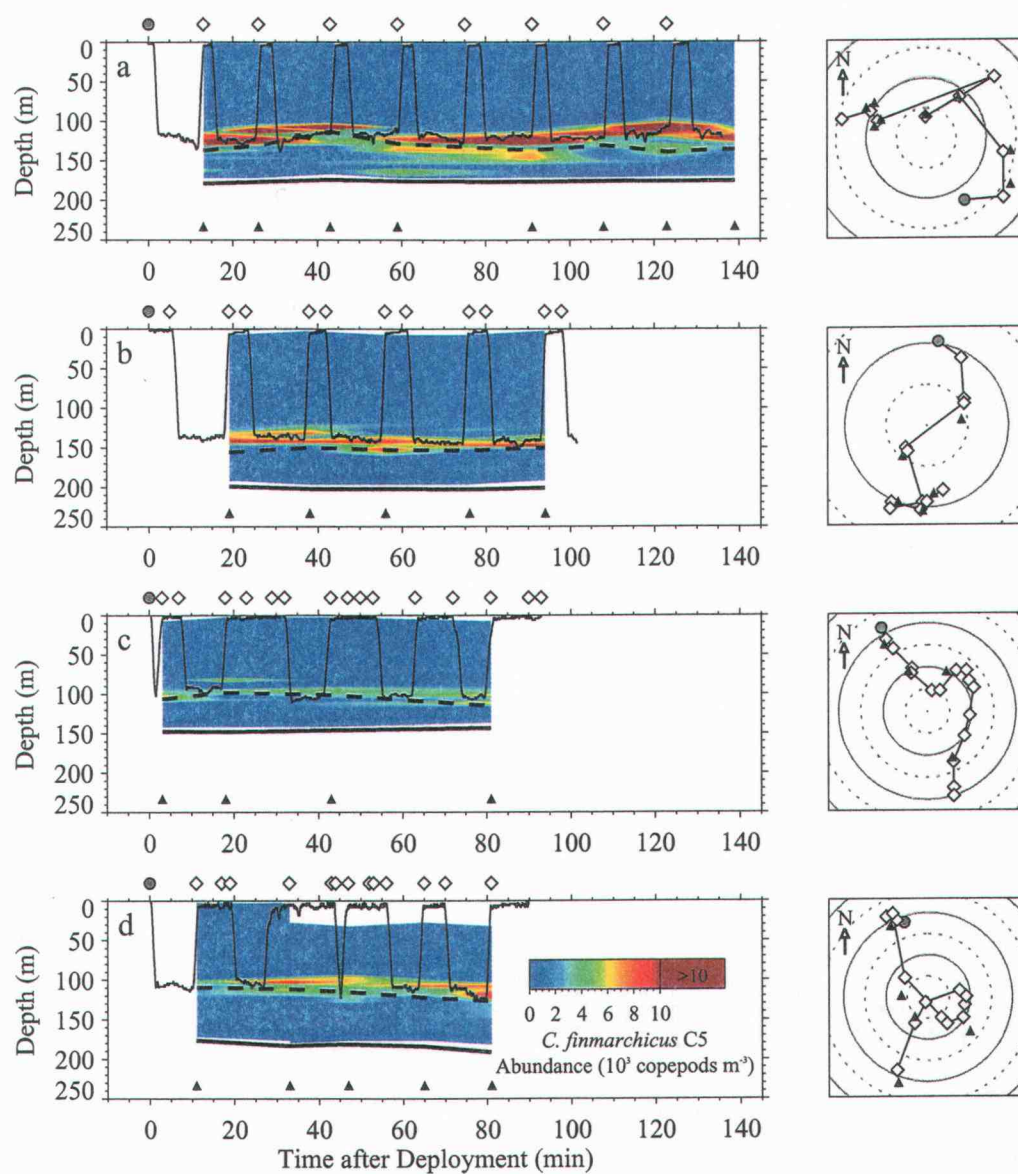


Figure 2.4. Examples of diving and tracking observations during feeding behavior. Contoured *Calanus finmarchicus* C5 abundance estimated from the OPC casts is shown. Color scale shown in (d) applies to all plots. Symbols and lines are the same as in Figure 2.3.

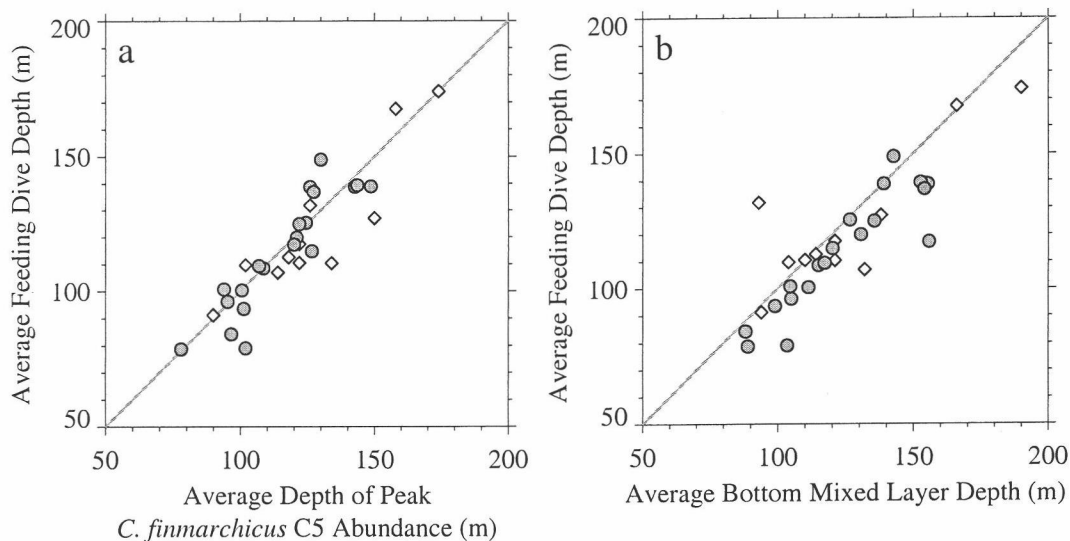


Figure 2.5. Scatterplots of (a) average depth of peak *Calanus finmarchicus* C5 abundance versus average depth of feeding dives and (b) average depth of the bottom mixed layer versus average depth of feeding dives. Filled circles represent tagged animals that had 2 or more feeding dives with accompanying CTD/OPC casts. Diamonds represent tagged animals with only one feeding dive with an accompanying CTD/OPC cast.

Table 2.2. Correlation matrix of feeding dive characteristics for tagged animals that engaged in at least one feeding dive for which an accompanying OPC/CTD cast was conducted. $n = 31$ for each correlation coefficient.

	Dive duration	Duration at depth	Descent speed	Ascent speed	Peak C5 abundance	Depth of peak C5 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***
Peak C5 abundance						0.031

Note: “***” indicates $p < 0.001$, “**” indicates $0.001 \leq p < 0.01$, “*” indicates $0.01 \leq p < 0.05$ and “.” indicates $0.05 \leq p < 0.10$.

finmarchicus C5 upon which the whales presumably fed were often observed near the bottom mixed layer (Figure 2.4). Consequently, the whales’ average dive depth was strongly correlated with the average depth of the bottom mixed layer ($r = 0.865$, $p < 0.0001$, Figure 2.5b). 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 *C. finmarchicus* C5 abundance, total ingestion (I_d from equation 2.1) 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 equation 2.2) were estimated only for those animals tracked over 1 hour (Table 2.3). Of the 22 tagged animals 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 hours at the observed ingestion rates to meet this requirement. Four of the 14 would have needed less than 5 hours to meet their daily metabolic

Table 2.3. Number of feeding dives, duration of attachment, percent time feeding, average minimum speed between diving and resurfacing positions, average peak *Calanus 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 equation 2.4. Data are from deployments lasting over 1 hour. The first column contains the label used for each animal in Figure 2.6. Figure numbers are also provided for those deployments shown in Figures 2.3 and 2.4. Minimum speeds were not calculated for animals tagged in 2000 (see text for explanation). Missing values for T_{req} indicate $T_{\text{req}} > 24$ hr.

Label in Fig. 2.6	Number of Feeding Dives	Deployment Duration (min)	% Time Feeding	Average		I' (10^4 W)	I' ($\times I'_{\text{BMR}}$)	T_{req} (hr)	Fig.
				Minimum Speed (m s^{-1})	Peak Abundance (copepods m^{-3})				
1 ^a	0	69	0.0	—	—	0.00	0.00	—	2.3c
2 ^a	0	63	0.0	—	—	0.00	0.00	—	2.3d
3	0	92	0.0	—	—	0.00	0.00	—	
4 ^b	1	93	5.1	1.94	5592	0.45	0.38	—	2.3b
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	—	2.4c
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 ^c	4	90	33.7	1.54	8672	4.64	3.87	8.4	2.4d
19	6	86	64.2	0.61	9871	7.69	6.41	4.4	
20 ^a	6	68	48.0	—	12,867	7.78	6.49	4.4	
21 ^d	5	102	57.7	0.68	11,893	8.47	7.06	4.0	2.3a,2.4b
22 ^a	8	136	68.0	—	14,945	12.48	10.41	2.6	2.4a
Average			40.4	0.96	6618	3.55	2.96		

^a Animals tagged in 2000. All other animals tagged in 2001.

^b Animals tagged in Roseway Basin on southwestern Scotian Shelf. All other animals tagged in Grand Manan Basin of the lower Bay of Fundy.

^c Pregnant female.

^d Adult (presumably female) with calf.

^e Calf.

requirement. 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 (Figure 2.6). The resulting regression equation ($I' = [6.58 \text{ m}^3 \text{ W}] \times C$) 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 hr day^{-1} to meet this requirement). The minimum peak concentration observed near whales that were tagged for over 1 hour and that engaged in feeding dives was ca. 3000 copepods m^{-3} (Table 2.3), which is in good agreement with the minimum concentration required to meet daily metabolic requirements. One of the tagged animals engaged in behavior that we interpret as searching (Figure 2.3d) and peak concentrations of *C. finmarchicus* C5 near this animal averaged ca. 1300 copepods m^{-3} . A whale feeding continuously on this concentration (i.e., 24 hr day^{-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 peak *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.

2.5. 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 positive

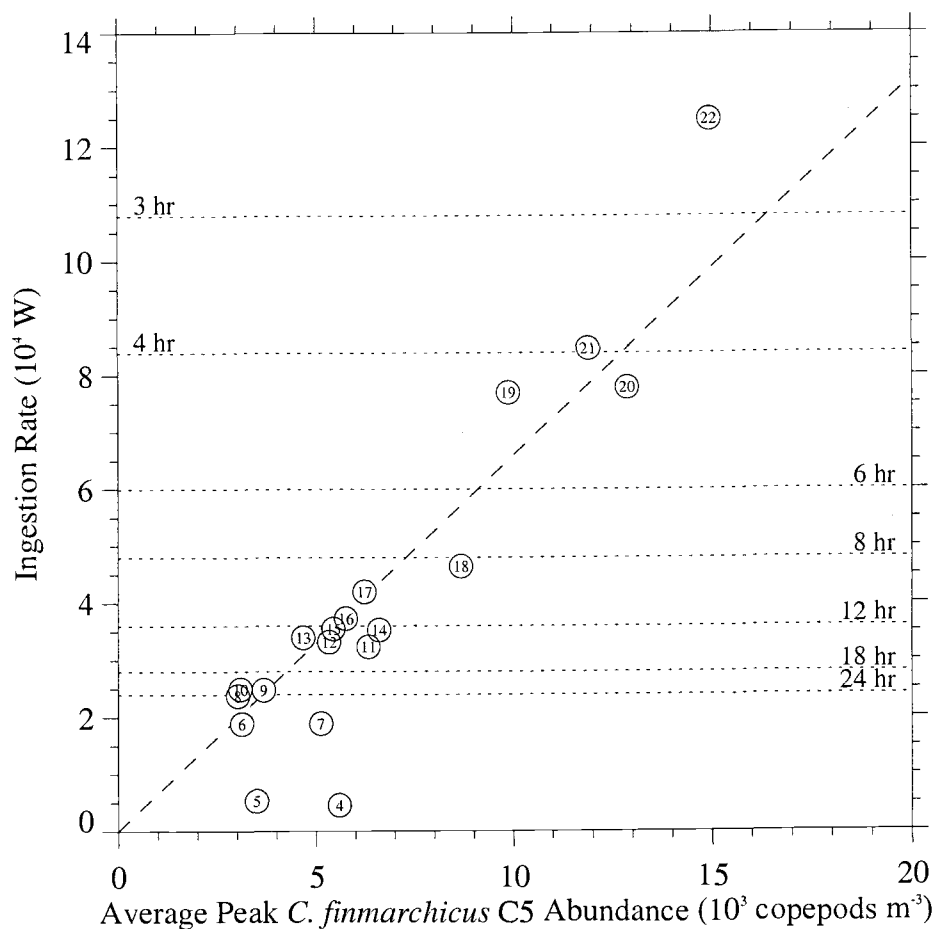


Figure 2.6. Scatterplot of average peak *Calanus finmarchicus* C5 abundance versus estimated ingestion rate. Labels reference data in Table 2.3. A linear regression forced through the origin was fitted to the data and is shown as the dashed line. Horizontal, dotted lines indicate the ingestion rates and times spent foraging required to meet daily metabolic needs (e.g., ingestion for 6 hr per day at a rate of 6×10^4 W would be sufficient to meet daily metabolic requirements).

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 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 were significantly 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 family (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, is 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 and 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) estimate total O_2 stores for blue and fin whales to be an average $55.6 \text{ ml } O_2 \text{ kg}^{-1}$. Assuming right whales have similar total O_2 stores and that a calf's $DMR = 4 \times BMR$ (i.e., $DMR = 4 \times [70M^{0.75} \text{ kcal day}^{-1}] / [4.8 \text{ kcal (l } O_2)^{-1}] / [1440 \text{ min day}^{-1}]$), a 5000 kg calf (New England Aquarium unpublished 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 ($n = 5$, $SD = 2.04 \text{ min}$, range = 8.84 – 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 O_2 stores and diving metabolic rate for right whales.

The strong correlation between dive depths and the depth of maximum *C. 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 extraordinary. 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 collosities 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 tens of meters 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 *C. 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 (Figure 2.7). If DMR values for right whales also exceed $4 \times BMR$, then only 4 of the 22 animals with tag attachments lasting over 1 hour would have been ingesting *C. finmarchicus* C5 at a rate sufficient to meet their daily metabolic requirement (Figure 2.7). 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.

Despite the uncertainties in DMR, it is clear that some of the tagged whales were easily ingesting *C. 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

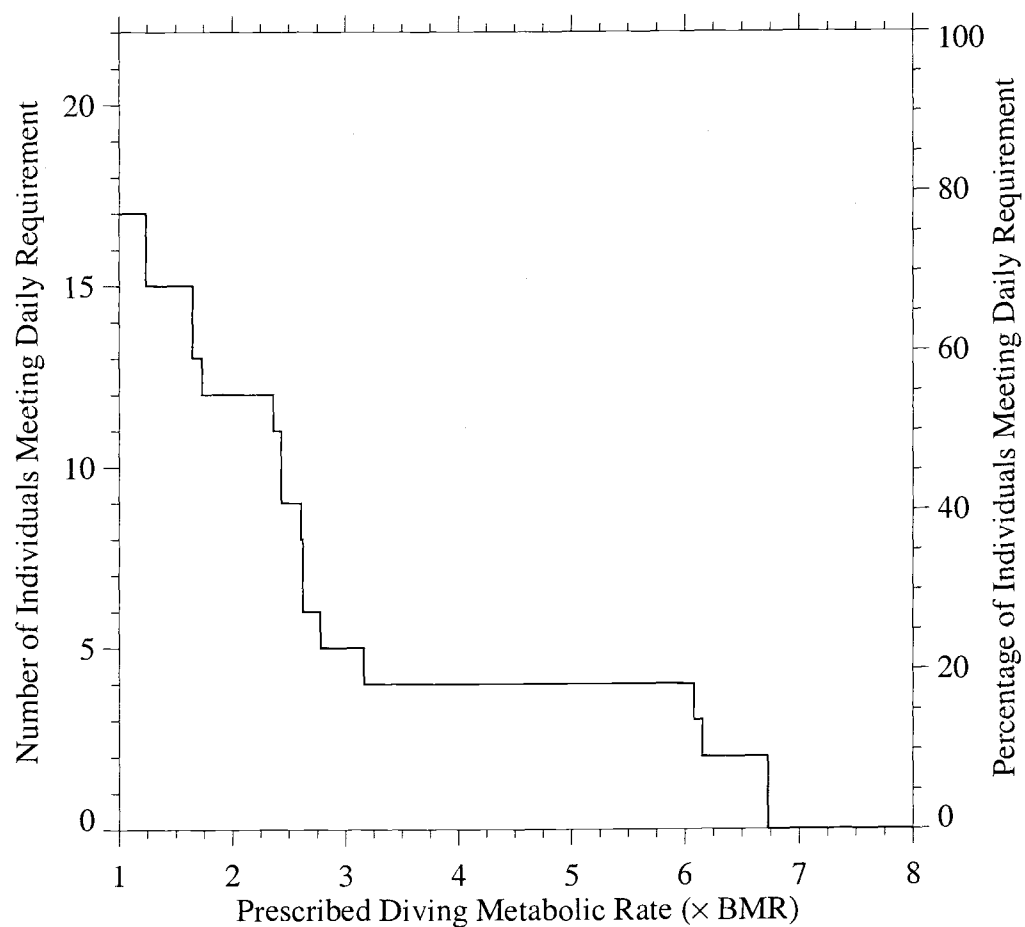


Figure 2.7. Number (and percentage) of animals shown in Table 2.3 that ingested at a rate sufficient to meet daily metabolic requirements for different choices of the diving metabolic rate (DMR). DMR shown as a multiple of the estimated basal metabolic rate (BMR).

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 animals 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 2.3). 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 hours. Therefore, the ingestion rates estimated here may not accurately reflect daily ingestion rates. Since we observed a few animals foraging on abundances of *C. finmarchicus* C5 in excess of 10000 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 hr. 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 equation 2.3), 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 similar 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 one feeding habitat, then, might provide a distorted view of whether sufficient food resources exist to support right whale population growth.

2.6. ACKNOWLEDGMENTS

We are indebted to chief scientists Tim Cole and Phil Clapham (NMFS), the master, officers and crew of NOAA Ship *Delaware II* and the many professional and volunteer observers who made field operations possible. Particular thanks go to our able drivers, Barb Lagerquist (OSU) and Fred Wenzel (NMFS), and Tom Fernald, John Nicolas and Pete Duley for special assistance in the field. Several people graciously loaned equipment and expertise for which we are grateful: Maureen Taylor (NMFS) provided the CTD, Rick Trask (WHOI) provided the rosette cage, Bill Percy (OSU) provided the acoustic receiver, Heidi Dewar (Stanford University) provided the directional hydrophone and Tomas Follett (OSU) contributed considerable expertise to the construction of the tags. Roz Rolland (NEAq) conducted the fecal steroid hormone analysis to identify the pregnant female tagged in Roseway Basin. This research was supported by the National Marine Fisheries Service, Office of Naval Research, Oregon State University Marine Mammal Endowment and by the Space Grant and Earth System Science fellowship programs of the National Aeronautics and Space Administration.

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3. NORTH ATLANTIC RIGHT WHALE HABITAT IN THE LOWER BAY OF FUNDY AND ON THE SOUTHWESTERN SCOTIAN SHELF DURING 1999–2001

3.1. ABSTRACT

Simultaneous visual and oceanographic surveys were conducted in the lower Bay of Fundy and in Roseway Basin of the southwestern Scotian Shelf during the summers of 1999, 2000 and 2001. Sightings of right whales were recorded in a grid of 9.3×9.3 km survey units within each region. Oceanographic measurements were collected with a conductivity-temperature-depth instrument (CTD) and an optical plankton counter (OPC) at a station in the center of each survey unit. Remotely-sensed, synoptic images of sea surface temperature (SST), surface chlorophyll and their respective horizontal gradients were acquired from the satellite-borne advanced very high resolution radiometer (AVHRR) and the sea-viewing wide field-of-view (SeaWiFS) sensor, respectively, and were averaged over each survey unit. Zooplankton and OPC sampling both in proximity to whales and in areas where whales were absent demonstrated that right whales feed on *Calanus finmarchicus* copepodite stage 5 (C5) in these regions. Spatial variability in right whale occurrence was associated with both water depth and bottom mixed layer depth. Our results suggest that *C. finmarchicus* C5 aggregated in the deepest part of the basins in each region and that right whales forage in areas where the bottom mixed layer forces discrete layers of *C. finmarchicus* C5 to occur shallower in the water column. Foraging on shallower layers of *C. finmarchicus* C5 is more energetically beneficial because the reduction in transit time allows feeding for up to 20% longer on these layers than on deeper ones. Annual increases in right whale occurrence were associated with decreases in SST in both regions. This association may be a consequence of increased productivity or survivorship of *C. finmarchicus*

C5 with decreased SST throughout the year or, in the case of Roseway Basin, the disappearance of warm water, predatory, gelatinous zooplankton that may reduce *C. finmarchicus* C5 survivorship or inhibit filter feeding by right whales. There was also evidence to suggest that both spatial and interannual variability in right whale occurrence in Roseway Basin was associated with SST gradient, a proxy for ocean fronts. The prospects for using the results of habitat research in a predictive model of right whale spatial distribution are discussed.

3.2. INTRODUCTION

Despite protection from hunting since the mid 1930's, the North Atlantic right whale (*Eubalaena glacialis*) remains one of the most endangered large whales (Clapham et al., 1999). Mortality from fishing gear entanglement and collisions with ships is of great concern (Kraus, 1990; Kenney and Kraus, 1993; Knowlton and Kraus, 2001) and conservation efforts may be improved with the protection of right whale habitat. Our understanding of what constitutes right whale habitat, though, is quite poor. Many studies have indicated that the presence of large aggregations of the right whale's primary prey, older stages of the calanoid copepod *Calanus finmarchicus*, is probably the single most important component of right whale habitat (Watkins and Schevill, 1976; Wishner et al., 1988, 1995; Murison and Gaskin, 1989; Mayo and Marx, 1990; Beardsley et al., 1996; Woodley and Gaskin, 1996; Kenney, 2001). However, the physical and biological oceanographic features or conditions that promote high abundance and discrete aggregation of this prey over time and space are not well understood, nor are the means by which right whales locate and exploit these food resources.

North Atlantic right whales can be found in Cape Cod and Massachusetts Bays in the late winter and early spring, where they primarily feed on *C.*

finmarchicus, but they have also been observed feeding on *Pseudocalanus* spp., *Centropages* spp., barnacle larvae and euphausiids (Watkins and Schevill, 1976; Mayo and Marx, 1990). By mid-spring, right whales are typically found in the Great South Channel (Kenney et al., 1995). Here again, they primarily feed on older copepodite stages of *C. finmarchicus* (Wishner et al., 1988, 1995). In the later summer, right whales occupy the lower Bay of Fundy (Kraus et al., 1982) or the southwestern Scotian Shelf (Mitchell et al., 1986). Murison and Gaskin (1989) and Woodley and Gaskin (1996) concluded that the primary prey of right whales in the lower Bay of Fundy was *C. finmarchicus* while Stone et al. (1988) observed *C. finmarchicus* mandibles in right whale feces collected in Roseway Basin on the southwestern Scotian Shelf. By late fall, right whales abandon the lower Bay of Fundy and while some animals migrate southward to the only known calving grounds on the coast of the southeastern United States, the whereabouts of the rest of the population in late fall and early winter are, as yet, unknown. Although these seasonal movements between high-use areas have been well documented for some time (CETAP, 1982; Winn et al., 1986), recent evidence from whales outfitted with satellite-monitored radio tags suggests that inter-regional movements on much shorter time scales are quite common (Mate et al., 1997). Alterations to this general distribution pattern have also been observed in some years (Payne et al., 1990; Kenney, 2001), and there is evidence of other potential high-use areas (Weinrich et al., 2000).

Our study focused on the ecological relationship between right whale occurrence and several biological and physical oceanographic factors in the lower Bay of Fundy and in Roseway Basin on the southwestern Scotian Shelf during the summers of 1999-2001. We examined data from visual surveys and from both in-situ and satellite-borne oceanographic instrumentation to characterize right whale habitat features. We paid particular attention to the relationship between the occurrence of right whales and the abundance and distribution of the most lipid-rich

stage of their prey, *C. finmarchicus* copepodite stage 5 (C5), to elucidate ecological relationships among the physical environment, *C. finmarchicus* and right whales. These relationships were examined separately over space and time to determine what environmental factors influence both spatial and interannual variability in right whale occurrence within each study region. By better understanding the factors that influence right whale occurrence, we hope to provide a basis to predictively model right whale distribution for conservation purposes.

3.3. MATERIALS AND METHODS

3.3.1. Data collection and processing

Simultaneous visual and oceanographic surveys were conducted in the lower Bay of Fundy and Roseway Basin during the summers of 1999, 2000 and 2001. North-south (Bay of Fundy) or east-west (Roseway Basin) transects were visually surveyed through a grid of oceanographic stations (Figure 3.1). A single survey unit consisted of a 9.3 km (5 nmi) transect section centered on an oceanographic station. The survey unit length was selected as the approximate scale of horizontal variability in hydrographic properties observed on the Scotian Shelf by Herman et al. (1991). The effective width of the survey unit was estimated as the maximum distance perpendicular to the trackline at which a right whale was detected during the surveys. This distance was approximately 4.6 km (2.5 nmi), so a single survey unit was defined as a 9.3 by 9.3 km (5 by 5 nmi) area centered on an oceanographic station. Surveys were conducted during cruises designed to accommodate several research objectives, so not all survey units were sampled each year. After 1999 in the lower Bay of Fundy, the present study competed with

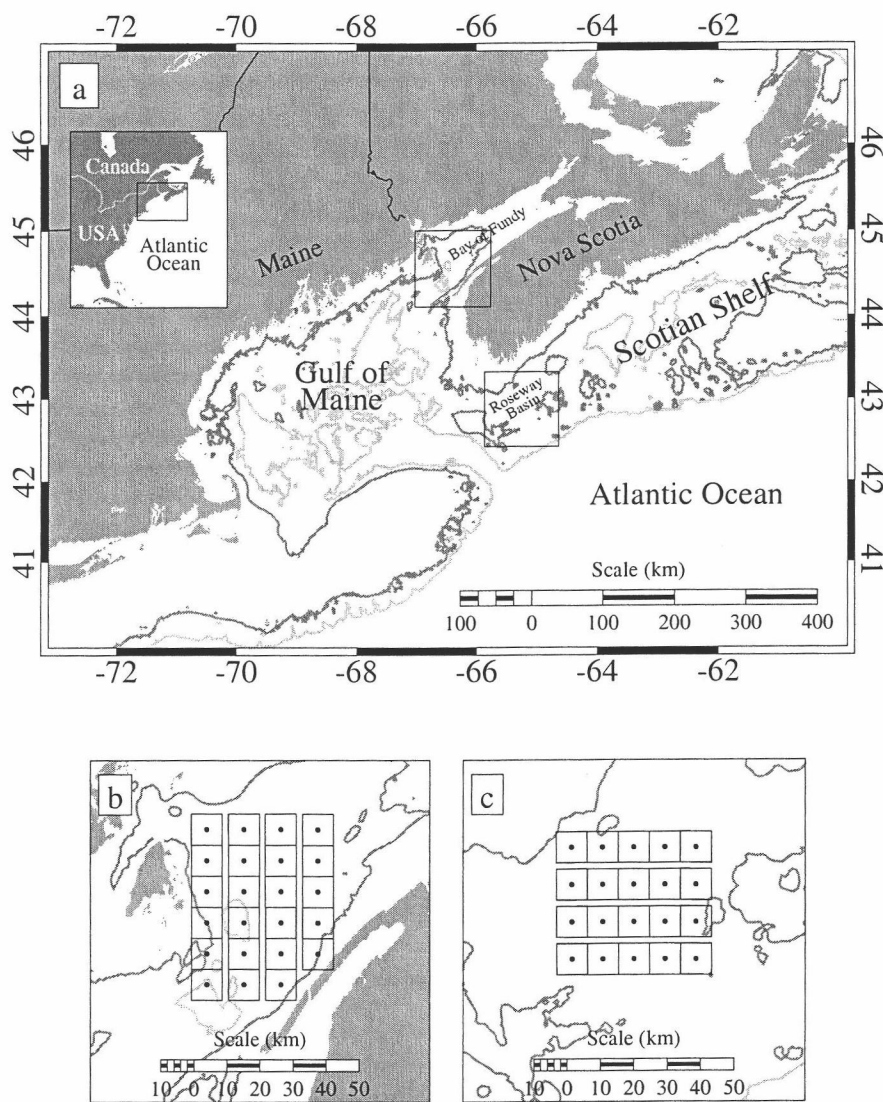


Figure 3.1. (a) Location of study areas in the lower Bay of Fundy and Roseway Basin. Survey units (boxes) and oceanographic stations (filled circles) in (b) the Lower Bay of Fundy and (c) Roseway Basin.

research objectives that required fair weather conditions and calm seas, so surveys were typically conducted in higher sea states. Each region (lower Bay of Fundy and Roseway Basin) was sampled once per summer except in 2000 when the lower Bay of Fundy was sampled twice (Figure 3.2).

Visual surveys were conducted from the flying bridge of NOAA Ship *Delaware II*. Two observers used mounted, 25×, “big eye” binoculars to scan from roughly -110 to +110° relative to the bow while a third observer scanned with hand-held binoculars or with the naked eye. Sightings of marine mammals were recorded by this third observer using a hand-held data-entry system. The date, time, species, number of individuals and the distance and relative bearing to the animal or animals were logged for each encounter. The location of each sighting was later computed along a rhumb line using the observer’s bearing and distance estimates and the ship’s simultaneous gyro compass measurement. Sighting conditions, including sea state, glare magnitude and direction, visibility and swell height, were also recorded during the surveys with either paper forms or the hand-held data entry device. Visual effort was conducted only while steaming along the transect and not while on station. Ship speed during surveys was nominally 18.5 km hr⁻¹ (10 knots).

An instrument package, consisting of a Seabird model SBE19 conductivity-temperature-depth instrument (CTD) and a Focal Technologies model OPC-1T optical plankton counter (OPC), was deployed in a vertical cast at each station. The CTD provided vertical profiles of temperature and salinity while the OPC (Herman, 1988, 1992) yielded the vertical distribution of particles between 0.25 and 20 mm in size. The vertical distribution of *C. finmarchicus* C5 was estimated from the OPC data in 4 m depth strata using the prediction equation developed by Baumgartner (Chapter 5) from comparisons between collocated OPC casts and net samples collected during these same cruises.

Concurrent, high resolution, remotely sensed data were also collected from the advanced, very high resolution radiometer (AVHRR) and the sea-viewing wide

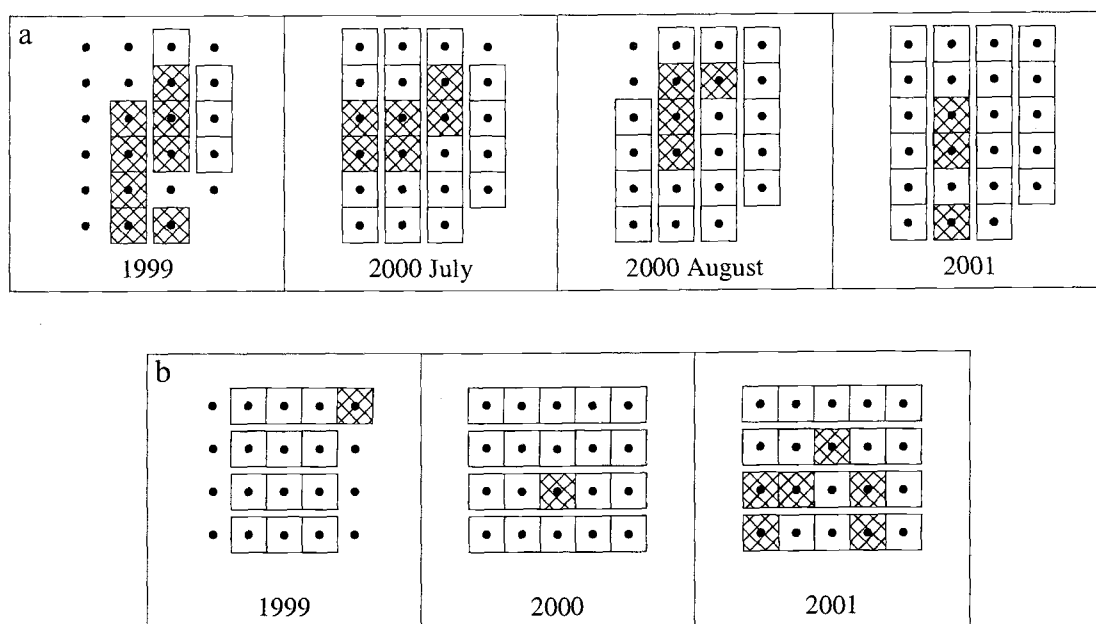


Figure 3.2. Visual survey results for (a) the lower Bay of Fundy and (b) Roseway Basin. Station plan (filled circles) and completed survey units (boxes) are indicated. Survey units with one or more right whales sighted are cross-hatched.

field-of-view (SeaWiFS) sensor and processed into sea surface temperature (SST) and surface chlorophyll, respectively. The AVHRR data were processed and archived at the University of Rhode Island (Cornillon et al., 1987) while the SeaWiFS data were processed by the first author with the SeaDAS software package (version 4.0). Synoptic images from both sensors were transformed to an equidistant, cylindrical projection (i.e., linear latitude/longitude) at a nominal resolution of 1.1 by 1.1 km and manually co-registered with a digital coastline. Horizontal gradients of both sea surface temperature and surface chlorophyll were computed using a 3 by 3 pixel Sobel gradient operator (Russ, 1995). A single, cloud-free, remotely-sensed image within ± 3 days of a survey day was selected and the corresponding SST or surface chlorophyll as well as its respective horizontal gradient magnitude were averaged over each 9.3 by 9.3 km unit surveyed on that day. The median time between midday on a survey day and the corresponding satellite overpass was 0.95 and 1.2 days for AVHRR and SeaWiFS images, respectively. Although higher frequency variability in SST and surface chlorophyll is expected within the ± 3 day temporal window (e.g., diurnal warming, tidal excursion of fronts), spatial and interannual variability in these properties at the scales examined here should be much larger in magnitude. Therefore, the ± 3 day temporal window is considered appropriate.

Zooplankton samples were obtained opportunistically in the lower Bay of Fundy and Roseway Basin both in the presence (within a few hundred meters) and absence of right whales. Depth integrated samples were collected with a 61 cm diameter bongo frame equipped with 333 μm mesh nets and two General Oceanics digital flowmeters. In the lower Bay of Fundy during 2001, depth-stratified samples were also obtained using a multiple opening-closing net and environmental sensing system (MOCNESS; Wiebe et al., 1976, 1985) equipped with 150 μm mesh nets. Zooplankton sampling was conducted in all years from NOAA Ship *Delaware II* and additional sampling was conducted from NOAA Ship *Albatross IV*

in 2001. Samples were preserved immediately after collection in a borate-buffered, 5% formalin-seawater solution. Subsamples containing approximately 100 or more of the most abundant species were drawn with a Hensen-stemple pipette and all organisms in these subsamples were identified and enumerated to the lowest taxa possible. *C. finmarchicus* C5 abundances from the net sampling were compared to independent OPC-derived abundances observed in survey units both with and without right whales present as well as to OPC-derived abundances observed in proximity to right whales tagged with time-depth recorders (data from Baumgartner and Mate, Chapter 2).

3.3.2. Environmental variables

Right whale occurrence was investigated with respect to several environmental variables (Table 3.1). Water depth was measured at each oceanographic station with a Simrad model EK500 scientific echosounder. A 1.1 by 1.1 km resolution digital bathymetric dataset was compiled from a variety of sounding and gridded bathymetric sources (e.g., National Ocean Service soundings, 2 by 2 minute topographic data [Smith and Sandwell, 1997], ETOPO5 gridded bathymetry [NGDC, 1988]) and depth gradient magnitude was computed from this dataset using the same 3 by 3 pixel Sobel gradient operator used for the AVHRR and SeaWiFS data. Both depth and depth gradient have been shown to be important habitat descriptors for a variety of cetacean species (Hui, 1979, 1985; CETAP, 1982; Selzer and Payne, 1988; Baumgartner, 1997; Baumgartner et al., 2001).

Murison and Gaskin (1989) and Woodley and Gaskin (1996) suggested that right whales occupy waters with high surface stratification in the lower Bay of Fundy, so changes in both density and temperature over the upper 50 m of the water

Table 3.1. Environmental variables used in the habitat analyses.

Variable	Source	Units
Depth	ship echosounder	m
Depth gradient	digital bathymetry	m km ⁻¹
Surface stratification (density)	CTD	kg m ⁻³ (50 m) ⁻¹
Surface stratification (temperature)	CTD	°C (50 m) ⁻¹
BML temperature	CTD	°C
BML salinity	CTD	PSU
BML density (sigma-t)	CTD	sigma-t units (kg m ³)
BML depth	CTD	m
Depth of maximum <i>C. finmarchicus</i> C5 abundance	OPC	m
Maximum <i>C. finmarchicus</i> C5 abundance	OPC	copepods m ⁻³
Average water column <i>C. finmarchicus</i> C5 abundance	OPC	copepods m ⁻³
<i>C. finmarchicus</i> C5 abundance above BML	OPC	copepods m ⁻³
Sea surface temperature (SST)	AVHRR	°C
SST gradient	AVHRR	°C km ⁻¹
Surface chlorophyll	SeaWiFS	mg m ⁻³
Surface chlorophyll gradient	SeaWiFS	mg m ⁻³ km ⁻¹

column were extracted from the CTD data and included in the analysis.

Baumgartner and Mate (Chapter 2) demonstrated that right whales equipped with archival tags dove to and presumably foraged just above the bottom mixed layer (BML) in the lower Bay of Fundy and Roseway Basin. Therefore, BML properties were derived from the CTD data and included in this analysis. BML depth was defined as the depth at which the density differed from the bottom density by 0.05 kg m⁻³. Since the BML is uniformly mixed, the temperature, salinity and density measured at the bottom were taken as representative of the BML hydrographic properties.

The depth of right whale feeding dives has been shown to be strongly correlated with the depth of the maximum *C. finmarchicus* C5 abundance (Baumgartner and Mate, Chapter 2), so this variable was computed from the OPC data and included in the analysis. Several measures of *C. finmarchicus* C5 abundance were also derived from the OPC and examined. These included the

maximum *C. finmarchicus* C5 abundance observed in the water column, the average water column abundance and the abundance of *C. finmarchicus* C5 found above the BML. The latter abundance was computed over a depth stratum spanning 20 m above to 5 m below the BML depth. Each *C. finmarchicus* C5 abundance (X) was transformed as $\log_{10}[X+1]$ prior to analysis.

Remotely-sensed SST and surface chlorophyll concentration were examined not only for their capacity to represent relevant oceanographic features, but also for their potential as easily acquired, synoptic datasets upon which predictive models of right whale distribution may be based for management purposes. High horizontal SST and surface chlorophyll gradients can indicate the presence of ocean fronts, so derived gradient data were included in the analysis to determine whether right whales utilize ocean fronts as habitat as suggested by Gaskin (1987).

3.3.3. Logistic regression

Since adjacent right whale sightings collected during these systematic surveys were not expected to be always independent of one another, associations between right whale presence and the environmental variables were investigated using logistic regression analysis. The response variable for each survey unit was coded as 1 if one or more right whales were sighted in that unit and 0 if no right whales were sighted (Figure 3.2). The log-transformed odds of sighting a right whale in a survey unit (η), also known as the logit of the sighting probability (π), was then modeled as a linear function of the independent variables (V_i) as follows

$$\eta = \text{logit}(\pi) = \ln \left[\frac{\pi}{1 - \pi} \right] = \beta_0 + \sum_{i=1}^p \beta_i V_i \quad (3.1)$$

where β_0 is the intercept, β_i are the model coefficients and p is the number of independent variables in the model. The significance of terms in the models were assessed using drop-in-deviance (likelihood ratio) statistics (D) generated from the fitted model and a reduced model that lacked the term or terms of interest. Wald-based z tests can also be used to assess the significance of individual model terms, but these tests are not considered as accurate as the drop-in-deviance test (Ramsey and Schafer, 1997; Hosmer and Lemeshow, 2000). However, Wald-based z tests were conducted when a drop-in-deviance test was inappropriate or to supplement the drop-in-deviance test results. Wald-based 95% confidence intervals (CI) are also reported.

3.3.4. Analysis of sighting conditions

As a consequence of the sampling methodology, the probability of sighting a right whale is influenced by factors that may prevent a whale from being observed from the survey platform. These factors or sighting conditions include the sea state, atmospheric conditions affecting visibility (e.g., haze, fog) or reflection of the sunshine off the sea surface (i.e., glare). The effect of sighting conditions on sighting probabilities was investigated with a logistic regression model that included sea state, visibility and glare fraction as independent variables. Sea state was assessed on the Beaufort scale, visibility was estimated as the maximum distance at which a large object at the sea surface could be seen and the glare fraction was defined as the proportion of the area scanned from -90 to 90° relative to the bow that was obscured by glare.

3.3.5. Analysis of spatial variability

Associations between the spatial distribution of right whales and the environmental variables within each region were examined with logistic regression models that included terms to account for the sighting conditions and regional and annual differences in both sighting probabilities and environmental conditions. To understand how this was accomplished, consider the hypothetical case where right whales “prefer” waters with the warmest surface temperatures available in each region. In a single year, assume that the overall sighting probability and mean SST in the lower Bay of Fundy were 0.5 and 10°C, respectively, while in Roseway Basin, the overall sighting probability and mean SST were 0.1 and 18°C, respectively. Furthermore, assume that sighting conditions during all surveys in this year were always the same. Results from a logistic regression model including the observed SST would be confounded by the regional differences in both sighting probabilities and SST. Specifically, the regional trend of higher sighting probabilities in cooler waters would obscure the association between right whales and locally warm waters. To “remove” this regional variability, a single dummy variable representing the region can be included in the model to account for regional differences in sighting probabilities, and a regional anomaly of SST can be included to account for regional differences in SST. The regional anomaly of SST would be computed by subtracting 10°C and 18°C from the lower Bay of Fundy and Roseway Basin SST observations, respectively. The resulting model would be of the following form:

$$\text{logit}(\pi) = \beta_0 + \beta_1(\text{BOF}) + \beta_2(\text{SST regional anomaly}) \quad (3.2)$$

where BOF is a dummy variable with values indicating the lower Bay of Fundy (BOF = 1) or Roseway Basin (BOF = 0). The coefficient β_2 in this model indicates

the nature of the relationship between local spatial variability in right whale sighting probability and local spatial variability in SST.

In addition to regional variability, interannual variability in both sighting probability and SST can also confound the results of this analysis. To “remove” this source of variability from the model in equation 3.2, dummy variables representing year must be included in the model to account for annual differences in sighting probabilities, and SST anomalies must be determined by subtracting the mean SST over a region in a particular year from the observations in that region and year. The resulting model would be of the following form:

$$\begin{aligned} \text{logit}(\pi) = & \beta_0 + \beta_1(\text{BOF}) + \beta_2(\text{Y2000}) + \beta_3(\text{Y2001}) + \\ & \beta_4(\text{BOF} \times \text{Y2000}) + \beta_5(\text{BOF} \times \text{Y2001}) + \\ & \beta_6(\text{SST regional/annual anomaly}) \end{aligned} \quad (3.3)$$

where Y2000 and Y2001 are dummy variables indicating the years 1999 (Y2000 = 0, Y2001 = 0), 2000 (Y2000 = 1, Y2001 = 0) and 2001 (Y2000 = 0, Y2001 = 1). As above, the coefficient β_6 in this model indicates the nature of the relationship between local spatial variability in right whale sighting probability and local spatial variability in SST where “local” now refers to both space (within region) and time (within year). Models of the form in equation 3.3 were fit for each of the environmental variables. Additional terms to account for variations in sighting probabilities due to sighting conditions were included when warranted.

Finally, it is possible that the nature of the relationship between local spatial variability in sighting probability and an environmental variable may differ between regions. For example, right whale sighting probability may increase with SST in the lower Bay of Fundy, but may decrease with SST in Roseway Basin. To detect this situation, a model including an interaction term for the region and the environmental variable was fit. This model is of the form:

$$\begin{aligned}
\text{logit}(\pi) = & \beta_0 + \beta_1(\text{BOF}) + \beta_2(\text{Y2000}) + \beta_3(\text{Y2001}) + \\
& \beta_4(\text{BOF} \times \text{Y2000}) + \beta_5(\text{BOF} \times \text{Y2001}) + \\
& \beta_6(\text{SST regional/annual anomaly}) + \\
& \beta_7(\text{BOF} \times \text{SST regional/annual anomaly})
\end{aligned} \tag{3.4}$$

A significant drop-in-deviance test of the interaction term (the term involving β_7) provides evidence of an inter-regional difference in the association between sighting probability and SST. The sum of β_6 and β_7 indicates the nature of the relationship between sighting probability and SST in the lower Bay of Fundy ($\text{BOF} = 1$) whereas β_6 alone indicates the nature of this relationship in Roseway Basin ($\text{BOF} = 0$).

Overfitting is a major concern when applying logistic regression models to data containing rare events. Hosmer and Lemeshow (2000) informally suggest that there should be at least 10 events per model parameter (in this study, an event is a survey unit with one or more right whales sighted). The model described in equation 3.3 contains 7 parameters and would therefore require at least 70 survey units with right whale sightings to satisfy these conditions. We observed only 29 units with right whales present. To investigate the effect of this low number of events, the models of the form in equation 3.3 were refitted without accounting for regional or interannual variability in sighting probabilities. These parsimonious models were of the following form (shown for SST and excluding terms to account for sighting conditions):

$$\text{logit}(\pi) = \beta_0 + \beta_1(\text{SST regional/annual anomaly}) \tag{3.5}$$

The resulting coefficients and drop-in-deviance tests from these models were compared to the corresponding models of the form in equation 3.3. Substantial

differences in these coefficients and test results would indicate overfitting is a concern.

3.3.6. Analysis of interannual variability

Logistic regression was also used to investigate the environmental factors associated with interannual variability in sighting probabilities. However, since this study consists of only 3 years of data, we strongly urge that any such associations be considered as tentative trends only. The regression analysis was confined to survey units in which interannual variability actually occurred (i.e., survey units in which no right whales were ever encountered and survey units in which right whales were encountered in every year of the study were excluded). Data from the lower Bay of Fundy for this analysis consisted of surveys in August of 1999, 2000 and 2001 only (i.e., the July 2000 survey was excluded). It is impossible to remove the spatial variability in the sighting probabilities in a similar manner as the interannual variability in sighting probabilities was removed in the analysis of spatial distribution described above. However, the restriction of this analysis to only those survey units in which interannual variability occurred reduces the confounding due to this source of variability. Spatial variability in the environmental variables was “removed” by using temporal anomalies as independent variables in the models. These anomalies were determined by subtracting the 3 year mean of an environmental variable within a single survey unit from each of the observations in that survey unit. The resulting logistic regression model took the following form (excluding terms to account for sighting conditions):

$$\text{logit}(\pi) = \beta_0 + \beta_1(V_T) \quad (3.6)$$

where V_T denotes the temporal anomaly of an environmental variable and β_1 indicates the nature of the association between the interannual variability in sighting probabilities and the interannual variability in the environmental variable of interest. Inter-regional differences in the association between sighting probability and the environmental variables were also investigated using the following model (excluding terms to account for sighting conditions):

$$\text{logit}(\pi) = \beta_0 + \beta_1(V_T) + \beta_2(\text{BOF}) + \beta_3(\text{BOF} \times V_T) \quad (3.7)$$

A drop-in-deviance statistic was computed from a reduced model that lacked the last two terms in equation 3.7. A significant drop-in-deviance statistic suggested that the association between sighting probability and V_T was different in the lower Bay of Fundy and Roseway Basin.

3.4. RESULTS

3.4.1. Zooplankton sampling

C. finmarchicus C5 dominated the sampled zooplankton community near right whales. The proportion of *C. finmarchicus* C5 to all copepods was significantly higher in samples collected near right whales than in samples collected in the absence of right whales (333 μm mesh bongo tows only, two sample t-test after arcsine transformation, $t = -4.21$, $p = 0.0003$). No other copepod species or copepodite stage of *C. finmarchicus* exhibited a similar trend. The percent composition of *C. finmarchicus* C5 averaged 67% near right whales ($n = 12$) and ranged as high as 92% in the lower Bay of Fundy, whereas the percent composition

of *C. finmarchicus* C5 collected in the absence of right whales averaged only 26% ($n = 14$). Zooplankton sampling in the lower Bay of Fundy indicated that *C. finmarchicus* C5 average water column abundance near right whales decreased from 1145 copepods m^{-3} in 1999 ($n = 7$, $\text{SD} = 322$, 95% CI: 848 – 1443) to 457 copepods m^{-3} in 2000 ($n = 3$, $\text{SD} = 74$, 95% CI: 273 – 640) and 505 copepods m^{-3} in 2001 ($n = 6$, $\text{SD} = 186$, 95% CI: 311 – 700) (Figure 3.3). The respective 2.5 and 2.3 fold decreases in the average *C. finmarchicus* C5 abundance from 1999 to 2000 and from 1999 to 2001 in the lower Bay of Fundy were coincident with estimated 4.81 (95% CI: 1.14 – 20.3) and 6.84 (95% CI: 1.11 – 42.3) fold decreases in the odds of sighting a right whale in a lower Bay of Fundy survey unit over these same time periods. Although only two zooplankton samples were collected near right whales in Roseway Basin, the data derived from both the net samples and the OPC suggest that average water column abundance of *C. finmarchicus* C5 either near right whales or in survey units where whales were present may have increased from 1999 to 2001 (Figure 3.3). Interestingly, the OPC-derived average water column abundance of *C. finmarchicus* C5 in survey units where right whales were absent actually decreased over this same time period (Figure 3.3).

A clear spatial trend in OPC-derived *C. finmarchicus* C5 abundance is apparent in years when sample sizes were sufficient (during 2000 and 2001 in the lower Bay of Fundy and during 2001 in Roseway Basin). As sampling moves closer to the location of a right whale (i.e., from survey units with right whales absent to survey units with right whales present and finally to within a few hundred meters of a right whale), *C. finmarchicus* C5 abundance increases dramatically (Figure 3.3). OPC casts conducted along the track of right whales that were tagged with time-depth recorders (Baumgartner and Mate, Chapter 2) indicate that average water column abundance of *C. finmarchicus* C5 is roughly an order of magnitude higher in proximity to a right whale when compared to areas where right whales are

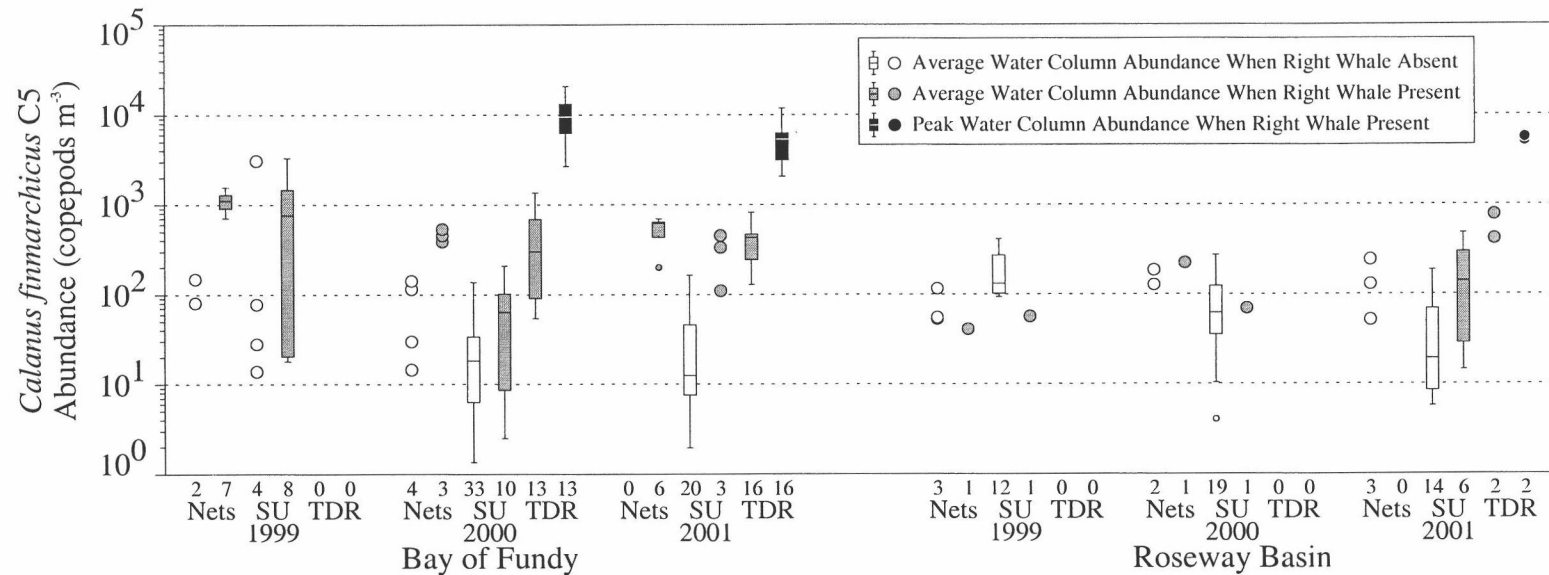


Figure 3.3. Distribution of *Calanus finmarchicus* C5 abundance derived from zooplankton samples (Nets), OPC casts conducted in the middle of each survey unit (SU) and OPC casts conducted in proximity to whales tagged with time-depth recorders (TDR) for each region and year. Average water column abundances in areas or survey units where right whales were absent (open) or present (gray) are indicated as either boxplots (for $n > 4$) or large circles (for $n \leq 4$). The peak water column abundance observed near tagged right whales is indicated as either black histograms or filled black circles. Sample sizes for each distribution are shown just below the lower ordinate axis. Sample sizes for abundances associated with tagged whales indicate the number of tagged whales for which a single, average *C. finmarchicus* C5 abundance was computed. Data for tagged whales are from Baumgartner and Mate (Chapter 2).

absent. Baumgartner and Mate (Chapter 2) found strong evidence to suggest that right whales feed at the depth of maximum *C. finmarchicus* C5 water column abundance. The abundance at this depth is at least an order of magnitude higher still than the average water column abundance of *C. finmarchicus* C5 observed in proximity to a right whale. The net-derived abundances of *C. finmarchicus* C5 obtained near right whales in the lower Bay of Fundy during 2000 and 2001 corroborate the corresponding, but independent OPC-derived average water column abundances obtained near tagged whales (Figure 3.3).

3.4.2. Sighting conditions

There was no evidence to suggest that the probability of sighting one or more right whales in a survey unit was associated with either visibility ($D = 1.91$, $df = 1$, $p = 0.17$) or glare fraction ($D = 0.293$, $df = 1$, $p = 0.59$). The potential impacts of both of these factors were largely controlled in the field by halting surveys when visibility was reduced to below 3.7 km (2 nmi) and by running survey transects in a direction opposite the sun when possible (i.e., to the west in the morning and to the east in the afternoon). There was, however, evidence to suggest an effect of sea state on the probability of sighting ($D = 6.166$, $df = 1$, $p = 0.013$) and the resulting logistic regression model indicated that the odds of sighting a right whale changed by a factor of 0.628 (95% CI: 0.428 – 0.921) for every unit increase in Beaufort sea state. Due to the significance of this effect, sea state was included in all subsequent logistic regression models.

3.4.3. Regional trends in sighting probabilities

Relative abundance and point estimates of sighting probability declined in the lower Bay of Fundy from 1999 to 2001 while relative abundance in Roseway Basin increased over these same 3 years (Table 3.2). The odds of sighting a right whale decreased significantly from 1999 to 2000 in the lower Bay of Fundy (Wald-based z test, $p = 0.033$), but there was no evidence of a change from 2000 to 2001 ($p = 0.64$). There was no evidence of a change in the odds of sighting a right whale from 1999 to 2000 in Roseway Basin ($p = 0.31$), however these odds increased significantly from 2000 to 2001 ($p = 0.037$). There was no evidence that the odds of sighting a right whale were different in the lower Bay of Fundy and Roseway Basin in 1999 (Wald-based z test, $p = 0.093$) or 2001 ($p = 0.54$), although the sample size in 1999 was small (Table 3.2). The odds of sighting a right whale in the Bay of Fundy were 9.44 (95% CI: 1.05 – 84.9) times higher than in Roseway Basin in 2000 ($p = 0.045$). These results support the use of dummy variables in the subsequent spatial models to account for interannual and inter-regional differences in sighting probabilities.

3.4.4. Spatial variability

There was strong evidence that within-region and within-year spatial variability in sighting probability was associated with spatial variability in depth, the depth of maximum *C. finmarchicus* C5 abundance, BML density, BML salinity, maximum water column *C. finmarchicus* C5 abundance, average water column abundance of *C. finmarchicus* C5, BML depth and the *C. finmarchicus* C5 abundance above the BML (Table 3.3). The most significant association detected was between sighting probability and depth ($D = 19.54$, $df = 1$, $p < 0.00005$). All of

Table 3.2. Location and dates of surveys. Average sea state during each survey is reported on the Beaufort scale and relative abundance is reported as the number of right whales sighted per 10 km of transect searched. The probability of sighting at least one right whale in a survey unit and the corresponding 95% confidence interval (CI) were estimated after accounting for the effect of sea state. Note that the Bay of Fundy survey transects were searched twice during 2000.

Year	Dates	Average Sea State	No. Units Sampled	No. Units with Whales Present	Probability of Sighting ¹	Wald's 95% CI ¹	Relative Abundance
<i>Bay of Fundy</i>							
1999	19 Aug	2.2	12	8	0.58	0.28 – 0.83	5.2
2000	20-22 Jul, 20-23 Aug	3.0	43	10	0.22	0.12 – 0.37	1.9
2001	9-27 Aug	3.9	23	3	0.17	0.05 – 0.42	0.5
<i>Roseway Basin</i>							
1999	30-31 Aug	4.4	13	1	0.13	0.02 – 0.57	0.1
2000	23-26 Jul	2.0	20	1	0.03	0.00 – 0.20	0.5
2001	24-26 Jul	2.6	20	6	0.25	0.11 – 0.49	1.0

¹ Estimated from logistic regression models with a reference level corresponding to the region and year of interest and a 3.0 Beaufort sea state [e.g., the log-odds of the sighting probability for Roseway Basin in 2000 at a Beaufort sea state of 3.0 was estimated to be β_0 in the following model: $\text{logit}(\pi) = \beta_0 + \beta_1(\text{Sea state} - 3.0) + \beta_2(\text{BOF}) + \beta_3(\text{Y1999}) + \beta_4(\text{Y2001}) + \beta_5(\text{BOF} \times \text{Y1999}) + \beta_6(\text{BOF} \times \text{Y2001})$].

Table 3.3. Test results for each environmental variable in the logistic regression analysis of spatial variability. Drop-in-deviance statistics (D), associated p-values (p) and the model coefficients (Coeff) are reported for models with and without an interaction term to account for inter-regional differences in the association between sighting probability and the environmental variable. Environmental variables were included in the models as anomalies from regional/annual means. Correlation coefficients reported for comparisons between regional/annual anomalies of depth and all other environmental variables. Abundances refer to those of *C.*

finmarchicus C5. All drop-in-deviance statistics have one degree of freedom.

$p = 0.0000$ indicates $p < 0.00005$ and $p = 1.00$ indicates $p \geq 0.995$. Significance denoted by asterisks: 1, 2 and 3 asterisks indicate $0.05 > p \geq 0.01$, $0.01 > p \geq 0.001$ and $p < 0.001$, respectively.

Table 3.3.

Variable	Correlation with Depth	Single variable model ¹			Model allowing inter-regional difference ²			
		D	p	Coeff	D	p	Bay of Fundy Coeff	Roseway Basin Coeff
Depth	—	19.54***	0.0000	0.0351	0.03	0.86		
Depth gradient	-0.280**	0.50	0.48	-0.0452	0.20	0.65		
Surface stratification (density)	-0.072	0.39	0.53	-0.396	0.22	0.64		
Surface stratification (temperature)	0.060	0.01	0.93	-0.0137	0.00	1.00		
BML temperature	-0.222*	1.59	0.21	-0.592	9.55**	0.0020	-4.00*	0.329
BML salinity	0.761***	12.99***	0.0003	3.57	0.37	0.54		
BML density	0.783***	14.96***	0.0001	4.71	0.01	0.93		
BML depth	0.868***	7.26**	0.0070	0.0219	0.01	0.94		
Depth of maximum abundance	0.749***	15.54***	0.0001	0.0340	2.00	0.16		
Maximum abundance	0.537***	11.58***	0.0007	1.65	1.37	0.24		
Average water column abundance	0.412***	8.01**	0.0047	1.21	0.00	0.97		
Abundance above BML	0.388***	3.97*	0.046	0.625	0.05	0.82		
SST	0.055	0.01	0.94	-0.0309	0.37	0.54		
SST gradient	-0.057	0.93	0.34	4.47	5.43*	0.020	-7.24	16.4*
Surface chlorophyll	-0.138	2.22	0.14	-0.660	3.66	0.056		
Surface chlorophyll gradient	-0.113	1.61	0.20	-4.34	7.19**	0.0073	-6.16	56.3*

¹ Model (equation 3.3): $\text{logit}(\pi) = \beta_0 + \beta_1(\text{Sea state}) + \beta_2(\text{BOF}) + \beta_3(\text{Y2000}) + \beta_4(\text{Y2001}) + \beta_5(\text{BOF} \times \text{Y2000}) + \beta_6(\text{BOF} \times \text{Y2001}) + \beta_7(\text{Variable})$. Drop-in-deviance test (D, p) and estimated coefficient (Coeff) reported for the term involving β_7 .

² Model (equation 3.4): $\text{logit}(\pi) = \beta_0 + \beta_1(\text{Sea state}) + \beta_2(\text{BOF}) + \beta_3(\text{Y2000}) + \beta_4(\text{Y2001}) + \beta_5(\text{BOF} \times \text{Y2000}) + \beta_6(\text{BOF} \times \text{Y2001}) + \beta_7(\text{Variable}) + \beta_8(\text{BOF} \times \text{Variable})$. Drop-in-deviance test (D, p) reported for the term involving β_8 . Estimated coefficients (Coeff) are $(\beta_7 + \beta_8)$ and β_7 for the lower Bay of Fundy and Roseway Basin, respectively. Only coefficients for models with a significant interaction term are shown. The Wald-based significance of these coefficients is indicated with asterisks.

the other variables with which sighting probability was significantly associated were correlated with depth (Table 3.3). There was also evidence of inter-regional differences in the association between sighting probability and BML temperature, SST gradient and surface chlorophyll gradient. Wald-based z tests suggest right whale sighting probability decreased significantly with increasing BML temperature in the lower Bay of Fundy, however this variable was also correlated with depth in this region ($r = -0.549$, $p < 0.0001$). The model that included depth as an independent variable (without a regional interaction term) indicated that the odds of sighting a right whale increased by a factor of 1.42 (95% CI: 1.19 – 1.69) for every 10 m increase in water depth. Because of the apparent importance of water depth, a second group of models was generated with depth as an additional independent variable (Table 3.4). Of the variables included in these models, only BML depth was found to be significant ($D = 5.61$, $df = 1$, $p = 0.018$). The resulting model (Table 3.5) indicated that the odds of sighting a right whale increased by a factor of 1.51 (95% CI: 1.06 – 2.14) for every 10 m decrease in the BML depth after accounting for the effect of water depth.

To verify that no other combination of variables produced a more significant model than the one reported in Table 3.5, models were constructed with sea state, dummy variables for region and year (with interactions) and all possible combinations of one or two environmental variables ($n = 136$ models). A reduced model with only sea state and dummy variables for region and year (with interactions) was used to generate drop-in-deviance statistics. The models with depth alone and both depth and BML depth were ranked well above all other models when ordered by the significance of the drop-in-deviance test. Parsimonious versions of the models shown in Tables 3.3 and 3.4 were fitted with only sea state and one or two of the environmental variables to investigate the potential effect of overfitting (see equation 3.5). The coefficients and drop-in-deviance test results from these models were nearly identical to those shown in

Table 3.4. Test results for each environmental variable in the logistic regression analysis of spatial variability after accounting for the influence of depth on sighting probabilities. Notation is the same as in Table 3.3.

Variable	Model including Depth ¹		
	D	p	Coeff
Depth	—	—	—
Depth gradient	0.01	0.92	0.00867
Surface stratification (density)	0.01	0.94	-0.0575
Surface stratification (temperature)	0.00	0.97	0.00750
BML temperature	0.07	0.79	-0.162
BML salinity	0.01	0.91	0.184
BML density	0.08	0.77	0.654
BML depth	5.61*	0.018	-0.0413
Depth of maximum abundance	1.21	0.27	0.0144
Maximum abundance	1.93	0.16	0.847
Average water column abundance	0.99	0.32	0.501
Abundance above BML	0.18	0.67	0.153
SST	0.01	0.92	-0.0402
SST gradient	2.10	0.15	8.01
Surface chlorophyll	1.17	0.28	-0.518
Surface chlorophyll gradient	0.83	0.36	-3.51

¹ Model: $\text{logit}(\pi) = \beta_0 + \beta_1(\text{Sea state}) + \beta_2(\text{BOF}) + \beta_3(\text{Y2000}) + \beta_4(\text{Y2001}) + \beta_5(\text{BOF} \times \text{Y2000}) + \beta_6(\text{BOF} \times \text{Y2001}) + \beta_7(\text{Depth}) + \beta_8(\text{Variable})$. Drop-in-deviance test (D, p) and estimated coefficient (Coeff) reported for the term involving β_8 .

Tables 3.3 and 3.4. We are therefore confident that overfitting is not a concern for the results of the analysis of spatial variability in right whale occurrence.

3.4.5. Interannual variability

There was evidence that the sighting probability in survey units in which interannual variability occurred was associated with interannual variability in

Table 3.5. Logistic regression model of spatial variability with depth and BML depth anomalies (n = 131 survey units, 29 units with right whales present). Residual deviance = 90.39 (df = 122), null deviance = 138.50 (df = 130) and overall drop-in-deviance = 48.11 (df = 8, $p < 0.00005$).

Term	Coefficient	Std. Error	Wald z statistic	p	Drop in Deviance	df	p
Intercept	1.14	1.75	0.65	0.51			
Sea state	-0.871	0.330	-2.64**	0.0083	8.15**	1	0.0043
Region ¹					10.24*	3	0.017
BOF	1.70	1.46	1.17	0.24			
Year ¹					15.42**	4	0.0039
Y2000	-2.80	1.75	-1.60	0.11			
Y2001	-0.00422	1.36	0.00	1.00			
Region × Year					6.52*	2	0.038
BOF × Y2000	0.808	2.03	0.40	0.69			
BOF × Y2001	-2.53	1.89	-1.33	0.18			
Depth	0.0708	0.0193	3.67***	0.0002	17.88***	1	0.0000
BML depth	-0.0413	0.0179	-2.31*	0.021	5.61*	1	0.018

¹ Reduced models for Region and Year drop-in-deviance tests lack both main effects and interaction terms.

surface density stratification and SST (Table 3.6). The logistic regression model for SST (Table 3.7) indicated that the odds of sighting a right whale in a survey unit increased by a factor of 3.19 (95% CI: 1.12 – 9.07) for every 1°C annual decrease in SST within that survey unit. Moreover, a value of 0.918 for this model's area under the receiver operating characteristic (ROC) curve indicated that SST discriminated very well between right whale presence and absence (an area under the ROC curve of 0.9 or greater is considered outstanding discrimination; Hosmer and Lemeshow, 2000). Surface density stratification was included as an additional term in the model shown in Table 3.7, but the drop-in-deviance test for this new term was not significant ($D = 0.078$, $df = 1$, $p = 0.78$). There was no evidence, therefore, of an association between sighting probability and surface density stratification after accounting for SST. The models including regional interaction terms (equation 3.7)

Table 3.6. Test results for each environmental variable in the logistic regression analysis of interannual variability. Drop-in-deviance statistics (D), associated pvalues (p) and the model coefficients (Coeff) are reported for models with and without an interaction term to account for inter-regional differences in the association between sighting probability and the environmental variable. Environmental variables were included in the models as anomalies from within-survey-unit, 3 year means. Depth and depth gradient were excluded from this analysis since there is no interannual variability in these variables. Notation is the same as in Table 3.3.

Table 3.6.

Variable	Single variable model ¹			Model allowing inter-regional difference ²			
	D	p	Coeff	D	p	Bay of Fundy Coeff	Roseway Basin Coeff
Surface stratification (density)	5.53*	0.019	-4.33	1.33	0.51		
Surface stratification (temperature)	1.64	0.20	-0.630	3.69	0.16		
BML temperature	3.67	0.055	-1.02	4.03	0.13		
BML salinity	3.48	0.062	-5.67	6.46*	0.039	1.16	-13.3*
BML density	0.03	0.86	-1.27	4.29	0.12		
BML depth	0.31	0.58	0.0285	1.49	0.47		
Depth of maximum abundance	0.02	0.89	0.00302	0.48	0.79		
Maximum abundance	1.75	0.19	1.17	4.36	0.11		
Average water column abundance	2.05	0.15	1.06	2.45	0.29		
Abundance above BML	1.49	0.22	0.860	3.56	0.17		
SST	7.07**	0.0079	-1.16	3.29	0.19		
SST gradient	1.03	0.31	6.70	8.20*	0.017	-8.48	50.0
Surface chlorophyll	1.58	0.21	-0.866	4.82	0.090		
Surface chlorophyll gradient	1.68	0.20	-8.49	1.07	0.59		

¹ Model (equation 3.6): $\text{logit}(\pi) = \beta_0 + \beta_1(\text{Sea state}) + \beta_2(\text{Variable})$. Drop-in-deviance test (D, p) and estimated coefficient (Coeff) reported for the term involving β_2 . Drop-in-deviance statistics have one degree of freedom.

² Model (equation 3.7): $\text{logit}(\pi) = \beta_0 + \beta_1(\text{Sea state}) + \beta_2(\text{Variable}) + \beta_3(\text{BOF}) + \beta_4(\text{BOF} \times \text{Variable})$. Drop-in-deviance test (D, p) reported for terms involving β_3 and β_4 . Drop-in-deviance statistics have two degrees of freedom. Estimated coefficients (Coeff) are $(\beta_2 + \beta_4)$ and β_2 for the lower Bay of Fundy and Roseway Basin, respectively. Only coefficients for models with a significant drop-in-deviance statistic are shown. The Wald-based significance of these coefficients is indicated with asterisks.

Table 3.7. Logistic regression model of interannual variability with SST anomaly ($n = 27$ survey units, 10 units with right whales present). Residual deviance = 18.33 ($df = 24$), null deviance = 35.59 ($df = 26$) and overall drop-in-deviance = 17.26 ($df = 2$, $p = 0.0002$).

Term	Coefficient	Std. Error	Wald z statistic	p	Drop in Deviance	df	p
Intercept	1.68	1.30	1.29	0.20			
Sea state	-0.928	0.508	-1.83	0.068	4.66*	1	0.031
SST	-1.16	0.533	-2.18*	0.030	7.07**	1	0.0079

provided evidence of an inter-regional difference in the association of sighting probability with annual variation in BML salinity and SST gradient (Table 3.6). The odds of sighting a right whale in a survey unit in Roseway Basin increased significantly (Wald-based z test, $p = 0.021$) by a factor of 3.78 (95% CI: 1.22 – 11.68) for every 0.1 PSU annual decrease in BML salinity within that survey unit, however there was no evidence to suggest that the odds of sighting a right whale in a lower Bay of Fundy survey unit changed with annual variation in BML salinity ($p = 0.81$). There was only suggestive, but inconclusive evidence of an association between the probability of sighting a right whale in a Roseway Basin survey unit and annual variation in SST gradient (Wald-based z test, $p = 0.068$) and no evidence of a similar association in the lower Bay of Fundy ($p = 0.56$).

3.5. DISCUSSION

Our zooplankton and OPC sampling results strongly indicate that right whales feed on *C. finmarchicus* C5 in the lower Bay of Fundy and Roseway Basin. Younger stages of *C. finmarchicus* caught by the bongo nets (C3 and C4) did not exhibit similar trends in dominance or abundance as did *C. finmarchicus* C5 near

right whales. Adult *C. finmarchicus* were significantly more abundant near right whales than in areas where right whales were absent, but average *C. finmarchicus* C5 abundance was 20 times greater than that of adults near right whales. The depth stratified samples, collected with the MOCNESS in the lower Bay of Fundy during 2001, confirm the existence of deep layers of *C. finmarchicus* C5 observed by Murison and Gaskin (1989) and Baumgartner and Mate (Chapter 2). Because of their deep distribution and stage composition, these layers are likely composed of animals in diapause. A study of *C. finmarchicus* diel vertical migration in the lower Bay of Fundy during 2001 showed that these layers remain at depth throughout the day and night (M.F. Baumgartner, unpublished data). Although the sample size is low, data presented by Baumgartner and Mate (Chapter 2) suggest that similar discrete aggregations of diapausing *C. finmarchicus* C5 also occurred in Roseway Basin during 2001 (see Figure 2.4c).

It is interesting, then, that the *C. finmarchicus* C5 abundance variables did not emerge as the most important factors in the analyses of either spatial or interannual variability in right whale occurrence. This is likely a consequence of the sampling methodology. The *C. finmarchicus* C5 abundance variables were derived from OPC casts conducted in the center of each survey unit. Since *C. finmarchicus* C5 average water column abundances for these casts were typically lower than those observed near tagged whales (Figure 3.3), we infer that *C. finmarchicus* C5 abundance varied on short spatial scales (i.e., copepod patch sizes were small relative to the size of a survey unit). The spatial scales of variation for the physiographic and physical oceanographic variables were expected to be significantly longer. Therefore, the *C. finmarchicus* C5 abundance measured at the station in the center of a survey unit was not always representative of the abundance near right whales in that unit, whereas the corresponding physical observations at the station were probably representative of conditions over most of the survey unit. Since a less ecologically relevant measurement of *C. finmarchicus* C5 abundance

was made during the surveys, the strength of the association between right whales and *C. finmarchicus* C5 abundance in the logistic regression analyses was obscured.

The correlation between average water column abundance of *C. finmarchicus* C5 and water depth suggests that the deepest parts of both Roseway Basin and Grand Manan Basin in the lower Bay of Fundy are sites of closed circulation that passively aggregate and retain resting stocks of *C. finmarchicus* C5. These deep regions would thus provide the best foraging grounds within each region, which would account for the higher probability of sighting right whales in deeper waters. This correlation is not as strong in Roseway Basin ($r = 0.302$, $p = 0.0278$) as it is in the lower Bay of Fundy ($r = 0.417$, $p = 0.0001$), so it is possible that other mechanisms promote aggregation in the former region (see below). Woodley and Gaskin (1996) also found evidence to indicate that right whales utilize the deeper areas of the lower Bay of Fundy and invoked a similar explanation for the accumulation of *C. finmarchicus*. The baroclinic (density-driven) component of the flow in these basins can be estimated from the hydrographic data obtained in this study, but the residual barotropic flow (generated primarily by the tides) is an important constituent of the mean currents in these regions that cannot be easily quantified with ship-based methods (Greenberg, 1983). Because of our inability to adequately measure the mean currents, it is difficult to demonstrate that gyres did indeed exist in these basins during this study. Other investigators, however, have inferred a cyclonic gyre about Grand Manan Basin both at the surface (Fish and Johnson, 1937; Hachey and Bailey, 1952 cited in Bumpus, 1960; Godin, 1968 cited in Greenberg, 1983) and at the bottom (Lauzier, 1967) with northeasterly flow along the southwestern margin of the Bay of Fundy and return southerly flow along the eastern edge of Grand Manan Island. The modeling results of Lynch et al. (1996) suggest that tidal rectification produces this cyclonic gyre. We conducted an unintended drifter experiment in Grand Manan Basin during the summer of 2000 by failing to immediately recover an

archival tag that had been attached to a right whale for a foraging ecology study (Baumgartner and Mate, Chapter 2). The tag was relocated via radio telemetry 6.5 days later and only 10.5 km away from its last known location (net speed = 1.9 cm s^{-1}). This fortunate recovery suggests that at least the surface circulation in Grand Manan Basin can retain particles over weekly time scales. The importance of the barotropic component suggests that this same capacity to retain particles in the basin may also exist at depth (Greenberg, 1983).

The probability of sighting a right whale was also higher in waters with shallow BML depths after accounting for the effect of water depth on sighting probability. One possible explanation for this result is that a shallow BML depth promotes concentration of *C. finmarchicus* above it (Figure 3.4b) whereas the vertical distribution of *C. finmarchicus* C5 is more uniform above a deep BML (Figure 3.4a). These conditions may arise particularly if *C. finmarchicus* C5 actively avoid the upper layers of the water column, perhaps due to increased illumination (and hence predation) or warmer temperatures. Our observations suggest, however, that this scenario does not occur. *C. finmarchicus* C5 abundance above the BML was *positively* correlated with BML depth ($r = 0.345$, $p = 0.0001$), which implies that *C. finmarchicus* C5 became more abundant or were more discretely concentrated as the BML depth deepened. A more plausible explanation is that foraging on similar concentrations of *C. finmarchicus* C5 at shallower depths (Figure 3.5b) rather than deeper depths (Figure 3.5a) affords a right whale more feeding time, and thus more energy can be acquired per dive for similar energy expenditure. For a constant total dive time, duration at depth can be extended by reducing transit times between the surface and the depth at which feeding occurs. This can be accomplished by increasing descent and ascent rates and by foraging at shallower depths. Baumgartner and Mate (Chapter 2) provide evidence of the former and the present study suggests the latter. Using the average dive duration (12.2 min), descent speed (1.40 m s^{-1}) and ascent speed (1.47 m s^{-1}) from

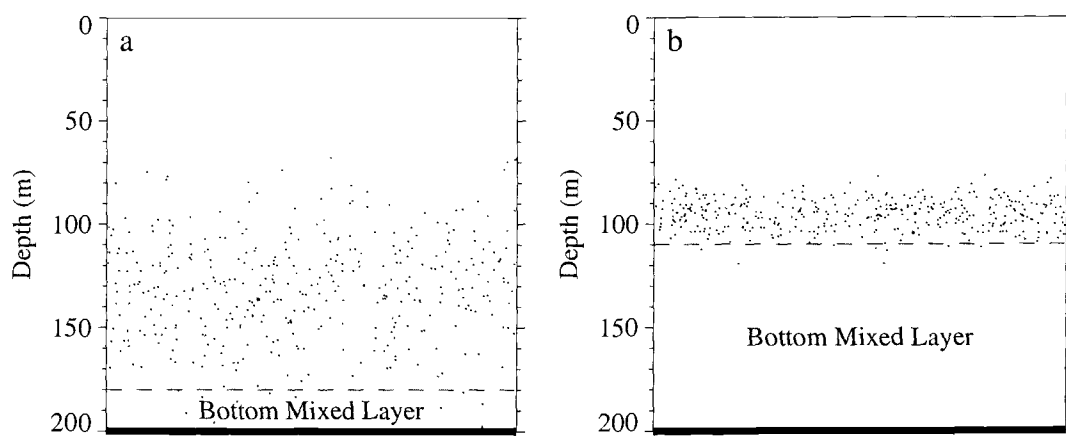


Figure 3.4. Prey availability scenario depicting (a) a deep BML depth without a discrete layer of *Calanus finmarchicus* C5 above the BML and (b) a shallow BML depth with a discrete layer above the BML. Horizontal lines indicate the sea surface (thin line), sea floor (thick line) and BML depth (dashed line). The vertical distribution of *C. finmarchicus* C5 is represented with dots.

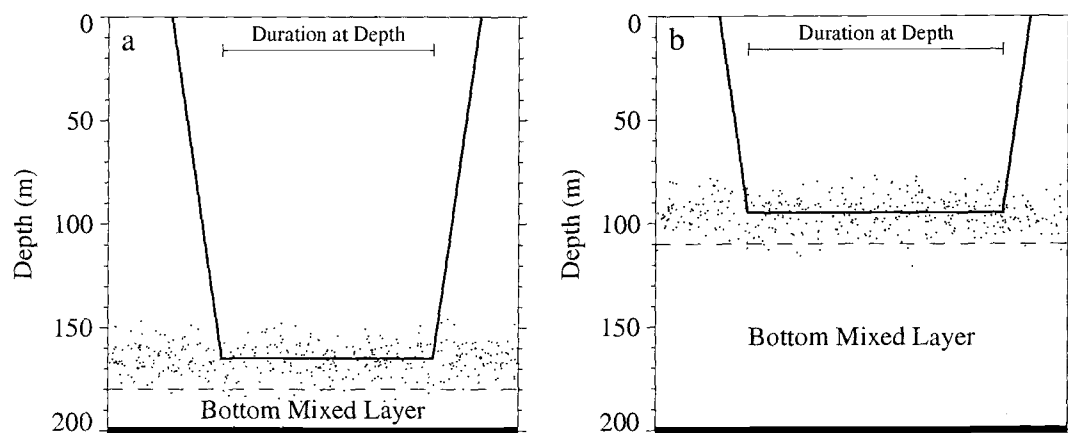


Figure 3.5. Prey availability scenario depicting (a) a deep BML depth with a discrete layer above the BML and (b) a shallow BML depth with a discrete layer above the BML. Stereotypical right whale dive profiles with a constant dive time are superimposed. The horizontal axis represents time for the dive profiles.

Baumgartner and Mate (Chapter 2) and the observed range of BML depths for waters of approximately 200 m depth in this study, we predict that right whales could extend their feeding time nearly 20% by foraging above a BML depth of 110 m (Figure 3.5b) rather than foraging above a BML depth of 180 m (Figure 3.5a).

Woodley and Gaskin (1996) reported higher surface temperatures in lower Bay of Fundy areas where right whales were present than in areas without them, but we found no evidence of this. Although Murison and Gaskin (1989) and Woodley and Gaskin (1996) state that right whales in the lower Bay of Fundy tend to frequent waters of high surface stratification, we found no evidence of this when measurements of surface stratification were made and the association was statistically tested.

Gaskin (1987) suggested that the transition zone between tidally-mixed and thermally stratified areas is a feature of right whale habitat in the lower Bay of Fundy and on the Scotian Shelf. Despite some supportive anecdotal evidence from Murison and Gaskin (1989), neither they, Woodley and Gaskin (1996) nor we found any quantitative evidence to support this hypothetical association between right whales and ocean fronts in the lower Bay of Fundy. However, we did find an association between spatial variability in right whale occurrence in Roseway Basin and the two proxies for ocean fronts: SST gradient and surface chlorophyll gradient. Furthermore, there was some indication that interannual variability in right whale occurrence in Roseway Basin might also be related to SST gradient (Table 3.6). As SST decreased in Roseway Basin from 1999 to 2001, the regional abundance of fronts increased (Figure 3.6). These changes were accompanied by an increase in the occurrence of right whales in the survey region. At the spatial scales investigated here, ocean fronts on the southwestern Scotian Shelf may serve a similar aggregative role as the closed circulation believed to be present in the lower Bay of Fundy. Both physics and animal behavior at the front may promote

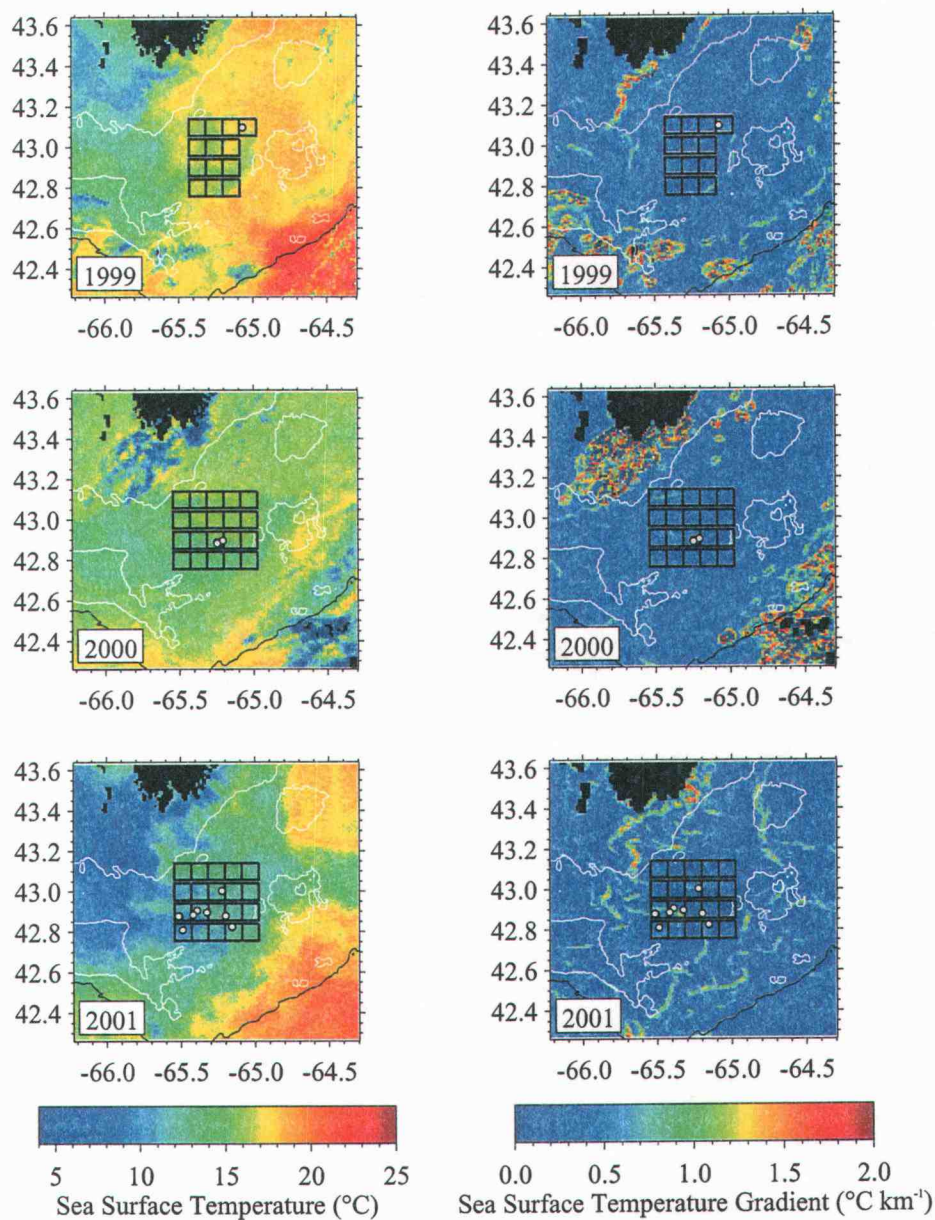


Figure 3.6. Sea surface temperature (left) and corresponding SST gradient (right) images associated with the 1999 (top), 2000 (middle) and 2001 (bottom) Roseway Basin surveys. Completed survey units are indicated with boxes and right whale sightings are shown as filled circles. Cloud contamination occurs as areas of regionally colder temperatures and unrealistically high gradients in the southern and eastern portions of the 1999 images and in the northwestern (off Cape Sable) and southeastern portions of the 2000 images. The 2001 images are cloud-free.

horizontal and vertical aggregation of *C. finmarchicus* (Olson and Backus, 1985; Epstein and Beardsley, 2001), which would provide greater prey concentrations at the comparatively small spatial scales required by filter-feeding right whales.

An association between right whales and ocean fronts was reported for the Great South Channel by Brown and Winn (1989), but surface temperature gradients near whales were low, and the whales were observed at a median distance of 11.4 km from the persistent front that occurs there in late spring. Brown and Winn (1989) demonstrated that right whales remain on the northern, stratified side of this front in a region characterized by warmer surface temperatures. These stratified conditions occur in deep water depths (> 100 m) and are associated with cyclonic currents (Chen et al. 1995) that provide closed circulation in the central Great South Channel (the "SCOPEX" gyre). The modeling results of Miller et al. (1998) suggest that late-stage *C. finmarchicus* from two separate generations accumulate in this gyre during the spring. The existence of two aggregative mechanisms in the Great South Channel, namely a persistent ocean front and closed circulation, may provide profitable foraging grounds for right whales in years of high *C. finmarchicus* productivity and survivorship.

The logistic regression analysis of interannual variability in right whale occurrence must be viewed with caution in light of the short duration of the study. Moreover, interannual variation for some environmental observations was not independent in adjacent survey units. For instance, observations of SST in all Roseway Basin survey units simultaneously decreased from 1999 to 2000 and again from 2000 to 2001 (Figure 3.6). Nonetheless, the tentative trends identified here (i.e., increasing sighting probability with decreasing SST) seem consistent with conditions that promote increased abundance of *C. finmarchicus*. Interannual (Meise-Munns et al., 1990; Conversi et al., 2001) and spatial (Meise and O'Reilly, 1996) variability in *C. finmarchicus* C5 abundance are negatively correlated with water temperature in the Gulf of Maine in the summer and fall. These relationships

likely reflect more complex variability in factors that affect *C. finmarchicus* productivity at time scales of several years, such as wind mixing, surface stratification and phytoplankton production (Fromentin and Planque, 1996; Conversi et al., 2001). Interannual and spatial variability in hydrographic conditions can potentially affect survivorship of *C. finmarchicus* as well. *C. finmarchicus* C5 are not thought to feed while in diapause (Hirche, 1983; but see Durbin et al., 1995), but instead rely on their abundant oil reserves to survive throughout the summer and fall. Warmer temperatures increase the rate at which these oil reserves are metabolized and may ultimately cause mortality when oil reserves are depleted (Sameoto and Herman, 1990).

Survival of *C. finmarchicus* C5 may also decrease in warmer temperatures due to an increase in the abundance of predatory, warm-water gelatinous zooplankton. The hydrographic conditions in Roseway Basin changed rather dramatically from warm, salty waters in 1999 ($n = 13$, average SST = 16.10°C , average BML temperature = 6.87°C , average BML salinity = 33.41 PSU) to cool, fresher waters in 2001 ($n = 20$, average SST = 11.76°C , average BML temperature = 4.64°C , average BML salinity = 33.06 PSU) (Figure 3.6). Zooplankton samples from this region in 1999 contained high abundances of gelatinous zooplankton ($n = 4$), but none of these animals were found in samples collected in 2000 ($n = 3$) and 2001 ($n = 3$). Predation by gelatinous zooplankton may have reduced *C. finmarchicus* C5 abundance in Roseway Basin, making this region unsuitable for right whales in 1999. Alternatively, an abundance of gelatinous animals may be a nuisance to filter-feeding right whales because these zooplankton can clog the whales' baleen. Mayo and Marx (1990) reported observations of right whales "flushing" their baleen in Cape Cod Bay, which probably functions to remove the viscous organic material and small particulates (including zooplankton) that are abundant in these waters during the spring. In contrast, we observed no flushing behavior in the lower Bay of Fundy, likely

because right whales prey on the rather large *C. finmarchicus* C5 at depths where the concentration of suspended organic material and small zooplankton is very low. If the vertical distributions of *C. finmarchicus* C5 and predatory gelatinous zooplankton coincide in Roseway Basin, then the baleen of feeding right whales would be subject to clogging. The consequent reduction in filtering efficiency or the increase in time required to clear the baleen of debris may make foraging in Roseway Basin unprofitable in years of high gelatinous zooplankton abundance.

Predictive modeling of right whale distribution is a management objective with important conservation implications. Provided the appropriate environmental variables are readily available for input into such a model, one would be able to predict regions where right whales are likely to occur. The present research suggests specific variables that may be useful for predicting the spatial distribution of right whale occurrence in the study areas within a particular year. These include depth and BML depth for both the lower Bay of Fundy and Roseway Basin as well as SST gradient for Roseway Basin. However, prediction within each of these survey areas is of limited use. A better system would predict right whale occurrence in other areas as well. Extrapolation of our results to other regions of the spring-summer-fall feeding grounds is unwise, however, since *C. finmarchicus* abundance is likely influenced by other factors in other regions and at other times. For instance, *C. finmarchicus* probably do not associate with a bottom mixed layer during the spring since feeding is observed in the upper portion of the water column (Watkins and Schevill, 1976; Mayo and Marx, 1990; Winn et al., 1995). Also, the importance of depth in this study is related to the aggregation of *C. finmarchicus* C5 in shelf basins, however a similar relationship would not be expected in Cape Cod Bay where right whales feed in areas less than 20 m deep (Mayo and Marx, 1990). Further quantitative examination of right whale occurrence in relation to environmental factors is needed in the other major feeding areas to provide the scientific foundation for a predictive model.

One obstacle to overcome in this endeavor is the availability of relevant environmental variables for inclusion in a predictive model. A hypothetical model for the lower Bay of Fundy and Roseway Basin might require depth, BML depth and SST gradient. Depth is available as a gridded, bathymetric dataset and SST gradient is available as a remotely-sensed product from an AVHRR archive (e.g., Cornillon et al., 1987), but BML depth cannot presently be obtained remotely. One attractive solution to this problem is to use the output from an operational ocean model (e.g., Aikman et al., 1996; Kelley et al., 1997). These regional models can provide synoptic estimates of vertically-resolved temperature, salinity and currents and forecasts with which right whale distribution may be predicted for several days in advance. While much work remains to be done, including additional right whale ecology research, habitat model development, integration with existing ocean model forecast products and rigorous validation of model predictions, a predictive model with forecast capabilities has compelling promise: improved management of human activities within ephemeral right whale habitat to reduce anthropogenic sources of mortality in this endangered population.

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4. SUMMER AND FALL HABITAT OF NORTH ATLANTIC RIGHT WHALES INFERRED FROM SATELLITE TELEMETRY

4.1. ABSTRACT

Satellite-monitored radio tags were attached to North Atlantic right whales (*Eubalaena glacialis*) in Grand Manan Basin of the lower Bay of Fundy during the summer and early fall seasons of 1989-1991 and 2000. Monte Carlo tests were used to examine the distribution of the tagged whales in space, time and with respect to a variety of environmental variables to characterize right whale habitat on the northern feeding grounds. These environmental variables included depth, depth gradient, climatological surface and bottom hydrographic properties and remotely-sensed surface temperature, chlorophyll and their respective horizontal gradients. Site fidelity in the Bay of Fundy was very low during 1989-1991 and high during 2000. When the tagged animals left the Bay, they did not frequently visit the deep basins of the Gulf of Maine and Scotian Shelf where high abundances of their primary copepod prey, *Calanus finmarchicus*, are thought to exist. Instead, right whales visited areas characterized by low bottom water temperatures, high surface salinity and high surface stratification. No evidence was found to suggest that the tagged right whales associated with ocean fronts or regions with high standing stocks of phytoplankton. These results are considered in the context of the distribution and ecology of *C. finmarchicus*.

4.2. INTRODUCTION

The North Atlantic right whale (*Eubalaena glacialis*) is one of the most highly endangered whales (Clapham et al., 1999) and recent population assessments

indicate about 300 individuals remain (IWC, 2001). Recovery of this population after centuries of whaling and subsequent international protection in the 1930's has been slow or perhaps even non-existent (IWC, 2001). The hypothesized reasons for this lack of recovery have been numerous and include inbreeding, habitat degradation, competition for food, pollution and human-caused mortality (IWC, 2001). Knowlton and Kraus (2001) reported that 9 of the 19 known right whale mortalities during 1990-1999 were linked to ship strikes and Kraus (1990) reported that 57% of photographed right whales bear scars from fishing gear entanglement. At current mortality rates, population models suggest that the North Atlantic right whale will be extinct in the next two centuries (Caswell et al., 1999). To help mitigate human-caused mortality, information about the distribution and habitat of right whales is desperately needed.

Traditional, large-scale habitat studies have combined ship- or aerial-based surveys with oceanographic observations to elucidate associations between cetaceans and the environment (e.g., CETAP, 1982; Reilly, 1990; Baumgartner et al., 2001). These studies are limited in spatial and temporal coverage by the expense of operating a research vessel for long periods of time. Radio tracking is a comparatively low-cost alternative that provides a unique, animal-based perspective that is only limited in spatial and temporal coverage by technological challenges such as attachment duration and battery life. To date, location data from satellite telemetry have been used largely in a descriptive fashion (e.g., demonstrating where animals go, when they go there and how long they stay) and have yet to be exploited profitably in a quantitative habitat study. These data, consisting only of dates and positions, seem simple, but statistical methods for exploring habitat associations with them are lacking. With the increasing availability of synoptic oceanographic information such as remotely-sensed data, climatological datasets and ocean model output, telemetry data can now be combined with a wealth of environmental data to investigate the habitat of marine animals.

We report here on a study of North Atlantic right whales tagged with satellite-monitored radio tags on their northern feeding grounds during the summer and early fall of 1989-1991 and 2000. We used Monte Carlo methods to examine the distribution of the tagged right whales in space, time and with respect to a variety of environmental variables. The environmental variables were chosen with specific hypotheses in mind. Right whales feed on older stages of the copepod *Calanus finmarchicus* in every major high use area of their feeding grounds in the northwestern Atlantic Ocean: Cape Cod Bay (Watkins and Shevill, 1976; Mayo and Marx, 1990), the Great South Channel (Wishner et al., 1988, 1995; Beardsley et al., 1996), lower Bay of Fundy (Murison and Gaskin, 1989; Woodley and Gaskin, 1996) and Roseway Basin (Stone et al., 1988). Large concentrations of *C. finmarchicus* have been observed deep in the basins of the Scotian Shelf (Sameoto and Herman, 1990) and modeling studies suggest similarly large concentrations exist below 200 m in the deep Gulf of Maine basins (Lynch et al., 1998). We examined the hypothesis (denoted H1) that the tagged right whales use these basins to exploit the *C. finmarchicus* aggregations found there. Tidal mixing fronts are frequently observed in the study area (Ullman and Cornillon, 1999) and we examined the hypothesis (H2) that the tagged right whales associate with these fronts because they provide improved feeding opportunities via the accumulation of biomass (Olson and Backus, 1985; Epstein and Beardsley, 2001). We also tested the hypothesis (H3) that the tagged right whales frequent areas with high surface chlorophyll concentrations because these conditions presumably provide feeding opportunities for their copepod prey.

Finally, we examined associations between the distribution of the tagged right whales and a variety of hydrographic properties. Baumgartner and Mate (Chapter 2) observed right whales foraging on discrete layers of *C. finmarchicus* stage 5 copepodites (C5) just above the bottom mixed layer in the lower Bay of Fundy and Roseway Basin, so we investigated associations between the tagged

whales and bottom water properties. Studies in the Great South Channel (Brown and Winn, 1989; Wishner et al., 1988, 1995; Beardsley et al., 1996) and the lower Bay of Fundy (Murison and Gaskin, 1989; Woodley and Gaskin, 1996) have observed that right whales frequent stratified waters (but see Baumgartner et al., Chapter 3), so we also examined associations between the tagged whales and surface stratification.

4.3. METHODS

Right whales were tagged with a satellite-monitored radio transmitter and tracked via the ARGOS system carried aboard the National Oceanic and Atmospheric Administration (NOAA) Polar Orbiting Environmental Satellites (POES). The tag consisted of a Telonics ST-3 (1989), ST-6 (1990-1991) or ST-15 (2000) UHF radio transmitter housed in a surface-mounted (1989-1991) or an implantable (2000) stainless steel cylinder. A salt water switch and microprocessor were used to conserve battery power by limiting transmissions to times when the tag was out of the water and when the NOAA POES were likely overhead. Further details about the tag design and deployment methods can be found in Mate et al. (1997, 1998, 1999). Right whales were also photographed and individually identified when possible (after Kraus et al., 1986).

The environmental data for this study came from either static or temporally varying gridded datasets. We constructed a digital bathymetry from a variety of sources, including U.S. National Ocean Service sounding data, 2 by 2 minute data from satellite altimetry (Smith and Sandwell, 1997) and ETOPO 5 gridded bathymetry (NGDC, 1988). Depth gradient was computed from the digital bathymetry to examine associations between right whales and sea floor topography. Horizontal gradients for depth, SST and surface chlorophyll (see below) were

computed as vector quantities by using a 3 by 3 pixel Sobel gradient operator (a weighted average of finite differences; Russ, 1995) and for brevity, the scalar gradient magnitude will be referred to as the gradient.

Remotely-sensed sea surface temperature data (SST) with a nominal resolution of 1.1 km were acquired from the University of Rhode Island's advanced very high resolution radiometer (AVHRR) archive (Cornillon et al., 1987). Reliable automated cloud masking was performed by URI on only the 1989-1991 data, so we masked SST values in the 2000 dataset that were judged extreme within a fixed temporal (10 days) and spatial (36 by 36 km) window about a pixel. Due to the crudeness of this approach, only 1989-1991 SST data are presented, however the results of our analyses were similar using SST data from all years. Raw, ocean color radiance data for 2000 were acquired from the sea-viewing wide field-of-view sensor (SeaWiFS) and processed into gridded estimates of surface chlorophyll with a nominal resolution of 1.1 km using SeaDAS software (v. 4.0). Both SST and surface chlorophyll were co-registered to a digital coastline by hand with an accuracy of approximately ± 1 pixel. Ocean fronts can often be observed from remotely-sensed data as regions of coherent horizontal variability in either SST or surface chlorophyll, so both SST and surface chlorophyll gradient were computed as proxies for the presence of ocean fronts. To investigate whether right whales visit areas historically rich in ocean fronts, a climatology of monthly front presence probabilities (Ullman and Cornillon, 1999) was also examined.

The hydrography of the Gulf of Maine and the Scotian Shelf is quite variable in space due to a variety of physical processes acting in a topographically complex region (Mountain and Jessen, 1987). These processes include tidal mixing, slope water intrusions, wintertime convective and mechanical mixing, buoyancy forcing due to local and remote (e.g., St. Lawrence River) fresh water inputs and stratification due to vernal warming. To examine associations between right whales and hydrographic features, a summertime climatology of surface

temperature, salinity and stratification (density difference in the top 50 m of the water column) and bottom temperature and salinity was utilized (Loder et al., 1997).

Randomly-generated, simulated tracks were created from the observed ARGOS data for Monte Carlo tests (described below). For each tagged animal's track, 9999 corresponding simulated tracks were generated such that the initial location (tag deployment site), the total distance traveled and the between-location distances and speeds for each simulated track were identical to that of the observed track, but the direction of travel between locations was randomly selected from a uniform distribution of angles between 0 and 360 degrees. The simulated locations were not allowed to occur on land, but straight-line paths between locations were allowed to cross small islands. The static environmental data were spatially averaged within a radius of 7.5 km around each observed and simulated location. All remotely-sensed data were first temporally averaged within ± 1 day of a location acquisition time and then spatially averaged within a radius of 7.5 km around an observed or simulated location. Spatially averaged front probabilities were computed from the monthly climatology that corresponded to the location acquisition time. If the location was beyond the domain of the gridded environmental dataset or, in the case of the remotely-sensed variables, more than 50% of the data in the spatial average were missing because of cloud contamination, the environmental datum for that location was flagged as a missing value. The spatial averaging radius was chosen as 7.5 km based on accuracy tests reported in Mate et al. (1997). They found that 68% of the poorest quality ARGOS locations (class 0) were within 7.5 km of the true transmitter location. Even if the location error is negligible, a right whale could potentially move up to 6 km at a maximum swimming speed of 18 km hr^{-1} during a NOAA POES overpass that can take up to 20 min. Therefore, the 7.5 km radius also accounts for any location uncertainty due to movement of the tagged whale during a satellite overpass.

Right whales generally remained in the lower Bay of Fundy in 2000 (see Results) and so a second simulation dataset was created to minimize confounding due to selection of this habitat. The lower Bay of Fundy is a well-known habitat for right whales, so movements outside of the Bay are of particular interest. For each tagged animal's track outside the Bay of Fundy, 9999 corresponding simulated tracks were generated. The first location in each simulated track was the last acquired location in the Bay of Fundy before the animal exited the Bay. As before, the total distance traveled outside the Bay and the between-location distances and speeds for the simulated tracks were identical to that of the observed track. Only the direction of travel between locations was randomly selected. The simulated track ended if and when the tagged animal returned to the Bay of Fundy. Separate, simulated tracks were generated each time a tagged animal left the Bay.

We used Monte Carlo tests to determine if the tagged right whales' observed distribution in space, time and with respect to each of the environmental variables could have occurred by chance (i.e., by simply moving at random). The null hypothesis in all of these tests is that the tagged right whales' distribution is random. Rejection of the null hypothesis in a two-tailed test provides evidence for either resource selection (preference) or resource rejection (avoidance) and the p-value from such a test is denoted p_2 . The p-value from a one-tailed tests for resource selection is denoted p_U and the p-value from a one-tailed tests for resource rejection is denoted p_L .

The first Monte Carlo test was conducted to determine if the tagged right whales preferred or avoided particular regions or topographic features in the study area. To accomplish this, the total number of locations occurring over a particular feature were tallied for all of the tagged right whales. For each of the 9999 simulated track sets, the total number of locations over the topographic feature were similarly tallied. The total number of locations occurring over the feature is regarded as a statistic of interest and the 10000 values for this statistic (9999 from

the simulated track sets and 1 from the observed data) make up the sampling distribution of this statistic under the null hypothesis. Consider first a one-tailed test of resource selection. The null hypothesis is rejected if less than 5% of the 10000 values in the sampling distribution are greater than or equal to the observed statistic. Rejection of the null hypothesis would suggest that the tagged right whales preferred the topographic feature in question since more locations occurred there than expected. A one-tailed p-value (p_U) can be assigned to the observed statistic as the fraction of values in the sampling distribution that are greater than or equal to the observed statistic. Similarly, the p-value in a one-tailed test of resource rejection (p_L) can be assigned to the observed statistic as the fraction of values in the sampling distribution that are less than or equal to the observed statistic. A two-tailed p-value for either resource selection or rejection (p_2) is constructed as the smaller of $2p_U$ and $2p_L$ (Manly, 1997).

In addition to the number of locations occurring over a particular topographic feature, the number of individuals was also tested in the same manner as described above. Because the Bay of Fundy is a well known high-use area, selection of this habitat was examined over time with one-tailed Monte Carlo tests of the number of locations and individuals occurring there in biweekly time intervals.

A two-dimensional frequency histogram was constructed to examine the null hypothesis of random spatial distribution. The study area was partitioned in 0.685° longitude by 0.5° latitude bins (nominally 56 km by 56 km) and separate, one-tailed Monte Carlo tests were conducted on the number of locations and individuals in each bin. Bins containing significant results represent areas that the tagged right whales visited more than expected had they moved about at random.

Monte Carlo tests were also used to examine the null hypothesis that the tagged right whales were distributed randomly with respect to the environmental variables. Separate, two-tailed Monte Carlo tests were conducted for the mean,

standard deviation, skewness and kurtosis of each environmental variable (Manly, 1997). Significant results for any of these tests was interpreted as evidence that the tagged right whales' distribution was different from an expected distribution under the null hypothesis. To further examine the relationship between the tagged whales and the environmental variables, univariate frequency histograms were constructed for each variable and separate, one-tailed Monte Carlo tests were conducted on the number of locations and individuals occurring in each histogram bin. Frequency histogram bin sizes were allowed to vary and were determined such that the average number of locations from the 10000 values in the sampling distribution for each bin was the same. Plots of collocated temperature and salinity measurements are useful for investigating water masses, so we constructed a bivariate frequency histogram for bottom salinity and bottom temperature to investigate the tagged right whales' distribution with respect to bottom water masses. The two-dimensional bin sizes were fixed at 0.25 PSU and 1°C for bottom salinity and bottom temperature, respectively. Separate, one-tailed Monte Carlo tests were conducted on the number of locations and individuals in each bin.

For the univariate and bivariate one-tailed tests of resource selection, all bins with observed counts greater than zero were considered as well as those in which 2 or more locations occurring in a bin could be found significant (i.e., where 5% or more of the values in the sampling distribution exceeded zero). Resource rejection in a one-tailed test could only be detected when less than 5% of the values in the sampling distribution (2.5% for a two-tailed test) were zero. To illustrate this constraint, consider the most extreme case of potential resource rejection when zero observed locations or individuals occur in an area. Then only 5% or less of the values in the sampling distribution can be zero in order to achieve statistical significance for the observed result in a one-tailed test (i.e., to achieve $p_L < 0.05$). In other words, an area must be *potentially* visited often, but infrequently or never visited at all in order to successfully detect resource rejection.

In the analyses described above, many Monte Carlo tests are carried out to determine the significance of an area or a single environmental variable. This multiple testing increases the likelihood of obtaining a significant result when, in fact, the null hypothesis is true (i.e., increases the probability of identifying resource selection when there is none). Since our study is exploratory with the goal of identifying potential habitat, this Type I error is far more acceptable than a Type II error (i.e., failing to identify resource selection when, in fact, it exists). Therefore, we chose not to use a multiple-testing adjustment to the selected significance level of 0.05 (e.g., Bonferroni adjustment), but we instead rely on coherent patterns in the results to judge ecological significance.

4.4. RESULTS

Thirty five right whales were tagged with satellite-monitored radio tags in Grand Manan Basin of the lower Bay of Fundy during the summer or early fall seasons of 1989-1991 and 2000 (Figure 4.1). Eighteen whales were tracked for 6 days or more (Table 4.1) and locations for these animals were acquired an average 2.1 times day⁻¹ for 20.5 days in 1989-1991 and 0.9 times day⁻¹ for 43.2 days in 2000. Location acquisition rates varied because programmed transmission rates were reduced in 2000 to conserve battery power. Only the 18 whales shown in Table 4.1 were used in the analyses. This sample size precluded an investigation of habitat differences among sex, age and reproductive classes. One of the whales (23039 in 2000, NEA ID #2320) migrated from the northern feeding grounds in mid-November to the only known wintering area off the U.S. Florida/Georgia coast. The migration portion of this whale's track was omitted from the analysis since we are concerned here only with habitat use on the northern feeding grounds. When the tagged right whales left the Bay of Fundy, they moved extensively

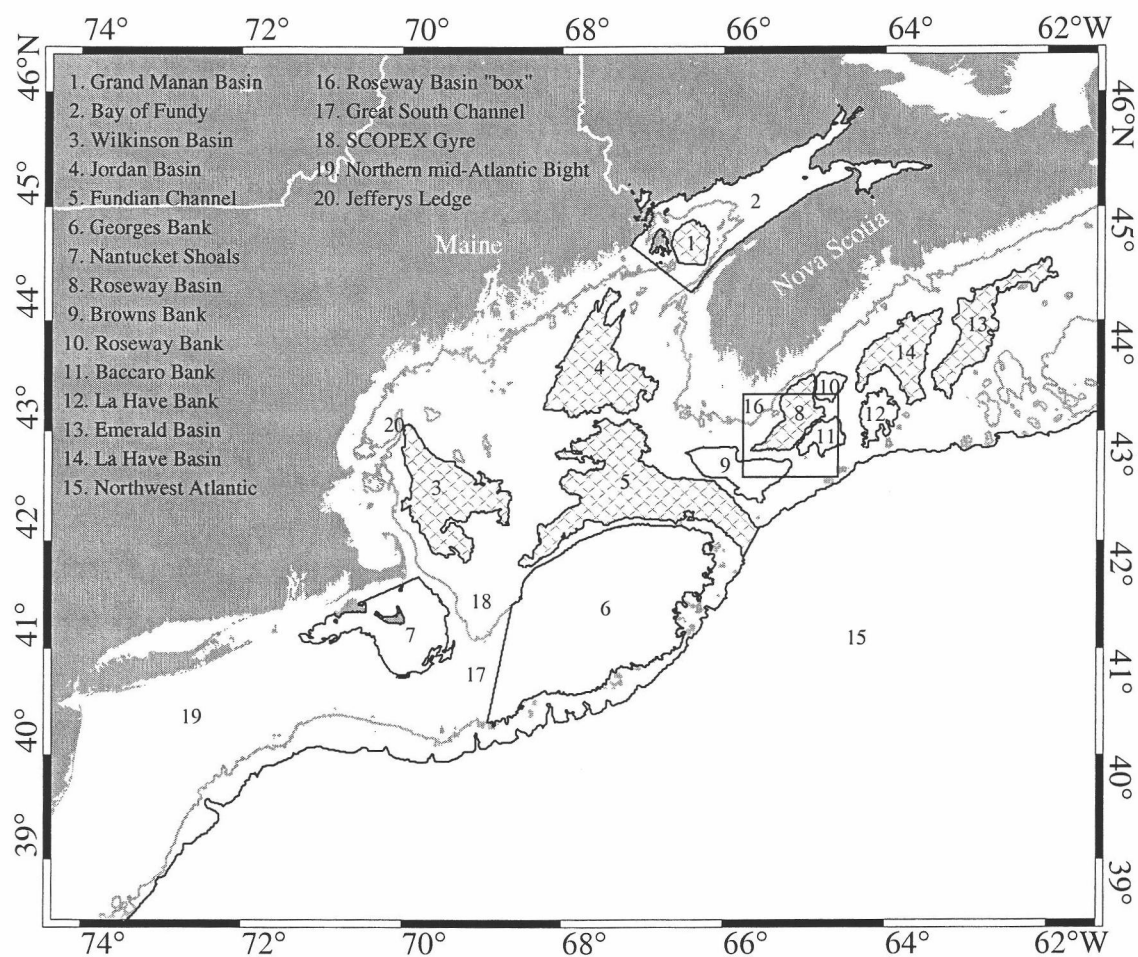


Figure 4.1. Map of the study area with location names mentioned in the text. The 91 m (50 fathom) isobath is shown in gray. Basins are crosshatched.

Table 4.1. Summary data for each tag deployment, including the New England Aquarium (NEA) right whale catalog ID, tagging date, total number of locations, percentage of locations outside the Bay of Fundy (BOF), total (minimum) distance traveled (calculated as sum of rhumb line distances between ARGOS locations) and total duration of location acquisitions. Location data are shown in Figure 4.2. Animals with a missing NEA ID were not identified.

Tag ID	NEA ID	Tagging Date	Total Locations	Locations outside BOF (%)	Total Distance (km)	Total Duration (days)	Label (Fig. 4.2)
<u>1989</u>							
843	1146	10/15/89	71	94.4	1511	21.2	A
<u>1990</u>							
840	1135	8/24/90	15	66.7	770	6.4	B
839	1140	8/24/90	108	88.0	3614	41.5	C
833	1981	8/25/90	25	0.0	367	10.6	D
825	1629	8/26/90	8	0.0	196	9.9	E
823	1421	9/12/90	137	97.8	3104	42.1	F
<u>1991</u>							
1385	1243	9/27/91	6	83.3	218	7.9	G
1386	1608	9/28/91	38	84.2	1787	23.7	H
1387	1406	10/05/91	46	87.0	1321	21.4	I
<u>2000</u>							
848		7/09/00	5	60.0	504	23.1	J
4174	2645	7/13/00	63	3.2	1400	52.9	K
23039*	2320	8/11/00	114	53.5	6006	125.8	L
10829		8/11/00	26	23.1	1547	66.0	M
1387	2617	8/12/00	4	0.0	36	18.9	N
23040	1114	8/12/00	14	35.7	708	18.9	O
824	1027	8/12/00	16	0.0	266	6.3	P
823	2310	8/12/00	24	4.2	513	23.2	Q
828		8/12/00	39	61.5	2606	52.1	R

* Non-migrating portion: total locations = 101, 47.5% of locations were outside BOF, total distance = 3718 km and total duration = 94.8 days

throughout the Gulf of Maine, western Scotian Shelf, northern mid-Atlantic Bight and on the continental slope at an average 79 km day^{-1} (Figure 4.2).

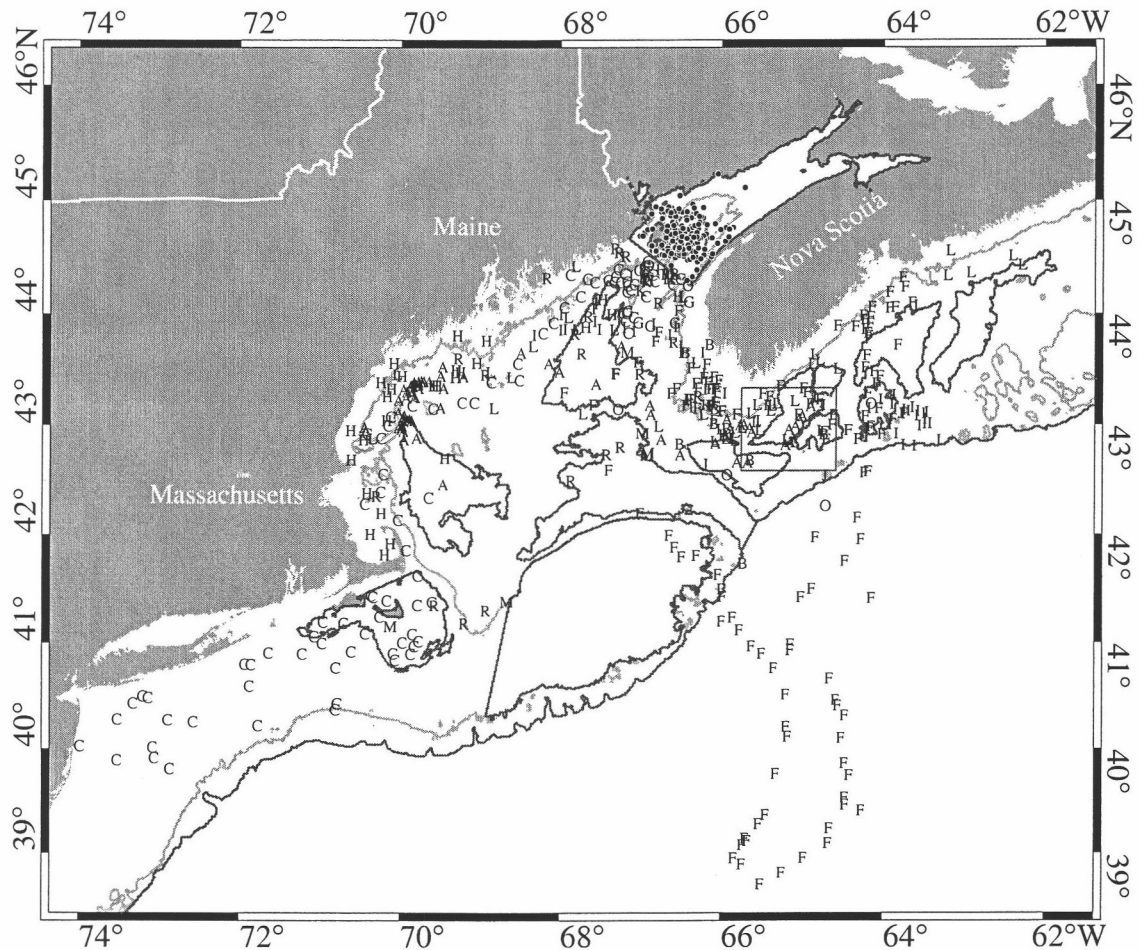


Figure 4.2. ARGOS-acquired locations for all tagged right whales. Because of the high number of locations in the Bay of Fundy, locations there are indicated as filled circles. Locations for animals outside the Bay of Fundy are lettered. Summary data for each animal are included in Table 4.1. The 91 m (50 fathom) isobath (gray) and the features from Figure 4.1 are shown.

During 1989-1991, only 16% of all acquired locations ($n = 71$ of 454, $p_2 = 0.060$) occurred in the lower Bay of Fundy (Table 4.2). In contrast, 70% of all locations ($n = 203$ of 292, $p_2 = 0.0008$) acquired in 2000 occurred in the lower Bay of Fundy (Table 4.2). To examine whether these differences were an artifact of the tag deployment times (late August through mid-October in 1989-1991 and early July through early August in 2000), we conducted one-tailed Monte Carlo tests on the biweekly occurrence of locations and individuals in the Bay of Fundy (Table 4.3). These tests demonstrate that from late August to mid October, significantly more locations and individuals occurred in the Bay of Fundy during 2000 than expected. During this same period in 1989-1991, the observed number of locations in the Bay of Fundy was consistently less than the mean of the sampling distribution. Because right whales exhibited such strong selection for the lower Bay of Fundy in 2000, the simulation dataset for track segments outside the Bay was used for all subsequent analyses.

The number of locations in the deep basins of the Gulf of Maine and Scotian Shelf for all years was quite low ($n = 37$, Table 4.3) and there was some suggestive, but inconclusive evidence that the tagged whales that moved out of the Bay of Fundy actually avoided these deep basins ($p_2 = 0.093$). The observed number of locations in the Fundian Channel ($n = 5$) and Jordan Basin ($n = 19$) were much lower than the mean of the sampling distribution (Table 4.4), albeit these results were not significant ($p_2 = 0.065$ and $p_2 = 0.21$, respectively). More of the tagged right whales visited the banks of the southwestern Scotian Shelf than expected ($n = 7$ individuals, $p_2 = 0.0012$), but only 4.5% of the locations outside the Bay of Fundy were found on these banks ($n = 22$ of 491, $p_2 = 0.073$). Interpretation of the tagged right whales' use of Roseway Basin depended on the definition of where this basin is actually located. No more locations or individuals were found in the basin area bounded by the 130 m isobath than were expected (region 8 in Figure 4.1), however significantly more locations ($n = 42$, $p_2 = 0.041$) were found

Table 4.2. Two-tailed Monte Carlo test results for the observed number (n) of locations or individuals occurring in the Bay of Fundy. The mean number of locations or individuals occurring in the Bay of Fundy from the sampling distribution is indicated by μ , and the total number of locations or individuals is indicated by n_t . Significance indicated with asterisks: 1, 2 and 3 asterisks indicate $0.05 > p \geq 0.01$, $0.01 > p \geq 0.001$ and $p < 0.001$, respectively.

Region	1989-1991				2000				All Years			
	Locations ($n_t = 454$)		Individuals ($n_t = 9$)		Locations ($n_t = 292$)		Individuals ($n_t = 9$)		Locations ($n_t = 746$)		Individuals ($n_t = 18$)	
	n	μ	n	μ	n	μ	n	μ	n	μ	n	μ
Bay of Fundy	71	147.9	9	9.0	203***	71.0	9	9.0	274	218.9	18	18.0
Inside Grand Manan Basin	47	40.9	9	8.7	126***	24.4	9	9.0	173***	65.3	18	17.7
Outside Grand Manan Basin	24**	107.0	7	7.9	77	46.7	9	6.8	101	153.6	16	14.7

Table 4.3. Results for one-tailed Monte Carlo tests of resource selection for the observed number (n) of locations or individuals occurring in the Bay of Fundy during two week intervals. The mean number of locations or individuals from the sampling distribution is indicated by μ .

Dates	1989-1991				2000			
	Locations		Individuals		Locations		Individuals	
	n	μ	n	μ	n	μ	n	μ
07/01 - 07/15					6	5.3	2	2.0
07/15 - 07/29					2	0.5	1	0.2
07/29 - 08/12					11	3.1	3	2.2
08/12 - 08/26	10	9.8	3	3.0	75*	40.4	7	6.3
08/26 - 09/09	39	60.3	4	3.9	44**	15.7	6**	3.2
09/09 - 09/23	3	25.1	1	1.7	33**	3.8	3**	0.8
09/23 - 10/07	13	23.9	4	3.5	20**	1.5	2**	0.2
10/07 - 10/21	6	19.6	2	1.9	12***	0.5	2***	0.1
10/21 - 11/04	0	8.9	0	0.7	0	0.1	0	0.0
11/04 - 11/18	0	0.2	0	0.1	0	0.0	0	0.0

in the high-use area described by Mitchell et al. (1986) as Roseway Basin (region 16 in Figure 4.1). More individuals visited this area in 1989-1991 than expected ($n = 4$, $p_2 = 0.040$) and more locations occurred here in 2000 than expected ($n = 12$, $p_2 = 0.035$). The locations in 2000 were, however, from a single animal. The area around Jefferys Ledge, bounded to the south by $42^{\circ}35'N$, to the north by $43^{\circ}20'N$, to the east by $69^{\circ}50'W$ and to the west by the coast (after Weinrich et al., 2000), had more locations ($n = 32$, $p_2 = 0.044$) and individuals ($n = 3$, $p_2 = 0.024$) than expected in 1989-1991, but there was no evidence that this area was frequented or avoided in 2000. Nantucket Shoals was visited by 3 individuals ($p_2 = 0.023$) and had more locations than expected ($n = 18$, $p_2 = 0.025$), however 16 of the 18 locations were from a single animal.

Significant concentrations of locations or individuals occurred in the western Gulf of Maine (north and west of Wilkinson Basin), on the southwestern Scotian Shelf, over Nantucket Shoals, in the northern mid-Atlantic Bight and over

Table 4.4. Two-tailed Monte Carlo test results for the observed number (n) of locations or individuals occurring in regions outside the Bay of Fundy. The mean number of locations or individuals occurring in these regions from the sampling distribution is indicated by μ and the total number of locations or individuals is indicated by n_i . Results were obtained using observed and simulated track segments outside of the Bay of Fundy.

Table 4.4.

Region	1989-1991				2000				All Years			
	Locations ($n_t = 391$)		Individuals ($n_t = 7$)		Locations ($n_t = 100$)		Individuals ($n_t = 7$)		Locations ($n_t = 491$)		Individuals ($n_t = 14$)	
	n	μ	n	μ	n	μ	n	μ	n	μ	n	μ
Deep Basins	26	56.1	5	5.4	11	15.6	3	3.7	37	71.6	8	9.1
Wilkinson Basin	9	5.3	3	1.0	0	1.7 ¹	0	0.9 ¹	9	7.0	3	1.9
Jordan Basin	13	30.3	4	4.7	6	7.4	2	2.8	19	37.8	6	7.5
Fundian Channel ²	1	19.3	1	2.9	4	6.1	2	2.3	5	25.4	3	5.2
La Have Basin	3	0.8	1	0.2	0	0.2 ¹	0	0.1 ¹	3	1.0	1	0.3
Emerald Basin	0	0.4 ¹	0	0.1 ¹	1	0.1	1	0.1	1	0.5	1	0.2
Scotian Shelf Banks	18	5.3	4*	1.4	4	1.5	3*	0.8	22	6.8	7**	2.2
Browns Bank	4	3.8	2	1.1	2	1.1	2	0.6	6	4.9	4	1.8
Roseway Bank	0	0.3 ¹	0	0.2 ¹	1	0.1	1	0.1	1	0.4	1	0.2
Baccaro Bank	6	0.7	3**	0.3	0	0.2 ¹	0	0.1 ¹	6	0.9	3*	0.4
La Have Bank	8*	0.4	2*	0.2	1	0.1	1	0.1	9*	0.6	3**	0.3
Roseway Basin ³	10	2.2	2	0.7	2	0.6	1	0.4	12	2.8	3	1.0
Roseway Basin ⁴	30	7.9	4*	1.3	12*	2.0	1	0.9	42*	10.0	5	2.2
Jefferys Ledge	32*	3.5	3*	0.6	1	1.0	1	0.5	33*	4.4	4*	1.1
Georges Bank	4	13.1 ¹	1	1.6 ¹	0	4.7 ¹	0	1.7 ¹	4	17.9	1	3.3
Nantucket Shoals	16*	1.0	1	0.2	2	0.5	2	0.3	18*	1.5	3*	0.6
Northwest Atlantic	47	20.2	3	1.9	1	10.5 ¹	1	1.9 ¹	48	30.7	4	3.8

¹ p_L could not be assessed because more than 2.5% of the values in the sampling distribution were zero (see text)

² includes Georges Basin and Northeast Channel

³ area enclosed by the 130 m isobath (region 8 of Figure 4.1)

⁴ high-use area observed in Blanford whaling records (Mitchell et al., 1986) (region 16 of Figure 4.1)

the continental slope in the Northwest Atlantic Ocean (Figure 4.3). These latter three areas, however, were predominantly occupied by only one animal each (Figure 4.2). The large number of locations between the mouth of the Bay of Fundy and Jordan Basin was not significantly higher than expected and was primarily the result of the tagged animals using this region as a corridor when leaving and returning to the Bay.

Monte Carlo tests of the mean, standard deviation, skewness and kurtosis of the environmental variables suggest that the tagged right whales' distribution with respect to surface salinity, surface stratification, bottom temperature, bottom salinity and SST gradient may be different than a random distribution (Table 4.5). The mean surface salinity ($p_2 = 0.0088$) and bottom temperature ($p_2 = 0.016$) were lower than expected while the mean surface stratification ($p_2 = 0.023$) was higher than expected. The kurtosis of bottom salinity, surface stratification and SST gradient were different than expected ($p_2 = 0.024$, $p_2 = 0.024$ and $p_2 = 0.032$, respectively). Although depth was not found to be significant for any of these statistics, the high mean depth (Table 4.5) suggests confounding by the few individuals that moved off the shelf into the very deep waters of the Northwest Atlantic Ocean (Figure 4.2, Table 4.4). When the 48 points occurring in this region were removed from the analysis, all of the observed statistics for depth became highly significant ($\theta = 123.0$, $\mu = 312.7$, $p_2 = 0.0032$ for mean; $\theta = 53.5$, $\mu = 658.0$, $p_2 = 0.0002$ for standard deviation; $\theta = -0.03$, $\mu = 5.49$, $p_2 = 0.0024$ for skewness; $\theta = -0.58$, $\mu = 40.48$, $p_2 = 0.0068$ for kurtosis).

The patterns of significant results for either locations or individuals in the univariate frequency histograms (shown as probability density functions in Figure 4.4) suggest that the tagged whales' distributions with respect to surface salinity, surface stratification, bottom temperature, bottom salinity and depth were indeed different than expected. The number of locations or individuals outside the Bay of Fundy was significantly greater than expected in waters of low surface salinity

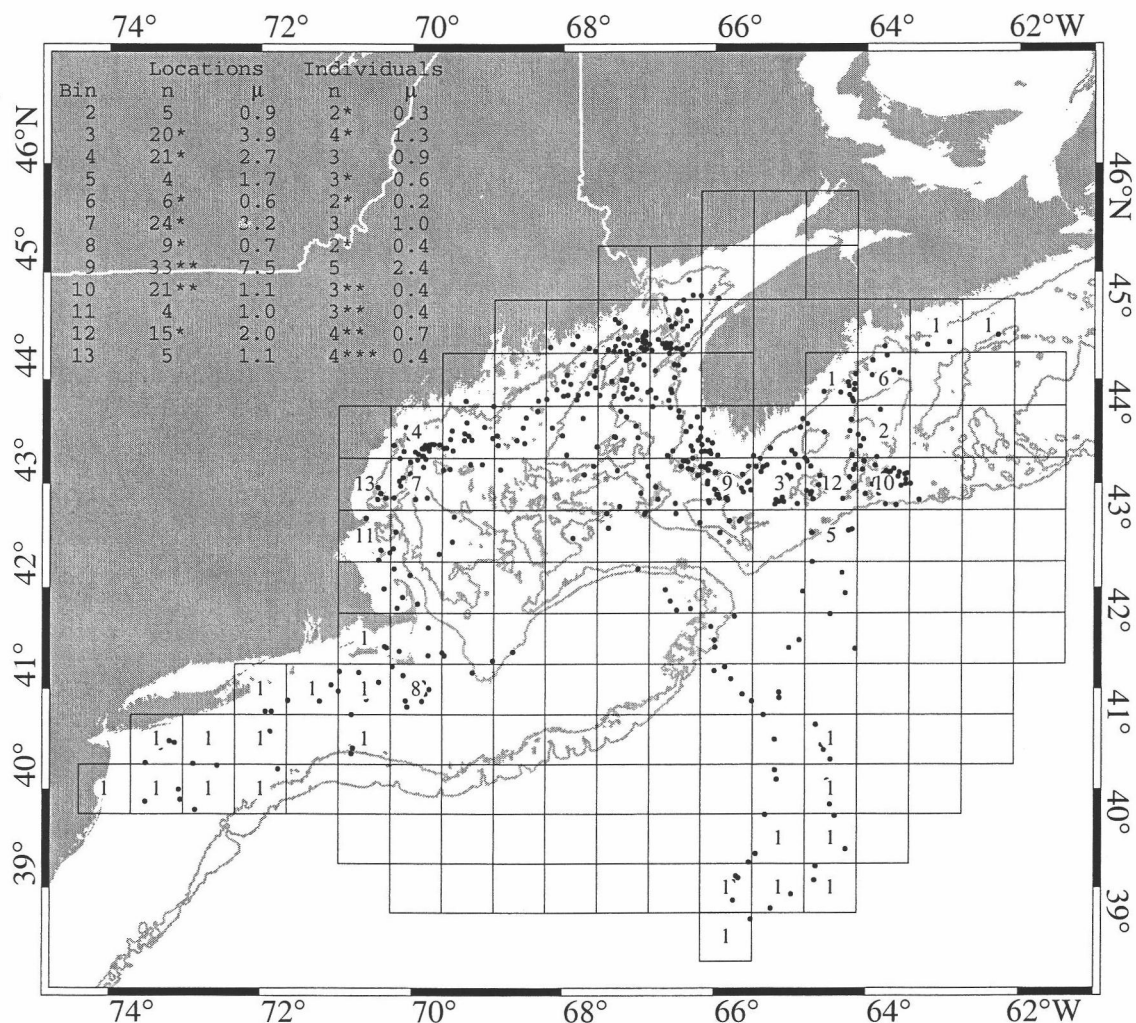


Figure 4.3. Distribution of ARGOS-acquired locations outside the Bay of Fundy (dots) and the results of one-tailed Monte Carlo tests of resource selection for the corresponding spatial frequency histogram. Boxes indicate two-dimensional bins in which each Monte Carlo test was conducted. A significant number of locations and/or individuals ($p_u < 0.05$) were found in bins labeled with numbers. The label "1" indicates only one individual occurred in the bin, but the number of locations was significantly higher than expected ($p_u < 0.05$). The observed number (n) of locations or individuals and the mean number (μ) of locations or individuals in the sampling distribution for all other labeled bins are shown in the inset table. The 91 (50 fathom) and 200 m isobaths are shown.

Table 4.5. Two-tailed Monte Carlo test results for the observed mean, standard deviation, skewness and kurtosis (θ) of each environmental variable. The mean statistic from the sampling distribution is indicated by μ . Results were obtained using only observed and simulated track segments outside the Bay of Fundy for all years.

Variable	Mean		Standard Deviation		Skewness		Kurtosis	
	θ	μ	θ	μ	θ	μ	θ	μ
Depth (m)	452.9	299.7	1099.1	632.6	3.27	5.73	9.32	44.14
Depth gradient (m km ⁻¹)	8.18	7.37	13.94	9.72	8.86	6.55	108.23	64.14
Surface temperature (°C)	14.10	13.53	2.74	2.47	0.14	0.66	-0.57	0.36
Surface salinity (PSU)	31.94**	32.18	0.54	0.41	0.29	0.41	1.20	6.54
Bottom temperature (°C)	6.93*	7.56	2.09	1.56	1.74	0.84	6.31	3.52
Bottom salinity (PSU)	33.33	33.37	0.79	0.87	0.23	0.04	-0.29*	-0.87
Surface stratification (kg m ⁻³)	1.72*	1.36	0.92	0.78	-0.01	0.28	-1.29*	-0.78
Remotely-sensed SST ¹ (°C)	14.43	13.48	3.33	2.40	0.71	0.89	-0.10	1.51
Surface chlorophyll ² (mg m ⁻³)	2.60	2.67	2.16	2.55	3.28	2.80	14.22	10.29
Front probability	0.02	0.02	0.02	0.02	1.13	1.10	1.32	1.47
SST gradient ¹ (°C km ⁻¹)	0.14	0.14	0.06	0.06	1.10	1.68	0.51*	4.59
Chlorophyll gradient ² (mg m ⁻³ km ⁻¹)	0.35	0.33	0.53	0.56	3.87	4.21	18.07	20.42

¹ 1989-1991 data only

² 2000 data only

Figure 4.4. Results of one-tailed Monte Carlo tests of resource selection for univariate frequency histograms. The frequency histograms have been converted to probability density functions to facilitate visualization because the frequency bin sizes vary. Shading with lines facing down and to the left or down and to the right indicate a significantly higher number of locations or individuals in the bin than expected ($p_U < 0.05$), respectively. A label appears above all bins for which significant results were found. The observed number (n) of locations or individuals and the mean number (μ) of locations or individuals in the sampling distribution for all significant bins are shown in the inset table. SST and SST gradient are from 1989-1991 only and surface chlorophyll and chlorophyll gradient are from 2000 only.

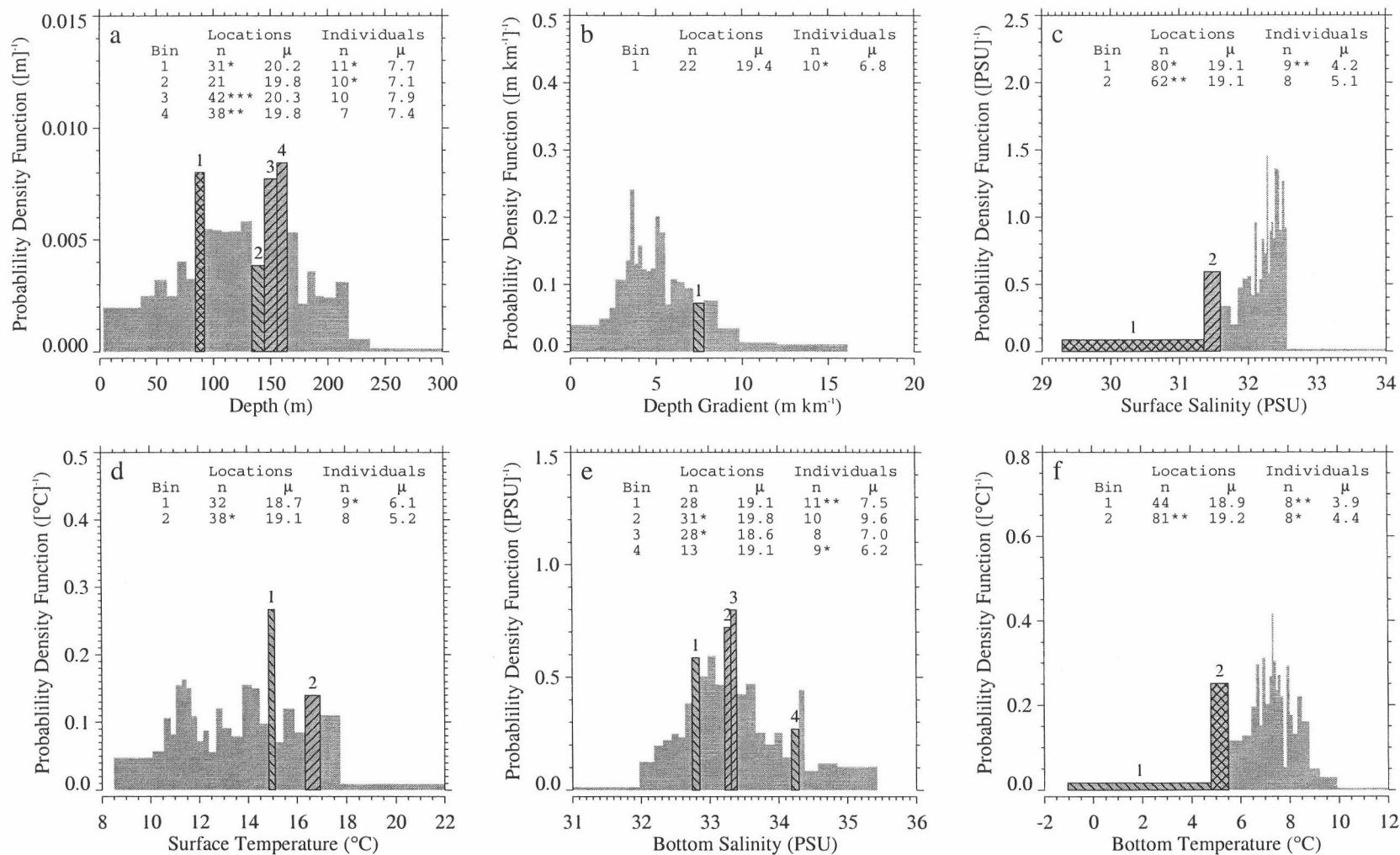


Figure 4.4.

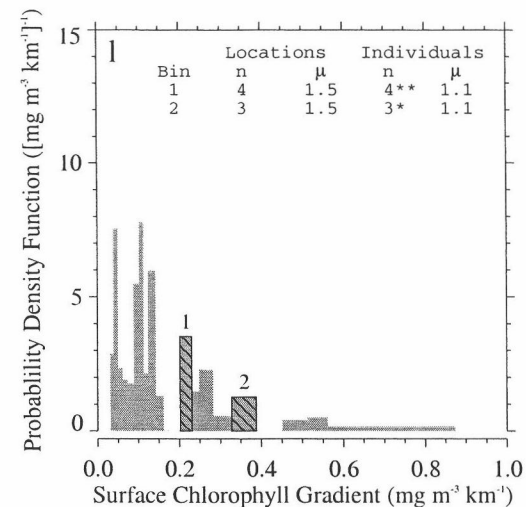
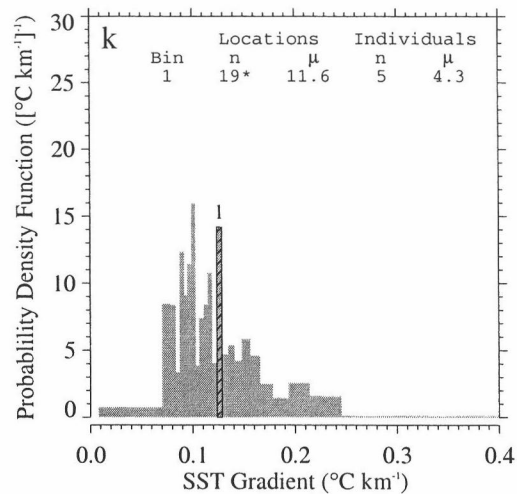
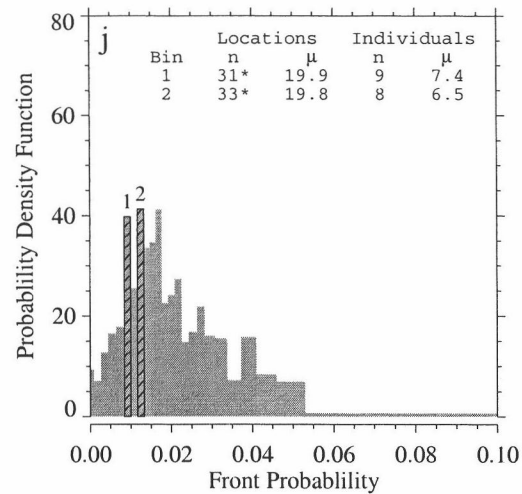
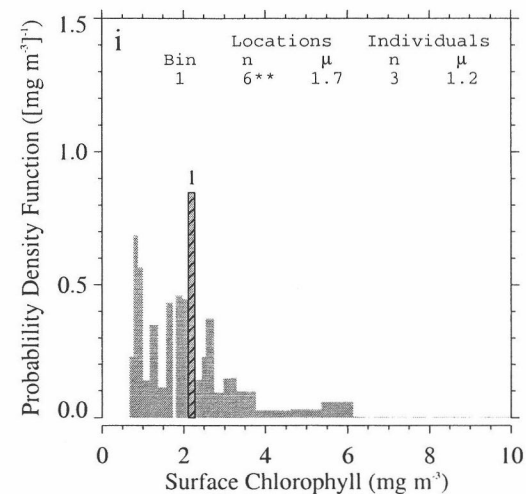
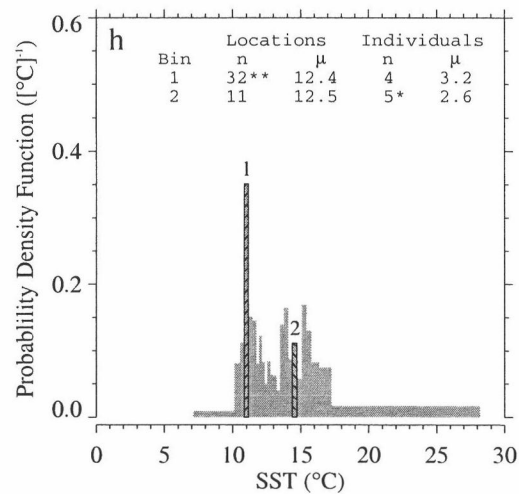
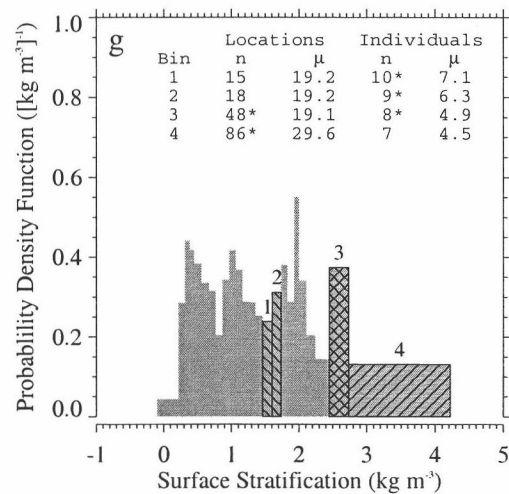


Figure 4.4. (continued)

(Figure 4.4c) and high surface stratification (Figure 4.4g). The lowest two frequency histogram bins for surface salinity contained 29% of all locations (142 of 491) whereas the highest two bins for surface stratification contained 27% of all locations (134 of 491). Since surface salinity and surface stratification are correlated in the data, it is not surprising that the same subset of locations contribute to the significance of both of these variables. Significantly more locations or individuals were found in waters with low bottom temperatures (Figure 4.4f) and the lowest two frequency histogram bins for this variable contained 25% of all locations (125 of 491). The pattern of significant results for bottom salinity is less coherent (Figure 4.4e), however it is worth noting that 37% of locations found inside the Bay of Fundy (102 of 274) fell within the range 33.21-33.39 PSU (bins 2 and 3 in Figure 4.4e). The number of locations or individuals in waters of 133–165 m depth (bins 2–4 in Figure 4.4a) was also significantly greater than expected and 24% of locations inside the Bay of Fundy (66 of 274) were found in this depth range. Finally, there was no evidence to suggest that the tagged right whales occurred more frequently at higher climatological front probabilities (Figure 4.4j), SST gradients (Figure 4.4k) or surface chlorophyll gradients (Figure 4.4l).

The results of the Monte Carlo tests for the bivariate frequency histogram of bottom temperature and bottom salinity (Figure 4.5a) suggest that particular bottom water properties were selected by the tagged right whales. Significantly more locations were found in the warmest and freshest bins, but all of these locations were from the single animal that visited Nantucket Shoals. Several of the bins found in cool and moderately fresh bottom waters had more locations and individuals than expected. In total, 30% of all locations outside the Bay of Fundy were found in bottom waters of less than 6°C and 33.75 PSU ($n = 131$, $p_U = 0.0005$) and more individuals were found in these bottom waters than expected ($n = 9$, $p_U = 0.022$). This bottom water mass was also characterized by low surface salinities, high surface stratification and depths between 75 and 175 m

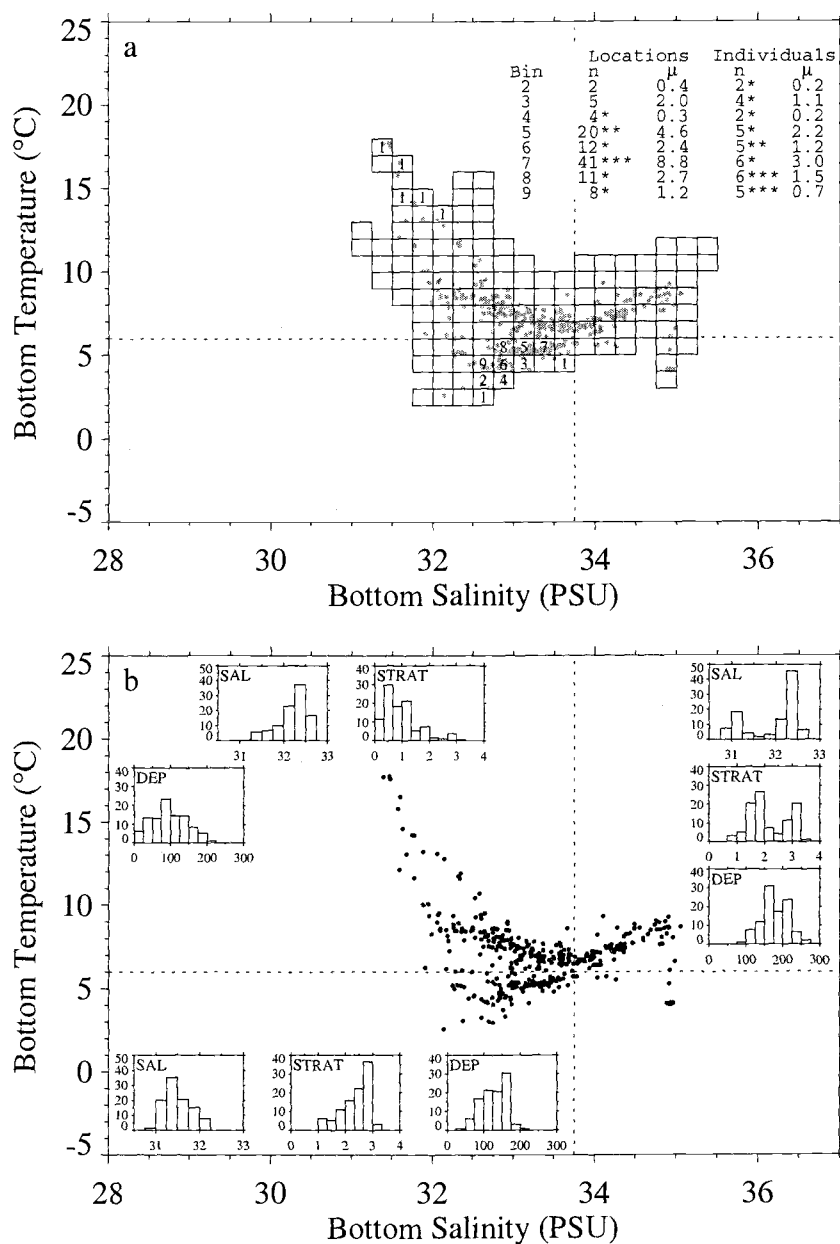


Figure 4.5. (a) Distribution of bottom salinity and temperature at ARGOS-acquired locations (gray dots) and results of one-tailed Monte Carlo tests of resource selection for the corresponding bivariate frequency histogram. Two-dimensional bins and significant results are indicated as in Figure 4.3. (b) Distribution of bottom salinity and temperature at the same locations as in (a) with percent frequency histograms of surface salinity (SAL), surface stratification (STRAT) and depth (DEP) for locations in quadrants defined by $BT < 6^{\circ}\text{C}$ and $BS < 33.75$ PSU (lower left), $BT \geq 6^{\circ}\text{C}$ and $BS < 33.75$ PSU (upper left) and $BT \geq 6^{\circ}\text{C}$ and $BS \geq 33.75$ PSU (upper right) where BS and BT are bottom salinity and bottom temperature, respectively.

(Figure 4.5b). In contrast, bottom waters greater than 6°C and less than 33.75 PSU were characterized by high surface salinities, low surface stratification and shallower depths between 25 and 150 m. The deep basins had bottom waters greater than 6°C and 33.75 PSU and were characterized by greater depths and bimodal distributions of surface salinity and surface stratification. These bimodal distributions indicate the lower surface salinities and higher surface stratification over the deep basins of the Scotian Shelf (Emerald and La Have Basins) and the high surface salinities and lower surface stratification over the deep basins of the Gulf of Maine (Wilkinson and Jordan Basins and the Fundian Channel). Bottom waters of less than 6°C and 33.75 PSU occur in the western Gulf of Maine to the north and west of Wilkinson Basin, in the SCOPEX gyre, on the southwestern Scotian Shelf and along the southern coast of Nova Scotia (Figure 4.6). The areas where the tagged right whales visited more than expected (Figure 4.3) correspond well with the spatial extent of these bottom waters.

4.5. DISCUSSION

Upon exiting the lower Bay of Fundy, the tagged right whales moved extensively about the Gulf of Maine, Scotian Shelf, northern mid-Atlantic Bight and the continental slope. Moving at an average speed of 79 km day^{-1} , right whales could circumnavigate the entire Gulf of Maine (including a visit to Roseway Basin) and return to the Bay of Fundy in only 15 days. Individual movements were highly variable (Figure 4.2) and no other area or oceanographic regime was used as much as the lower Bay of Fundy. Of the 14 tagged animals that left the Bay of Fundy, 50% returned to it before the tag stopped transmitting. Right whales have been observed during the summer and fall in some of the other areas frequently visited by the tagged animals, including the southwestern Scotian Shelf (Mitchell et al.,

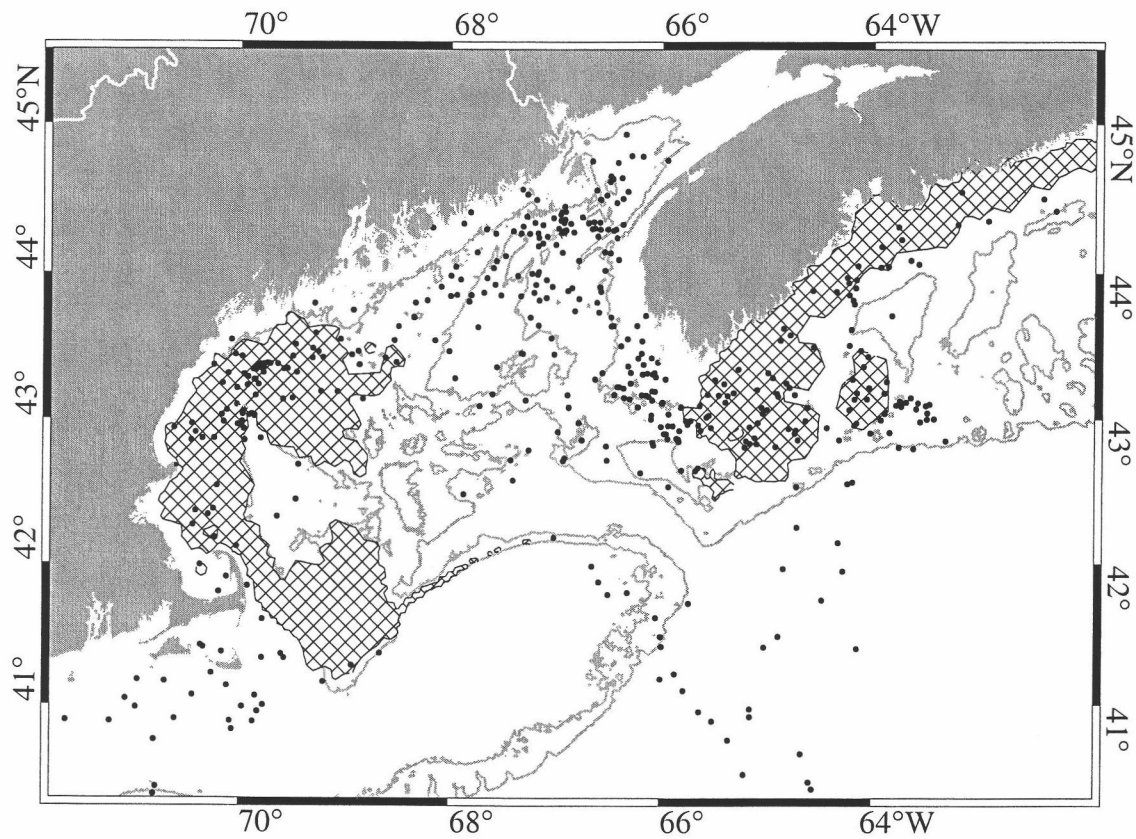


Figure 4.6. Map of areas with bottom temperature less than 6°C and bottom salinity less than 33.75 PSU (crosshatched regions). ARGOS-acquired locations outside the Bay of Fundy are shown. The 91 (50 fathom) and 200 m isobaths are also shown.

1986; Stone et al., 1988; CETAP, 1982), SCOPEX gyre (CETAP, 1982) and the western Gulf of Maine (CETAP, 1982; Payne et al., 1990; Weinrich et al., 2000).

The high site fidelity exhibited by tagged right whales in Grand Manan Basin in 2000 might suggest that food resources were abundant in that year when compared to 1989-1991. In the summer and early fall of 1989, Woodley and Gaskin (1996) reported late stage *Calanus finmarchicus* abundances of 1128 ± 637 copepods m^{-3} (mean \pm standard deviation) from 12 vertical tows near right whales in the basin. A single right whale was tagged in this same year and it left the Bay of Fundy soon after tagging and did not return during the 21 days it was tracked. In 2000, Baumgartner et al. (Chapter 3) observed late stage *C. finmarchicus* abundances of only 457 ± 74 copepods m^{-3} in Grand Manan Basin from 3 oblique bongo tows near right whales on long dives (a typical characteristic of feeding activity in this area). These low abundances were corroborated with independent, optical plankton counter (OPC; Herman, 1988, 1992) measurements (see Figure 3.3). The 2000 *C. finmarchicus* abundances represented a minimum in three years of zooplankton monitoring near right whales in Grand Manan Basin from 1999-2001 (Baumgartner et al., Chapter 3). Although extreme caution is warranted when attempting to characterize zooplankton abundance for an entire season with only a few plankton samples, the available data may tenuously suggest that right whales remain in Grand Manan Basin for reasons other than feeding. Sexual activity is common in the Bay (Kraus and Hatch, 2001), therefore it is possible that right whales remain in the Bay for breeding opportunities even when food resources are low.

There was no evidence to support the hypothesis (H1) that right whales used the deep basins of the Gulf of Maine and the Scotian Shelf. Moreover, there was suggestive, but inconclusive evidence that they actually avoided these basins. Sameoto and Herman (1990) and Herman et al. (1991) reported very high abundances of late stage *C. finmarchicus* below 200 m in the basins of the Scotian

Shelf (up to 20000 copepods m^{-3}). Meise and O'Reilly (1996) demonstrated that the 10-year average of late stage *C. finmarchicus* total water column abundance in the upper 200 m reaches a regional and annual maximum in the central Gulf of Maine in the summer and fall. Modeling results by Lynch et al. (1998) suggest that high abundances of *C. finmarchicus* exist below 200 m in the Gulf of Maine basins. In light of these studies, it is somewhat surprising that right whales do not visit these basins more often. The basins have average depths of 210-250 m, which is 40-67% deeper than the average depth in the Bay of Fundy or in Roseway Basin (150 m). It is plausible that the deepest portions of the basins are inaccessible to right whales, however we have observed right whales tagged with time-depth recorders diving to depths of 200 m in Grand Manan Basin (Baumgartner and Mate, Chapter 2). Furthermore, the satellite-monitored radio tag deployed in 1989 was equipped with a pressure sensor, and the maximum dive depth for the single whale on which it was used was between 272 and 306 m in Wilkinson Basin. Based on these observations, we think it is unlikely that right whales have diving limitations that would prevent them from exploiting *C. finmarchicus* concentrations below 200 m. Although right whales may be physiologically capable of reaching discrete layers of *C. finmarchicus* at these depths, right whales may still avoid foraging on these layers. Foraging at deeper depths affords less feeding time, and thus less energetic benefit per dive, than foraging at shallower depths (Baumgartner et al., Chapter 3).

Prey concentrations that are ecologically meaningful to right whales are difficult to measure at depth with plankton nets. The vertically-integrated tows upon which the Meise and O'Reilly (1996) climatology are based can only provide an average water column abundance of *C. finmarchicus*. This average abundance grossly underestimates the concentration of prey actually available to a right whale because the whales seek out and feed on prey that are distributed vertically in discrete layers (Baumgartner and Mate, Chapter 2). So despite the high total water

column abundances present in the Gulf of Maine basins, our results suggest that discrete, high concentrations of late-stage *C. finmarchicus* may not exist there. This is in contrast to the predictions of Lynch et al. (1998) that high concentrations of resting *C. finmarchicus* must exist below 200 m in these basins during the fall in order to explain the springtime distribution of younger stages of *C. finmarchicus*. We sampled Jordan and Wilkinson basins in the summer of 2001 with a vertically-profiled OPC and did not observe any discrete, high concentration layers of *C. finmarchicus* below 200 m (unpublished data). These layers were, however, readily observable at mid-depth near foraging right whales in Grand Manan Basin with the same instrument (Baumgartner and Mate, Chapter 2). The high concentrations observed by Sameoto and Herman (1990) and Herman et al. (1991) in the deep basins of the Scotian Shelf would certainly be attractive to right whales, but the paucity of ARGOS locations observed there suggests that these concentrations are not present every year.

There was no evidence to support the hypothesis (H2) that right whales associate with oceanic fronts or visit areas that are climatologically rich in fronts. Despite the presence of a strong tidal mixing front along the western margin of Grand Manan Basin, Murison and Gaskin (1989) and Woodley and Gaskin (1996) found that right whales occupied the central basin, well away from this front. Brown and Winn (1989) observed that right whales were nearly always on the stratified side of a persistent tidal mixing front in the Great South Channel during the spring, but were a median 11.4 km away from it. Wishner et al. (1995) found dense concentrations of *C. finmarchicus* at the leading edge of a low salinity plume during the two years of the SCOPEX study in the Great South Channel (Kenney and Wishner, 1995), but Beardsley et al. (1996) found no evidence of a physical concentrating mechanism near a right whale feeding on very large aggregations of *C. finmarchicus* during that same study. Baumgartner et al. (Chapter 3) found no evidence of an association between right whale occurrence and ocean fronts in the

lower Bay of Fundy, but they did find evidence of such an association in Roseway Basin. While it is possible that fronts may aggregate prey in particular regions, our results suggest that ocean fronts are not a common feature of right whale habitat.

There was no evidence to support the hypothesis (H3) that right whales frequent areas with high surface chlorophyll concentrations. This is not particularly surprising when considered in the context of *C. finmarchicus* life history. When *C. finmarchicus* reaches copepodite stage 5 (C5), they typically undertake an ontogenetic vertical migration to depth where they enter a resting state (termed diapause) (Hirche, 1996). *C. finmarchicus* C5 starve during diapause, relying on their considerable lipid reserves to support metabolism (although see Durbin et al., 1995). *C. finmarchicus* females spawn the year's first generation (G1) of copepods in mid- to late winter, which mature in early spring (Durbin et al., 1997, 2000). While most *C. finmarchicus* C5 enter diapause, some remain at the surface to become the progenitors of the next generation of copepods (G2). The G2 generation reaches stages 4 or 5 by late spring or early summer. Some G2 animals may remain at the surface to spawn a third generation (G3), but the bulk of the *C. finmarchicus* population can be found at depth as C5 by summer. Baumgartner and Mate (Chapter 2) observed right whales diving to and presumably feeding on deep layers of *C. finmarchicus* C5 in the lower Bay of Fundy and Roseway Basin during the summer. Moreover, diel vertical migration studies of *C. finmarchicus* in the lower Bay of Fundy at this time indicate that the animals in these layers have empty guts (R.G. Campbell, unpublished data) and do not migrate to the surface (M.F. Baumgartner, unpublished data). Since phytoplankton abundance is irrelevant to starving *C. finmarchicus* C5 in diapause during the summer and early fall, right whale distribution is accordingly unrelated to surface chlorophyll concentration.

The tagged right whales' preference for waters with low bottom temperatures suggests these conditions may improve feeding opportunities by promoting higher *C. finmarchicus* abundance or better quality food. Oceanic

populations of *C. finmarchicus* typically migrate to several hundred meters depth (Miller et al., 1991) where the ambient temperature is typically only a few degrees Celsius. Continental shelf populations, however, do not have access to such deep depths and cold temperatures. The lipid reserves upon which *C. finmarchicus* rely to survive starvation during diapause are depleted faster at higher temperatures because metabolic rates in resting stocks increase with warmer temperatures (Hirche, 1983). The colder bottom temperatures found in the areas visited by the tagged right whales, therefore, may promote higher abundances by improving *C. finmarchicus* survivorship relative to the warmer bottom waters of the deep basins or the coastal environment. Meise and O'Reilly (1996) demonstrated that late-stage *C. finmarchicus* average water column abundance was negatively correlated with average water column temperature in summer and fall, suggesting that indeed, cooler temperatures improve survivorship of resting stocks. Sameoto and Herman (1990) reported a large decrease in Emerald Basin *Calanus* spp. over the winter and they raised the possibility (among others) that copepods could not survive diapause in the 8.5 to 10°C waters at depth. For copepods that migrate to depth at the same time in the early summer, lipid reserves (and therefore energetic content) will be higher during the summer and fall in those animals that descend to colder temperatures. Therefore, right whales foraging in colder bottom water temperatures may also encounter higher quality food relative to what is available in waters with warmer bottom temperatures.

The tagged whales visited areas with depths of roughly 150 m more frequently than expected. These areas can be characterized as shallow basins. The structure, hydrography and physical processes of these basins may improve the availability, quality and aggregation of *C. finmarchicus*, respectively, for foraging right whales. Shoal layers of prey allow longer feeding times for right whales and thus are more energetically favorable. In contrast to deeper basins, the shoal depths of shallow basins guarantee shoal layers of prey. While the bottom waters of

deeper basins are warm due to slope water intrusions, colder temperatures prevail near the bottom of shallow basins. As discussed above, these conditions may improve survivorship and reduce oil depletion in resting *C. finmarchicus*, so prey abundance and quality may be enhanced in shallow basins. Strong tidal currents in the Gulf of Maine and Scotian Shelf act on the sea floor to generate turbulence and a well-mixed bottom layer. Baumgartner and Mate (Chapter 2) consistently found *C. finmarchicus* C5 in discrete layers just above this bottom mixed layer near feeding right whales in the lower Bay of Fundy and Roseway Basin. Unlike in very shallow regions, where the surface and bottom mixed layers interact and copepods may become uniformly distributed (e.g., Georges Bank, Nantucket Shoals), resting stocks of *C. finmarchicus* in shallow basins are vertically aggregated between surface and bottom mixed layers. The tide also produces cyclonic circulation over shallow basins via tidal rectification which, if sufficiently strong, may horizontally aggregate and retain *C. finmarchicus* as well. Tidal rectification generates a cyclonic gyre over Grand Manan Basin (Lynch et al., 1996) in which Baumgartner et al. (Chapter 3) suggest late-stage *C. finmarchicus* are aggregated and made available to foraging right whales.

The spatial and temporal scales of the present study (hundreds of kilometers, tens of days) would be impossible to study using ship- or aerial-based surveys. Even if these methods were viable, the rarity of right whale sightings over these spatial scales would make habitat analyses futile. Radio-tracking provides direct observations of resource selection and is therefore a useful tool for studying right whale habitat at these larger spatial scales. Considering the large volume of tracking data for marine vertebrates collected to date, improving the statistical methods to analyze satellite-acquired locations and associated environmental data is a particularly fruitful avenue of research. With approaches such as those presented here, much can be learned about marine habitats with data already in hand.

4.6. ACKNOWLEDGMENTS

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5. COMPARISONS OF *CALANUS FINMARCHICUS* FIFTH COPEPODITE ABUNDANCE ESTIMATES FROM NETS AND AN OPTICAL PLANKTON COUNTER

5.1. ABSTRACT

The response of an optical plankton counter (OPC) to concentrations of *Calanus finmarchicus* fifth copepodites (C5) ranging from 2 to 1621 copepods m^{-3} was examined during the summers of 1999-2001 in the lower Bay of Fundy and on the central and southwestern Scotian Shelf. Net tows from either a bongo or MOCNESS were collocated with vertical OPC casts to provide comparable data. Regression and validation procedures on independent datasets were used to determine the optimum particle size range in which *C. finmarchicus* C5 could be reliably detected. Particle abundances in the 1.5 to 2.0 mm equivalent circular diameter range were strongly correlated with net-derived abundances of *C. finmarchicus* C5. This optimum size range represents only the larger half of the full size distribution of *C. finmarchicus* C5 previously measured in the laboratory. The smaller half of this size distribution was often contaminated by smaller, more abundant particles. Particle abundance in the optimum size range increased with increases in the descent speed of the vertically profiled OPC, which indicated avoidance of the small sampling aperture by *C. finmarchicus* C5. A final regression model was developed to relate OPC particle abundance in the optimum size range to the abundance of *C. finmarchicus* C5 and the descent speed of the OPC. The data fitted the model well and excellent agreement was obtained with similar regressions by Heath et al. (*Fisheries Oceanography* 8 [Suppl. 1]:13-24, 1999). The inverted model was used as a calibration equation to predict *C. finmarchicus* C5 abundances from OPC measurements in an independent comparison to net abundances. In that case, the calibration equation underestimated net abundance by

an average factor of 2. However, anomalously low OPC particle abundances for some casts suggest spatial heterogeneity (patchiness) can confound such comparisons. Since the calibration equation was developed with net abundances that were collected over rather coarse depth strata, extrapolation from this equation is required to estimate *C. finmarchicus* C5 abundance at the smaller spatial scales resolvable by the OPC. Some considerations for this extrapolation are discussed.

5.2. INTRODUCTION

The calanoid copepod *Calanus finmarchicus* plays a pivotal trophic role in North Atlantic ecosystems by concentrating phytoplankton and microzooplankton biomass and making it directly available to higher trophic levels, such as fish, birds and some marine mammals. *C. finmarchicus* has garnered much attention in recent years (Wiebe et al., 2001; Tande and Miller, 1996) because its life history and population dynamics have a significant impact on so many other species. One such species is the North Atlantic right whale (*Eubalaena glacialis*). This highly endangered baleen whale feeds primarily on older copepodite stages of *C. finmarchicus* on its summer feeding grounds over the continental shelf of the northwestern Atlantic Ocean (Murison and Gaskin, 1989; Woodley and Gaskin, 1996; Stone et al., 1988). By summer, *C. finmarchicus* has already undertaken its ontogenetic downward migration and the population is primarily in the resting, fifth copepodite (C5) stage at depth (Hirche, 1996; Miller et al., 1991). To better understand important aspects of right whale ecology, particularly its habitat and foraging behavior, I required a method to rapidly assess the horizontal and vertical distribution and abundance of *C. finmarchicus* C5. The optical plankton counter (OPC; Herman, 1988, 1992) has been used as just such a rapid assessment tool in several applications (Sameoto and Herman, 1990; Herman et al., 1991; Heath,

1995; Huntley et al., 1995; Stockwell and Sprules, 1995; Checkley et al., 1997; Osgood and Checkley, 1997). The performance of the OPC has been examined in a wide variety of environments (Herman et al., 1993; Sameoto et al., 1993; Wieland et al., 1997; Sprules et al., 1998; Zhang et al., 2000; Woodd-Walker et al., 2000; Grant et al., 2000; Halliday et al., 2001) and it has shown promise in estimating the abundance of older stages of *Calanus* spp. (Osgood and Checkley, 1997; Heath et al., 1999).

The OPC consists of a light source and a detector housed in the middle of a flow tunnel through which water passes (Herman, 1988, 1992). Particles in the water partially occlude the collimated beam formed by the light source as they pass through the tunnel. The magnitude of the occlusion measured at the detector is related to the cross-sectional area of the aspect of the particle perpendicular to the light beam. The OPC, therefore, provides an estimate of the number of particles passing through the tunnel and a measure of each particle's size. The challenges of making sensible measurements with the OPC are similar to those faced by other rapid assessment methods. Both the OPC and video methods (e.g., Davis et al., 1992, 1996) sample relatively small volumes. In a patchy environment, significant concentrations of zooplankton may not be sampled by the instrument, so abundance may be underestimated. Statistical power is also reduced when estimating the concentration of less abundant mesozooplankton from small sample volumes. Furthermore, the small aperture through which particles pass to be sampled by these instruments is susceptible to avoidance by zooplankton. Unlike high-quality video, the OPC and acoustic methods (Holliday and Pieper, 1995) are hampered by their lack of taxonomic discrimination. In particular, a major constituent of OPC-observed particles in neritic waters is thought to be detrital material (Herman, 1992), which may impede taxonomic discrimination based on particle size alone. At high particle concentrations, the OPC is also prone to coincident counts, a phenomenon that occurs when two or more particles occlude the light beam

simultaneously and are recorded as a single, larger particle (Herman, 1988; Sprules et al., 1998).

Despite these challenges, the zooplankton community near feeding right whales has characteristics ideal for applying the OPC. The average water column abundance of *C. finmarchicus* C5 is typically in the upper hundreds to low thousands of copepods m^{-3} (Mayo and Marx, 1990; Murison and Gaskin, 1989; Woodley and Gaskin, 1996; Wishner et al., 1995) and the abundances at depth where the whales concentrate their feeding are likely much higher (Kenney et al., 1986). Statistical power, therefore, should not be a problem. *C. finmarchicus* C5 is typically the dominant zooplankton of its size near right whales, so discrimination based on size alone seems possible. Detrital material, however, is ubiquitous over the continental shelves, so size discrimination may be difficult. In fact, Heath et al. (1999) suggest that "the high incidence of detrital aggregates would seem to preclude the use of the OPC [for measuring late-stage *C. finmarchicus*] in continental shelf waters." Heath and his co-authors based this conclusion on poor correlations between OPC-derived particle abundances and net-derived abundances of *C. finmarchicus* C4 and C5 between 0.05 and 500 copepods m^{-3} in the upper 200 m of the Faroe-Shetland Channel.

This paper examines the response of the OPC to *C. finmarchicus* C5 abundances between 2 and 1621 copepods m^{-3} in a neritic environment. OPC particle abundances were compared to net-derived abundance estimates to determine which, if any, particle size range *C. finmarchicus* C5 could be detected. Avoidance of the OPC's small tunnel opening (2 by 25 cm) by *C. finmarchicus* C5 was also investigated by changing the descent speed for some OPC casts that accompanied net tows. A separate dataset consisting of paired OPC casts in which the descent speed was either varied or held constant between two successive casts was also used to examine avoidance by *C. finmarchicus* C5. Finally, a model relating OPC particle abundance and *C. finmarchicus* C5 abundance was developed

and tested with independent data for comparison to the results of Heath et al. (1999). This final model is also intended to be used to predict *C. finmarchicus* C5 abundance for the nearly 700 OPC casts collected during right whale and *C. finmarchicus* research conducted at the same time as this study (Baumgartner and Mate, Chapter 2; Baumgartner et al., Chapter 3; M.F. Baumgartner, unpublished data)..

5.3. METHODS

A model 1T OPC (Focal Technologies) was mounted in the center of an open, 0.8 m diameter by 1.0 m height, cylindrical, galvanized steel cage such that the downward-facing tunnel opening was 2-3 cm from the bottom of the cage. Two different instruments were used in this study: serial numbers TOW015 in 1999 and TOW047 in 2000 and 2001. A conductivity-temperature-depth (CTD) instrument was also housed in the cage, but was attached to one of the 6 stanchions connecting the top of the cage to the bottom. Flow into and around the OPC was unobstructed. The OPC was not equipped with a flowmeter, so the volume of water passing through the instrument was estimated simply as the product of the tunnel opening area (0.005 m^2) and the depth traversed by the OPC when profiled vertically. Instrument depth was measured via a pressure sensor in the CTD and, during 2000 and 2001, by a sensor in the OPC as well. When a cast was not exactly vertical, the calculated volume is an underestimate of the true sampled volume and the resulting particle abundance is overestimated. The percent error in the calculated volume for wire angles (θ) relative to the vertical is $100[\cos(\theta)-1]$ and is less than 10, 20 and 30% for angles as great as 25, 36 and 45°, respectively. Wire angles during casts were not explicitly measured, but were typically less than 30°. The OPC was always deployed in a vertical cast and only the data from the downcast were used.

Automated post-processing of the casts removed data associated with low descent speeds ($< 0.3 \text{ m s}^{-1}$), direction reversals (during periods of high swell), excessive changes in relative light attenuation, non-sequential timer values or invalid timer, depth or relative light attenuation values. Particle sizes are expressed as the diameter of a circle that has an area equal to the cross-section of the side of the particle facing into the light beam (or equivalently, the diameter of a sphere that has the same cross-sectional area as the side of the particle facing into the light beam).

5.3.1. Instrument calibration

The OPC calibration was checked by dropping nylon beads of known diameter through the tunnel while the OPC was mounted upright in the laboratory. These tests were conducted in air, not in water. A single trial consisted of dropping the same bead into the tunnel 10 times. Three trials were completed for each of the 1.588, 2.381 and 3.175 mm diameter beads both before and after the 2001 field season. The results were used to investigate the accuracy and precision of the OPC's particle size measurements and to detect any drift in the instrument over a single field season.

5.3.2. Collocated net and OPC sampling

Zooplankton samples were collected with 61 cm bongos equipped with 333 μm mesh nets. A CTD was affixed to the tow wire about 1 m above the bongo to telemeter the depth of the nets to the ship. The bongo was lowered at 0.50 m s^{-1} to within 5-10 m of the bottom and then hauled in at 0.33 m s^{-1} . The ship steamed

at 2.8 - 3.7 km hr⁻¹ (1.5 - 2.0 knots) during tows. A flowmeter was mounted in the center of each bongo to estimate the volume filtered by the nets. Depth-stratified, 1 m² multiple opening/closing net and environmental sensing system (MOCNESS; Wiebe et al., 1976, 1985) tows were conducted during 2001 in lieu of bongo tows. The MOCNESS was equipped with six, 150 µm mesh nets and the first of these remained open during the entire downcast to within 10 m of the bottom. The remaining 5 nets were towed through contiguous depth strata from the bottom of the downcast to the surface. The MOCNESS was towed at 1.9 - 3.7 km hr⁻¹ (1.0 - 2.0 knots) and paid out and hauled in at 0.33 m s⁻¹. The volume filtered by the nets was estimated from a flowmeter positioned outside of the net mouth. Zooplankton samples were preserved in a 5% borate-buffered formalin and seawater solution and were subsampled in the laboratory with a Hensen stempel pipette. Subsample volumes were obtained such that 100 or more of the most abundant copepod species were counted. *C. finmarchicus* copepodite stages C3 and higher were counted separately while all other taxa were identified to species or genus. More than 100 *C. finmarchicus* C5 were counted in 74% of the samples (52 of 70) and for those cases where less than 100 were counted, the *C. finmarchicus* C5 abundance was typically less than 55 copepods m⁻³ (14 of 18 cases) and always less than 200 copepods m⁻³.

Each bongo tow was collocated with a single OPC cast that was usually conducted immediately prior to the net sampling. A total of 26 collocated bongo tows and OPC casts were conducted on the central and southwestern Scotian Shelf (n = 12) and in the lower Bay of Fundy (n = 14) aboard NOAA Ship *Delaware II* (cruise DE9908) from 26 July to 3 September, 1999 (Figure 5.1; Table 5.1). Fourteen bongo tows with accompanying OPC casts were conducted in the lower Bay of Fundy (n = 11) and on the southwestern Scotian Shelf (n = 3) from 7 July to 31 August, 2000 aboard NOAA Ship *Delaware II* (cruise DE0007).

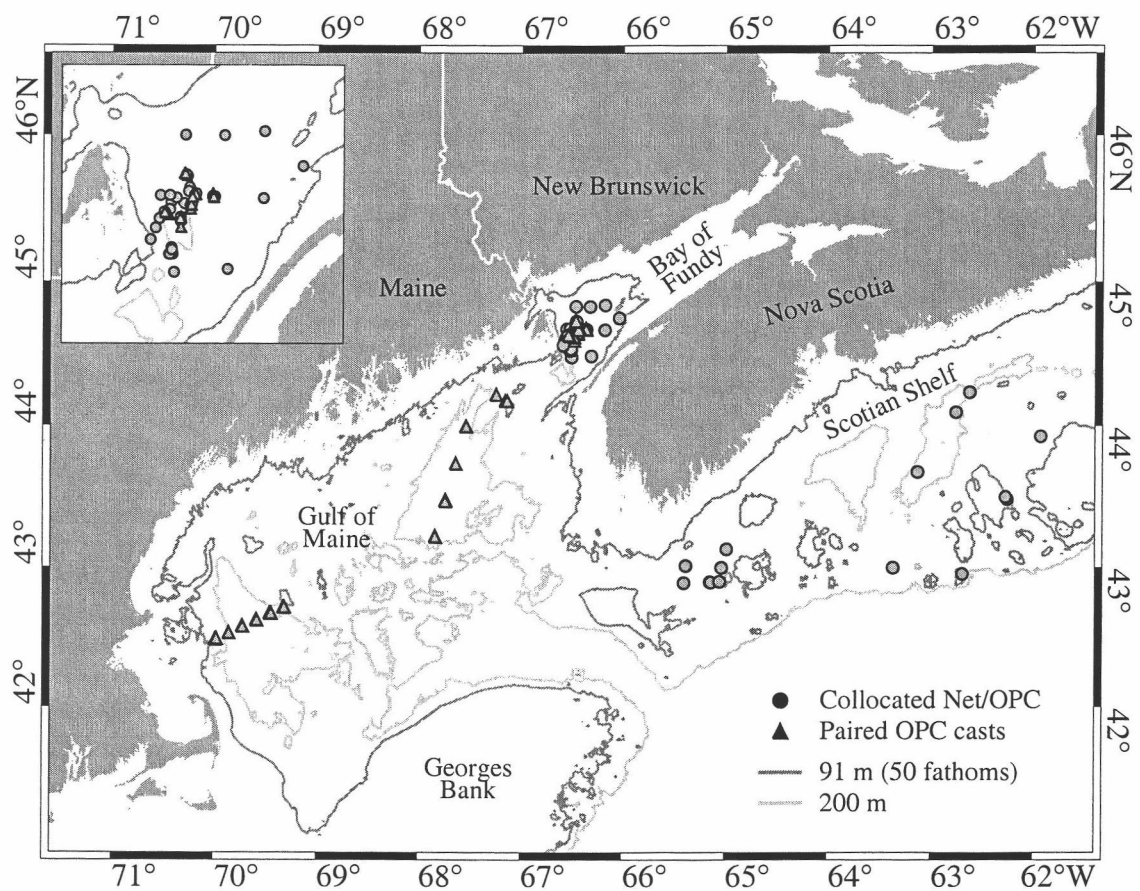


Figure 5.1. Study area and locations of collocated OPC casts and net tows (filled circles) and paired OPC casts (filled triangles). Inset shows the study area in the lower Bay of Fundy. The 91 (50 fathom) and 200 m isobaths are shown.

Table 5.1. Collocated net and OPC deployment information for each cruise.

Cruise	Sampling equipment	Tow type	Mesh size (μm)	Number of tows	Number of samples	OPC casts per tow	OPC descent speed range (m s^{-1})
DE9908	Bongo	double oblique	333	26	26	1	0.44 - 0.56
DE0007	Bongo	double oblique	333	14	14	1	0.60 - 0.92
AL0108	MOCNESS	depth stratified	150	3	15	4	0.59 - 0.66 ¹
AL0108	MOCNESS	depth stratified	150	3	15	4	0.87 - 0.98 ²

¹ referred to in the text as the “slow” AL0108 data

² referred to in the text as the “fast” AL0108 data

From 23 July to 3 August, 2001, 6 MOCNESS tows were conducted from NOAA Ship *Albatross IV* (cruise AL0108) in the lower Bay of Fundy (Figure 5.1; Table 5.1). These tows were conducted at slack tide and collocated with 4 OPC casts to reduce differences between the net and OPC abundance estimates attributable to advection of *C. finmarchicus* C5 and horizontal variability in copepod distribution. The local time of slack tide was predicted by 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 MOCNESS was towed through a station immediately after 2 OPC casts were completed there. After the tow, 2 more OPC casts would be conducted at the midpoint of the tow. To investigate the effect of copepod avoidance (see below), 3 of the MOCNESS tows were accompanied by OPC casts conducted at a nominal descent speed of just over 0.5 m s^{-1} (referred to as the “slow” AL0108 data). The remaining 3 MOCNESS tows were accompanied by OPC casts conducted at a nominal descent speed of just below 1.0 m s^{-1} (referred to as the “fast” AL0108 data).

OPC-derived particle abundances were computed only over the depths that were sampled during the bongo and MOCNESS tows to provide comparable data. The particle abundances from the 4 OPC casts accompanying each MOCNESS tow were averaged to obtain a single particle abundance estimate for each MOCNESS net sample.

5.3.3. Optimum size range detection

The size range in which *C. finmarchicus* C5 could be best detected was determined using similar methods to those employed by Heath et al. (1999). Particle abundances were computed from the OPC data over a matrix of size ranges

systematically defined by the minimum and span of the size range (equivalently, the mid-point and the span of the size range were used in Heath et al. [1999]). The minimum of the size range in the matrix varied from 0.25 to 3 mm in 0.05 mm increments and the span of the size range in the matrix varied from 0.20 to 2 mm in 0.05 mm increments. A regression procedure was first used to measure the strength of linear association between the log-transformed, OPC-derived particle abundances and the collocated, log-transformed, net-derived abundances of *C. finmarchicus* C5 in each of the size ranges of the matrix. The regression coefficients ($a_{i,j}$ and $b_{i,j}$) and the coefficient of determination ($r_{i,j}^2$) were estimated for the following model

$$\log_{10}(OPC) = a_{i,j} + b_{i,j} \log_{10}(NET) \quad (5.1)$$

where OPC is the particle abundance in the size range indexed by i and j in the matrix (i.e., with a minimum size indexed by i and a span of the size range indexed by j) and NET is the net-derived *C. finmarchicus* C5 abundance. Cases where the OPC-derived particle abundance was 0 particles m^{-3} were excluded from the model, and the regression was only performed when 50% or more of the cases had particle abundances greater than 0 particles m^{-3} . The regression procedure was conducted on data from a single cruise only. Data from a second cruise were used in a validation procedure to independently assess the predictive capabilities of the equations obtained in the regression procedure. Predicted abundances of *C. finmarchicus* C5 were computed from the OPC particle abundances in the validation dataset by inverting equation 5.1. A root mean square error (RMSE) for the predicted net abundances was computed as follows

$$RMSE_{i,j} = \sqrt{\frac{1}{n} \sum_{k=1}^n \left[\frac{\log_{10}(OPC_k) - a_{i,j}}{b_{i,j}} - \log_{10}(NET_k) \right]^2} \quad (5.2)$$

where $a_{i,j}$ and $b_{i,j}$ are the coefficients obtained in the regression procedure (equation 5.1) and OPC and NET are the particle and *C. finmarchicus* C5 abundances in the validation dataset, respectively. The RMSE was only computed when at least 50% of the validation cases had OPC-derived particle abundances greater than 0 particles m^{-3} (cases with particle abundances of 0 particles m^{-3} were excluded from the validation procedure). *C. finmarchicus* C5 was considered to be best detected in those size ranges in which the linear association between the particle abundance and the net-derived C5 abundance was strong (high $r_{i,j}^2$) and the applicability of the detected linear relationship to independent data collected in other years and at different locations was high (low $RMSE_{i,j}$). Based on these criteria, a single size range was selected for further analysis and is referred to as the optimum size range.

The OPC and net data from DE9908 ($n = 26$) were used in the regression procedure, and the OPC data from the “slow” casts during AL0108 and the corresponding MOCNESS net data ($n = 15$) were used in the validation procedure. Since the assignment of these datasets to the regression or validation procedures is arbitrary, a second analysis of the optimum size range was conducted with the “slow” AL0108 data and the DE9908 data assigned to the regression and validation procedures, respectively. The DE9908 and “slow” AL0108 data were chosen for these analyses because the descent speeds of the OPC casts do not vary much within each cruise and are nearly comparable between the two cruises (Table 5.1).

5.3.4. Avoidance: multiple linear regression analysis

To examine avoidance of the OPC by *C. finmarchicus* C5, the effect of descent speed on particle abundances in the optimum size range was tested using multiple linear regression analysis. Avoidance is expected to decrease as descent speed increases because the time for a copepod to react to the oncoming instrument decreases as the descent speed increases (Barkley, 1972). Therefore, measured particle abundance was expected to increase with increasing descent speed if avoidance occurs. The AL0108 MOCNESS tows were accompanied by OPC casts of different descent speeds to test this hypothesis (Table 5.1) and these data were used in the multiple linear regression analysis. The particle abundance in the optimum size range (OPC) was regressed against both the MOCNESS-derived abundance of *C. finmarchicus* C5 (NET) and the descent speed (SPEED) in the following model

$$\log_{10}(OPC) = \beta_0 + \beta_1 \log_{10}(NET) + \beta_2 SPEED \quad (5.3)$$

If significant, the back-transformed regression coefficient for the descent speed (10^{β_2}) indicates the multiplicative change in the median particle abundance corresponding to a 1 m s^{-1} increase in the descent speed after accounting for the effect of the net-derived abundance of *C. finmarchicus* C5 on the particle abundance (Ramsey and Schafer, 1997). The base 10 logarithm of the multiplicative change in the median particle abundance for any increase in descent speed from $SPEED_{slow}$ to $SPEED_{fast}$ can then be expressed as

$$\log_{10}\left(\frac{OPC_{fast}}{OPC_{slow}}\right) = \beta_2 (SPEED_{fast} - SPEED_{slow}) \quad (5.4)$$

5.3.5. Avoidance: paired OPC casts

OPC casts were also conducted in rapid succession at the same station (paired OPC casts) to investigate further the effect of descent speed on particle abundance. The descent speed for the two casts was either held constant ($< 0.1 \text{ m s}^{-1}$ difference between the two) or deliberately varied ($> 0.3 \text{ m s}^{-1}$ difference). The average water column particle abundance in the optimum size range was computed for each cast over the common depths sampled in both casts. The log-transformed ratio of these particle abundances was then regressed against the difference in descent speed between the two casts using the following equation

$$\log_{10} \left(\frac{OPC_{fast}}{OPC_{slow}} \right) = \alpha (SPEED_{fast} - SPEED_{slow}) \quad (5.5)$$

where OPC is the particle abundance, SPEED is the descent speed, α is the slope of the regression line forced through the origin and the indices “fast” and “slow” indicate the cast in the pair with the faster or slower descent speed, respectively. The back-transformed slope of the regression line (10^α) provides an estimate of the multiplicative change in the median particle abundance corresponding to a 1 m s^{-1} increase in the descent speed and is directly comparable to the coefficient β_2 in equations 5.3 and 5.4.

Paired OPC casts with varying descent speeds were conducted in Wilkinson and Jordan Basins in the Gulf of Maine during cruise AL0108 ($n = 9$) and during another cruise conducted aboard NOAA Ship *Delaware II* (cruise DE0108) from 7-31 August, 2001 ($n = 10$) (Figure 5.1). Paired OPC casts with nearly constant descent speeds were conducted in the Gulf of Maine during DE9908 ($n = 8$) and in the lower Bay of Fundy during AL0108 ($n = 12$). The latter paired OPC casts were the same casts conducted before and after each MOCNESS tow during AL0108.

5.3.6. Final model development

A final regression model of the form in equation 5.3 was developed as the “best fit” between the OPC data and the net-derived *C. finmarchicus* C5 abundance. This model was fitted using the DE9908 and all AL0108 data and inverted to produce the following calibration equation

$$\log_{10}(C5) = \frac{1}{\beta_1} [\log_{10}(OPC) - \beta_0 - \beta_2 SPEED] \quad (5.6)$$

where C5 is the abundance of *C. finmarchicus* C5 in copepods m^{-3} . Since the descent speeds of the DE0007 data varied much more than in any of the other datasets (Table 5.1), these data were excluded from the final model development and used to independently assess prediction errors in the calibration equation. One case was removed from the DE0007 data prior to this assessment because the OPC-derived particle abundance in the optimum size range was 0 particles m^{-3} (the corresponding net abundance for *C. finmarchicus* C5 was 29.0 copepods m^{-3}).

5.3.7. Caveats

All of the comparisons described above assume that the population of copepods remains the same during collocated sampling so that the OPC's performance can be directly evaluated. Violations of this assumption are caused by spatial heterogeneity in copepod distribution (patchiness) interacting with advection, ship drift or an incompatibility in the spatial scales over which different methods sample. When the assumption is not met, variability will occur in the comparisons, and serious violations will cause outliers. Patchiness at spatial scales

of meters to kilometers is a reality in copepod distributions (Pinel-Alloul, 1995), so it is important to recognize that substantial variability and even some outliers are expected to occur in the comparisons. This variability is the consequence of a genuine feature of copepod distribution in the ocean and is independent of the performance of the OPC.

5.4. RESULTS

5.4.1. Instrument calibration

The calibration check indicated that the measurement accuracy of the OPC decreased slightly with decreasing particle size, however the greatest mean error was less than 7% of the actual bead size (Table 5.2). These errors are well within the manufacturer specifications of 10% accuracy error (Focal Technologies, 1999). Ranges of the standard deviation for each of the six trials were 0.015-0.037, 0.020-0.031 and 0.025-0.044 mm for beads of 1.588, 2.381 and 3.175 mm diameter, respectively, which indicated very good precision in the OPC measurements. Statistically significant changes in the OPC calibration were detected during the 2001 field season (Table 5.2), however the magnitude of these changes was less than 2% of the actual bead size.

5.4.2. Optimum size range detection

The average particle size distribution in regions of high *Calanus finmarchicus* C5 abundance was characterized by a modal peak at approximately 1.55 mm (Figure 5.2). This mode was absent in regions of lower *C. finmarchicus*

Table 5.2. Results of the OPC calibration check before and after the 2001 field season. The 3 trials of $n = 10$ each were combined to give a single estimate of the errors before and after the 2001 cruises. Particle size is indicated as equivalent circular diameter (ECD) and as the raw, uncalibrated digital size (DS). The p-values for the following null hypotheses are shown: H_0 : mean error = 0, H_0 : mean pre/post-cruise ECD difference = 0, H_0 : mean pre/post cruise DS difference = 0.

Bead Size	n	Mean ECD (mm)	Mean Error (mm)	Mean % Error	Mean DS	pvalue for mean error or mean ECD difference	pvalue for mean DS difference
<u>1.588 mm</u>							
Pre-cruise	30	1.693	0.105	6.6	230.9	< 0.0001	
Post-cruise	30	1.668	0.081	5.1	224.7	< 0.0001	
Difference		0.024			6.2	0.0010	0.0011
<u>2.381 mm</u>							
Pre-cruise	30	2.443	0.062	2.6	462.8	< 0.0001	
Post-cruise	30	2.398	0.017	0.7	446.7	0.0017	
Difference		0.045			16.2	< 0.0001	< 0.0001
<u>3.175 mm</u>							
Pre-cruise	30	3.153	-0.022	-0.7	755.0	0.0249	
Post-cruise	30	3.128	-0.047	-1.5	743.5	< 0.0001	
Difference		0.025			11.4	0.0314	0.0303

C5 abundance. At intermediate abundances, the modal distribution is obscured by smaller particles. Herman (1992) measured the response of the OPC to preserved *C. finmarchicus* C5 in the laboratory (Figure 5.2). An offset between the modal peak observed here and Herman's (1992) laboratory-derived C5 peak of 0.1 to 0.15 mm is apparent (Figure 5.2), but this offset is consistent with the positive bias of 0.105 mm found in the calibration check for beads of 1.588 mm diameter (Table 5.2). After accounting for this offset, the distribution of particles associated with high *C. finmarchicus* C5 abundances observed in the field is nearly identical to that observed in the laboratory.

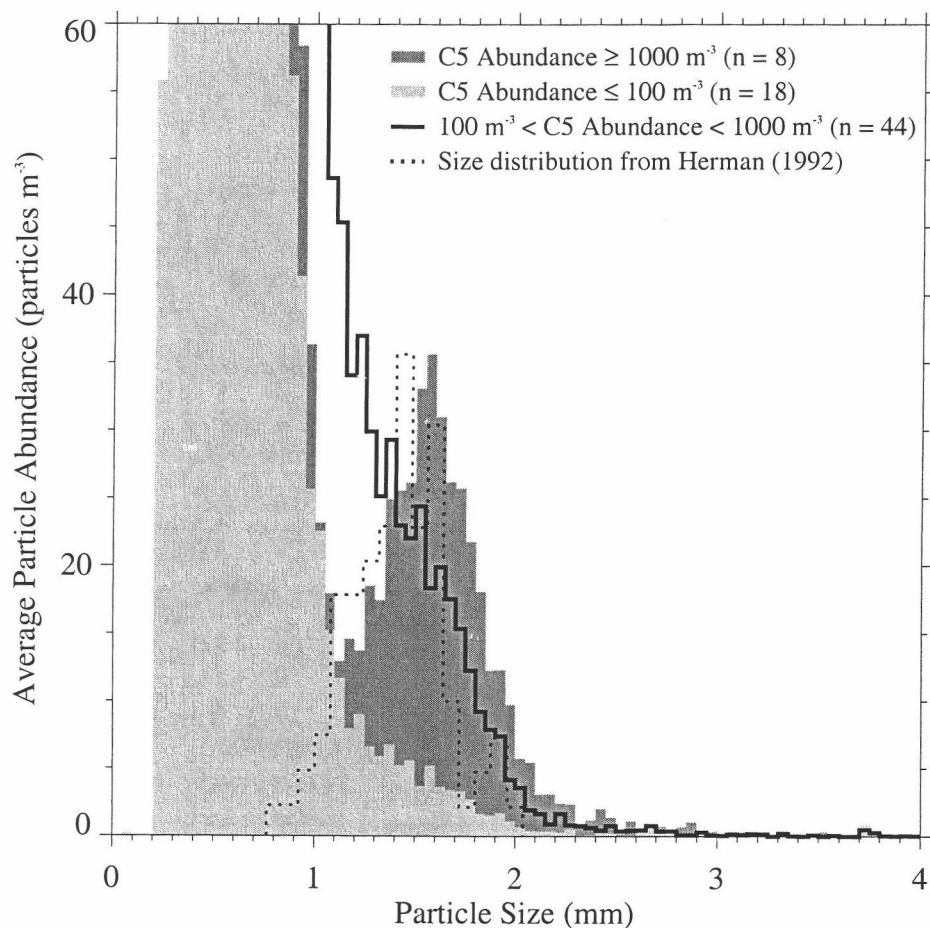


Figure 5.2. Average particle size distributions (in units of equivalent circular diameter) for OPC casts associated with tows that yielded *Calanus finmarchicus* C5 abundances in excess of 1000 copepods m⁻³ (dark gray), less than 100 copepods m⁻³ (light gray) and between 100 and 1000 copepods m⁻³ (solid line). Also shown (dotted) is the comparably scaled size distribution of preserved specimens obtained in the laboratory by Herman (1992).

The regression procedure on the DE9908 data indicated a peak in the coefficient of determination over the size range defined by a minimum of 1.90 mm and a span of 0.95 mm ($r^2 = 0.784$; Figure 5.3a). A similar result was obtained in the regression procedure on the “slow” AL0108 data, however the peak in the coefficient of determination occurred at a minimum size of 1.75 mm and a span of 0.40 mm ($r^2 = 0.843$). A local maximum occurred in both analyses at a minimum size of 1.5 mm, although this feature is more pronounced in the DE9908 data (Figure 5.3a). When the validation procedure was applied to the independent data, a single minimum was observed in the root mean square error for both analyses at a minimum particle size of 1.5 mm (Figure 5.3b). These results suggest that better correlation can be achieved between the OPC particle abundances and the net-derived C5 abundances at minimum sizes above 1.5 mm, but the best agreement between the regression equations and the independent data occurs in size ranges with a minimum of 1.5 mm. For both datasets, the coefficient of determination reaches an asymptote for the size range that has a minimum value of 1.5 mm and a maximum value of 2.0 mm (a span of 0.5 mm; Figure 5.3c) while the root mean square error reaches a minimum near this same size range (Figure 5.3d). An analysis of covariance (Zar, 1999) provided no evidence to suggest that the slopes ($p = 0.26$), elevations ($p = 0.47$) or overall regressions ($p = 0.40$) in the 1.5-2.0 mm size range were different in the two datasets (Figure 5.4). Based on these results, the 1.5-2.0 mm size range is considered the optimum size range.

5.4.3. Avoidance: multiple linear regression analysis

There was strong evidence that the particle abundance observed by the OPC in the optimum size range during AL0108 increased with increasing descent speed after accounting for the net-derived abundance of *C. finmarchicus* C5 ($p = 0.0009$;

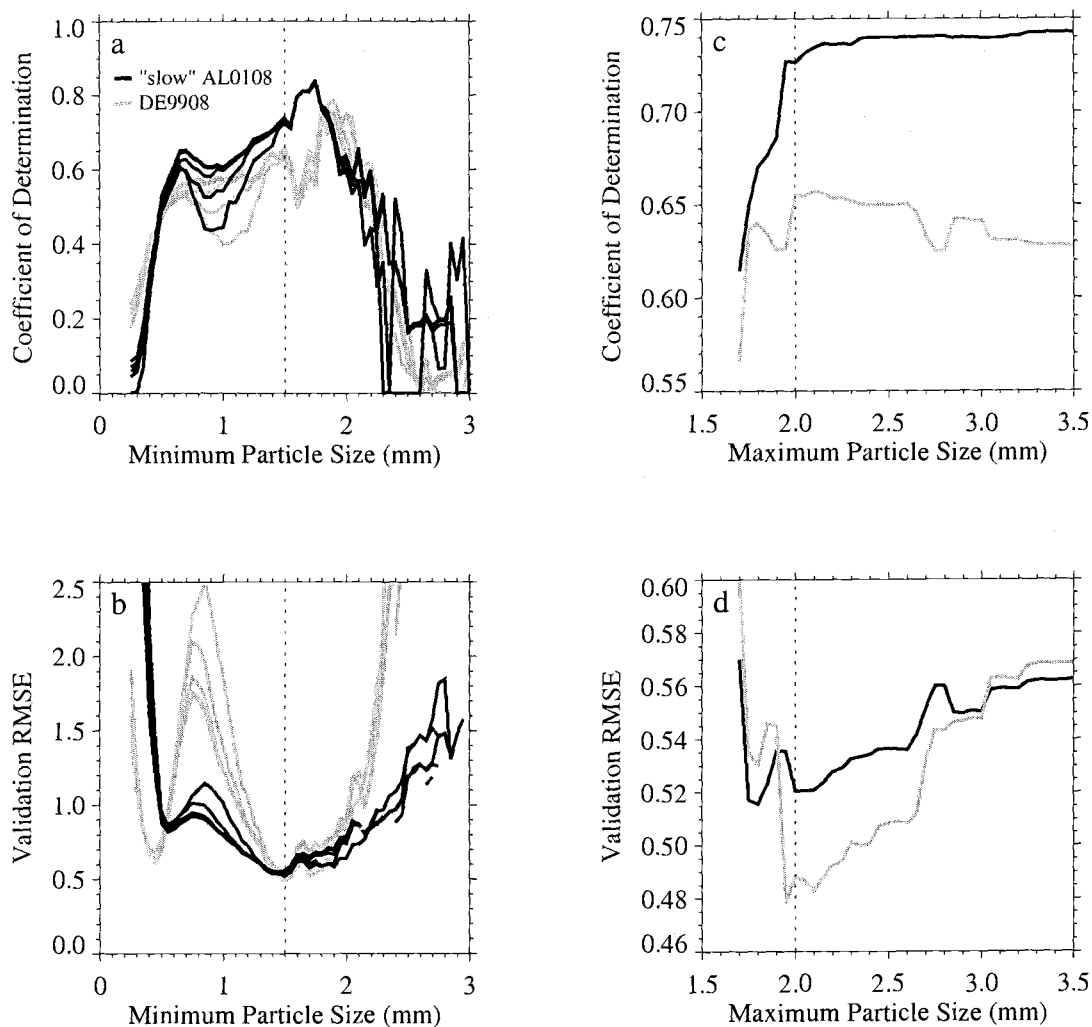


Figure 5.3. (a) Coefficients of determination (r^2) obtained in the regression procedure on the DE9908 (gray) and "slow" AL0108 (black) data for all minimum particle sizes and spans of 0.50, 0.75, 1.00, 1.25 and 1.50 mm. The spans are not differentiated because r^2 is primarily a function of minimum size. (b) Root mean square errors (RMSE) obtained by applying the DE9908 (gray) and "slow" AL0108 (black) regressions to the validation datasets for all minimum particle sizes and the same spans as in (a). (c) r^2 obtained in the regression procedure on the DE9908 (gray) and "slow" AL0108 (black) data for all maximum particle sizes associated with a minimum size of 1.5 mm. The maximum size is simply the sum of the minimum size and the span. (d) RMSE obtained by applying the DE9908 (gray) and "slow" AL0108 (black) regressions to the validation datasets for all maximum particle sizes associated with a minimum size of 1.5 mm. The dotted line indicates the minimum of the optimum particle size range (1.5 mm) in (a) and (b) and the maximum of the optimum particle size range (2.0 mm) in (c) and (d).

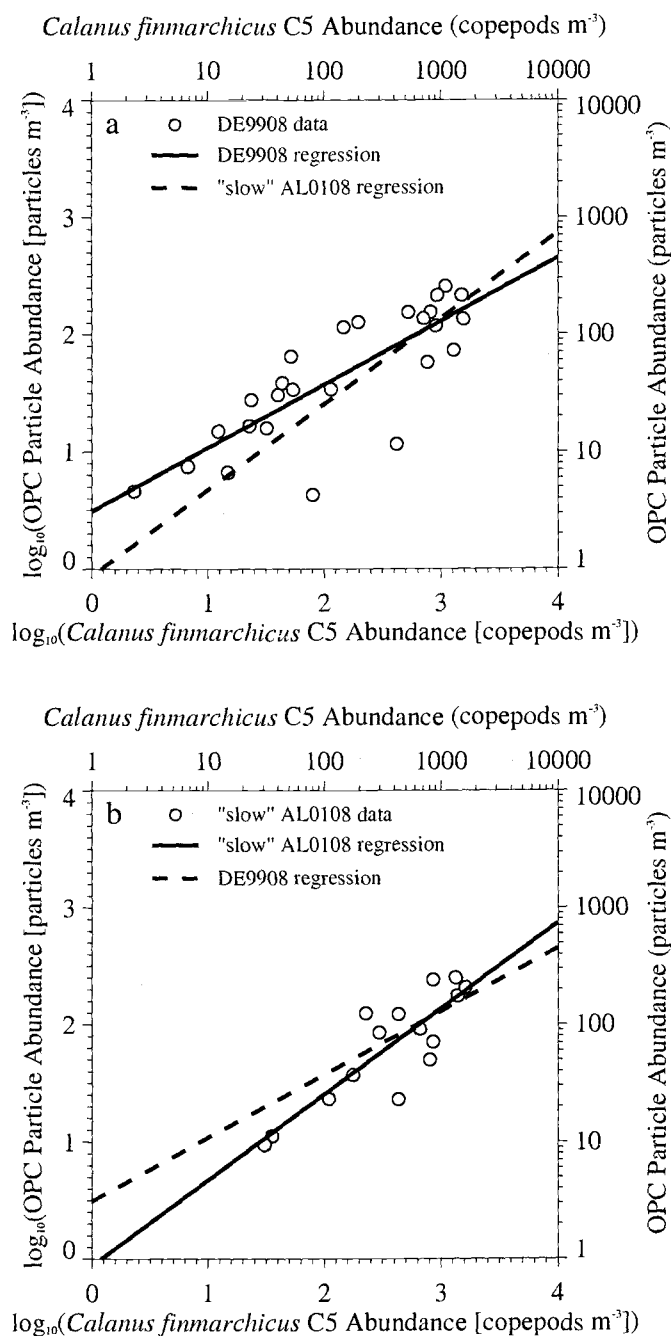


Figure 5.4. (a) Scatterplot of log-transformed *Calanus finmarchicus* C5 abundance and OPC particle abundance in the optimum size range of 1.5 to 2.0 mm for the DE9908 data (circles). The regression line is shown as a solid line and the independent regression of the "slow" AL0108 data for which the DE9908 data serve as the validation dataset is shown as a dashed line. (b) Similar scatterplot of "slow" AL0108 data (circles) with regression line (solid line). The independent regression of the DE9908 data for which the "slow" AL0108 data serve as the validation dataset is shown as a dashed line.

Table 5.3). The coefficient for the descent speed in the multiple linear regression model (β_2 in equation 5.3 and 5.4) was 1.21 s m^{-1} (95% CI: $0.541 - 1.88 \text{ s m}^{-1}$).

5.4.4. Avoidance: paired OPC casts

There was also strong evidence that an increase in particle abundance was associated with an increase in the descent rate during the paired OPC casts ($p = 0.0002$; Figure 5.5). Before fitting the model in equation 5.5, an intercept was included to test for a change in particle abundance when the descent speed was held constant, but this term was not found to be significant ($p = 0.11$). Note that 2 sets of paired OPC casts were excluded from the regression analysis because the ratios of the particle abundances were considered outliers (Figure 5.5). Each of these sets of casts was conducted near a right whale, an area where *C. finmarchicus* C5 abundance is typically patchy (Mayo and Marx, 1990; Wishner et al., 1988, 1995; Beardsley et al., 1996). I suspect that the two casts in each of the sets were not sampling the same population of copepods (i.e., one was in a patch upon which the right whale was probably feeding and the other was outside of it). The slope of the regression forced through the origin (α in equation 5.5) was 0.412 s m^{-1} (95% CI: $0.210 - 0.615 \text{ s m}^{-1}$), which was significantly lower than the comparable estimate of 1.21 s m^{-1} obtained in the multiple linear regression analysis ($p < 0.0001$).

5.4.5. Final model development

The final regression model fitted the DE9908 and AL0108 data well ($r^2 = 0.684$) and was highly significant ($p < 0.0001$) (Table 5.4; Figure 5.6). When applied to the DE0007 data using equation 5.6 (Figure 5.7), however, there was

Table 5.3. Multiple linear regression results for all AL0108 data fit to equation 5.3 to test for descent speed effects on OPC-measured particle abundance in the 1.5-2.0 mm size range ($n = 30$, $r^2 = 0.645$, $F = 24.55$, $p < 0.0001$).

Variable	Coefficient	Estimate	Standard Error	95% CI	t statistic	pvalue
Intercept	β_0	-0.5865	0.3749	-1.3558 – 0.1829	-1.56	0.1294
$\log_{10}(\text{NET})$	β_1	0.6310	0.1193	0.3861 – 0.8758	5.29	< 0.0001
SPEED	β_2	1.2101	0.3260	0.5412 – 1.8789	3.71	0.0009

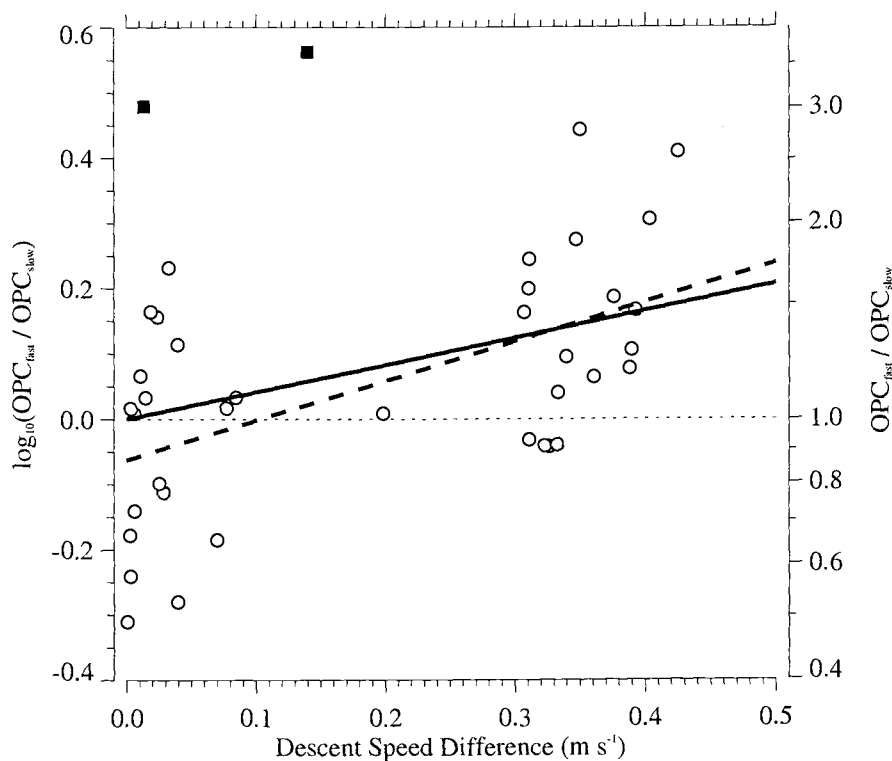


Figure 5.5. Scatterplot of descent speed difference and the ratio of OPC particle abundance in the optimum size range for paired OPC casts. The regression line forced through the origin (see equation 5.5 in the text) is shown as a solid line and the regression line with both a slope and intercept is shown as a dashed line. The regressions excluded the two observations with anomalously high ratios at low descent speed differences (filled squares).

Table 5.4. Final multiple linear regression model fit to all AL0108 and DE9908 data ($n = 56$, $r^2 = 0.684$, $F = 57.32$, $p < 0.0001$).

Variable	Coefficient	Estimate	Standard Error	95% CI	t statistic	pvalue
Intercept	β_0	0.0384	0.1825	-0.3276 – 0.4044	0.21	0.8341
$\log_{10}(\text{NET})$	β_1	0.5343	0.0626	0.4087 – 0.6598	8.53	< 0.0001
SPEED	β_2	0.8001	0.2370	0.3248 – 1.2754	3.38	0.0014

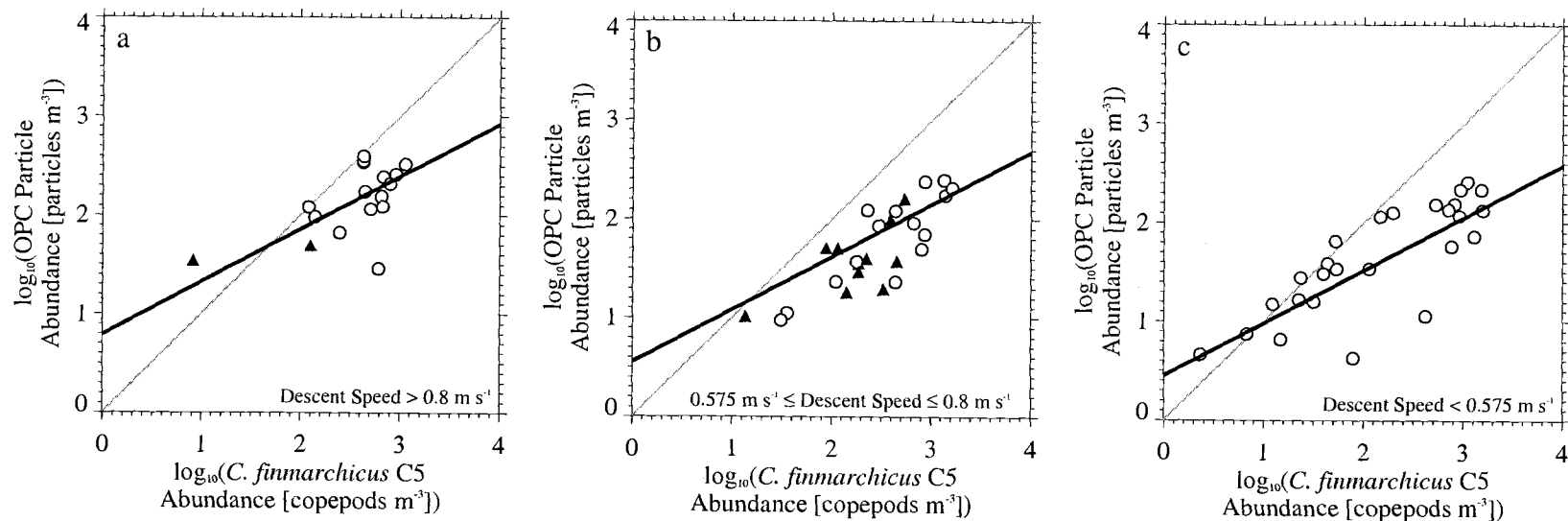


Figure 5.6. Scatterplots of log-transformed *Calanus finmarchicus* C5 abundance and OPC particle abundance in the optimum size range for descent speeds (a) greater than 0.8 m s^{-1} ("fast" AL0108 data), (b) between 0.575 and 0.8 m s^{-1} ("slow" AL0108 data) and (c) less than 0.575 m s^{-1} (DE9908). Data used to construct the final regression model (Table 5.4) are shown as open circles. Lines indicate the final model corresponding to average descent speeds of (a) 0.94 m s^{-1} , (b) 0.63 m s^{-1} and (c) 0.51 m s^{-1} . The independent DE0007 data are shown in (a) and (b) as black triangles.

suggestive, but inconclusive evidence that the mean prediction was different from the actual *C. finmarchicus* C5 abundance ($p = 0.060$). The predicted *C. finmarchicus* C5 net abundance was underestimated by an average factor of 1.95 (95% CI: 3.91 too low to 1.03 too high).

5.5. DISCUSSION

The modal peak in the average size distribution at 1.55 mm is unambiguous at high concentrations of *C. finmarchicus* C5, but is absent at lower concentrations (Figure 5.1). Furthermore, the regression and validation procedures suggest that the OPC-observed particles in the size range 1.5-2.0 mm are *C. finmarchicus* C5. These results indicate that in-situ *C. finmarchicus* C5 is best detected by the OPC in only the larger half of its laboratory-derived size distribution (Herman, 1992) where its abundance is not contaminated by other, smaller particles. The total abundance of smaller copepods (e.g., *C. finmarchicus* C3 or C4, *Centropages* spp., *Pseudocalanus* spp., *Metridia lucens*, *Temora longicornis* and *Acartia longiremis*) exceeded that of *C. finmarchicus* C5 in nearly 50% of the net samples, whereas the total abundance of larger copepods (e.g., *C. finmarchicus* adults, *Metridia longa*, *C. glacialis*, *C. hyperboreus*) only exceeded that of *C. finmarchicus* C5 on one occasion. Since smaller particles are more abundant than larger particles in general, the smaller half of the *C. finmarchicus* C5 size distribution is more likely to be contaminated by either smaller copepods or detrital particles. In contrast, the larger half of this modal size distribution is infrequently contaminated by less abundant, larger copepods or detrital material.

Avoidance of the OPC tunnel opening by *C. finmarchicus* C5 was inferred from the significantly higher particle abundances observed when descent speed was increased. This conclusion is also based on the observations of Miller et al. (1991)

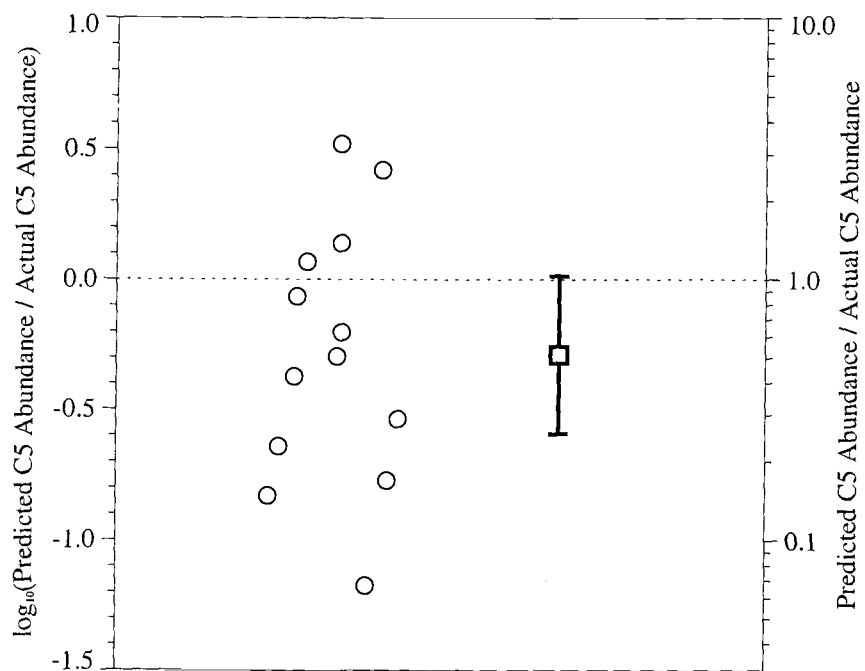


Figure 5.7. Ratio of predicted to actual *Calanus finmarchicus* C5 net abundance for DE0007 data (jittered circles) and the mean of the log-transformed ratio (square) with a 95% confidence interval (error bars).

that resting *C. finmarchicus* C5 in this region are still responsive and capable of a strong escape reaction. The magnitude of this effect may be substantial. For the 0.30 m s^{-1} average increase in descent speeds between the “fast” and “slow” AL0108 data, median OPC particle abundance increased by a factor of 2.31 (95% CI: 1.45 - 3.66). For the same 0.30 m s^{-1} increase in descent speed, the analysis of the paired OPC casts yielded a lower estimate of the factor increase in median OPC particle abundance: 1.33 (95% CI: 1.16 - 1.53). Avoidance is a function of the size of the sampling aperture and the reaction time and escape velocity of the zooplankton (Barkley, 1964, 1972). The reaction time, in turn, is a function of the distance at which the animal can detect the sampler and the speed of the sampler. Although the sampling aperture and tow speed of an OPC can be held constant across applications, differences in the structure of the vehicle carrying the OPC can alter the pressure wave in front of the sampler and hence, the distance at which zooplankton can detect the oncoming sampler. Therefore, the estimates of the magnitude of avoidance determined in this study are probably not directly applicable to other vehicles. However, the cage used in the present study was designed to reduce the pressure wave impacting the volume of water immediately in front of the OPC and so avoidance was probably minimized. For larger vehicles or vehicles with obstructions near the OPC, the effect of avoidance on OPC particle abundances will likely be worse.

The final model predicted median *C. finmarchicus* C5 abundances from the DE0007 data that were too low by a factor of nearly 2. Most of the predictions (7 of 13) were within a factor of 3, while four of the predictions were gross underestimates between a factor of 4.4 and 14.9 too low. Unreasonably low OPC particle abundances were also observed on two occasions during DE9908 (Figure 5.4a). Underestimation of this type suggests that the single OPC casts accompanying each of these bongo tows did not sample the same population of *C. finmarchicus* C5 as did the net (i.e., the net sampled a patch of copepods while the

OPC missed the patch). In a spatially heterogeneous environment, this would certainly be expected to happen occasionally. In fact, given this confounding by spatial heterogeneity and the differences in sampling methodology between the nets and the OPC, the correlations between the particle abundance and net-derived *C. finmarchicus* C5 abundance were remarkably high. Compared to the OPC, the nets integrated over a much larger horizontal spatial scale (hundreds of meters for towed nets versus discrete OPC vertical profiles), sampled a much larger volume of seawater (average net:OPC ratio of volume sampled was 300:1), probably experienced less avoidance (due to the larger sample aperture) and destroyed detrital particles that were counted by the OPC. Despite these significant differences, the coefficients of determination (r^2) were 0.655, 0.726 and 0.684 for the DE9908 data (Figure 5.4a), “slow” AL0108 data (Figure 5.4b) and the final multiple linear regression model (Figure 5.6, Table 5.4), respectively. When the two cases with unreasonably low OPC particle abundances are removed from the DE9908 data (Figure 5.4a), the agreement between the OPC and net abundances becomes much better ($r^2 = 0.840$). These coefficients of determination exceed those obtained by Heath et al. (1999) from samples and measurements collected in the Faroe-Shetland Channel between 500 and 1000 m with a side-by-side mounted plankton net and an OPC.

Using a similar regression procedure, Heath et al. (1999) obtained maximum correlations in size ranges that nearly encompass the complete laboratory-derived *C. finmarchicus* C5 size distribution (0.90 to 1.70 mm in January, 1.02 to 1.74 mm in March). The abundance of both *C. finmarchicus* C4 and C5 were included in their analysis, but C5 dominated in both months. Heath et al. (1999) reported that their OPC sampled volumes between 0.25 and 0.5 m³ during a single 60 s integration interval, which corresponds to tow speeds between 0.83 and 1.67 m s⁻¹. At the average descent speed used during the “fast” AL0108 casts (0.94 m s⁻¹), the final model determined in this study predicts lower OPC

particle abundances than those of Heath et al. (1999) for similar net abundances of *C. finmarchicus* C5 (Figure 5.8). Recall, however, that *C. finmarchicus* C5 was best detected in the larger half of its size distribution. Therefore, the final regression equation only models roughly half of the OPC particle abundance contributed by *C. finmarchicus* C5. The contribution of the smaller half of the size distribution can be taken into account simply by doubling the particle abundance obtained from the model. The resulting regression equation is now directly comparable to the Heath et al. (1999) regression and there is excellent agreement between the two (Figure 5.8). In fact, no evidence was found to suggest that the regression coefficient for the net abundance of *C. finmarchicus* C5 (Table 5.4) was different than the January ($H_0: \beta_1 = 0.492$, $p = 0.50$) or March ($H_0: \beta_1 = 0.461$, $p = 0.25$) slopes of the Heath et al. (1999) regressions. Because the results of these two studies are consistent, it seems reasonable to conclude that the regression lines in Figure 5.8 represent the true response of the OPC to varying abundances of *C. finmarchicus* C5 over nearly 5 orders of magnitude.

Since the OPC particle abundances used to develop the final regression model (Table 5.4) were between 4 and 395 particles m^{-3} , *C. finmarchicus* C5 abundances should only be prudently estimated with equation 5.6 when OPC particle abundances are in this range. These particle abundances were determined over very coarse depth strata to be comparable to the *C. finmarchicus* C5 abundances from the corresponding net tows. The OPC, of course, has the capability to provide much finer-scale abundance and distribution information, but calibrating particle abundances found in narrower depth strata is difficult. Near right whales, peak abundances in 5 m depth strata typically exceed 395 particles m^{-3} and can range as high as 1114 particles m^{-3} . Estimating abundances of *C. finmarchicus* C5 using these OPC data requires extrapolation from the calibration equation. The results presented here indicate that the regressions of Heath et al. (1999) could be successfully extrapolated to higher concentrations, which provides

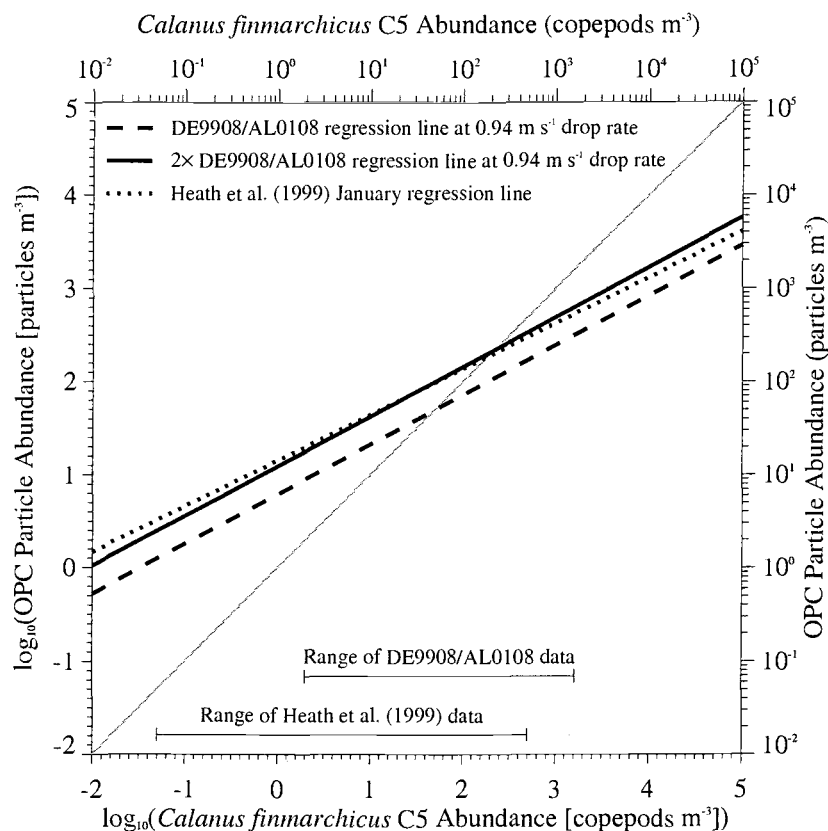


Figure 5.8. Final multiple linear regression model developed from the DE9908 and all AL0108 data for a descent rate of 0.94 m s^{-1} (dashed line), the final model at 0.94 m s^{-1} with particle abundances doubled (solid line) and the January regression of Heath et al. (1999) (dotted line). The ranges of net-derived *Calanus finmarchicus* C5 abundances used in each study are shown. Note that only 4% of the samples from Heath et al. (1999) had combined *C. finmarchicus* C4 and C5 abundances greater than 100 copepods m^{-3} whereas 74% of the samples in the present study had *C. finmarchicus* C5 abundances greater than 100 copepods m^{-3} .

some hope, yet no evidence, that these same regressions may apply to *C. finmarchicus* C5 abundances between 1000 and 10,000 copepods m^{-3} or higher.

At higher concentrations, coincidence counts (Herman, 1988) may occur if the concentration of smaller sized particles is also high. Coincidence would reduce the number of particles detected in the 1.5 to 2.0 mm size range and result in underestimation of the *C. finmarchicus* C5 abundance by the calibration equation. For OPC casts associated with net tows having *C. finmarchicus* C5 abundances greater than 1000 copepods m^{-3} , the total time spent detecting particles (i.e., the total time particles spent traversing the 4 mm wide light beam plus a 4 ms per particle electronics reset time) during each 0.5 s interval of a downcast was rarely greater than 0.25 s. If coincidence counting were frequent, this total processing time would be much closer to 0.5 s. Even near right whales, where discrete layers of particles in the optimum size range can exceed abundances of 1000 particles m^{-3} , total processing time remains below 0.25 s. These results suggest that coincident counting occurs infrequently, if at all, and it will not affect estimates from the calibration equation for the observed range of OPC particle abundances. There is also some indication that avoidance may decrease at higher concentrations (Fleminger and Clutter, 1965), which would result in overestimation of the *C. finmarchicus* C5 abundance by the calibration equation. A test of an additional interaction term ($\log_{10}[\text{NET}] \times \text{SPEED}$) in the model described by equation 5.3, however, provided no evidence that the effect of avoidance on the OPC particle abundance varied with *C. finmarchicus* C5 abundance over concentrations between 31 and 1621 copepods m^{-3} ($p = 0.31$). With no evidence of either persistent coincident counting or decreased avoidance at higher concentrations and with appropriate caution, extrapolation of the calibration equation to predict *C. finmarchicus* C5 concentrations from higher OPC particle abundances seems feasible.

The errors in the calibration equation indicated by the DE0007 data should be appropriately weighed by the challenges of comparing abundance estimates between the OPC and the nets. Independent of net comparisons, other data suggest that the OPC can provide very useful information about the abundance and distribution of *C. finmarchicus* C5. For instance, foraging right whales have been hypothesized to feed on late-stage *C. finmarchicus* in the lower Bay of Fundy. By tagging right whales with time-depth recorders and following their movements while sampling the water column with an OPC, Baumgartner and Mate (Chapter 2) demonstrated that right whales dive to and presumably forage at the depth of maximum particle abundance in the optimum size range described here. Agreement between the right whale diving behavior and the OPC-derived particle abundances was very strong, which indicates that the OPC is providing ecologically meaningful observations. I and co-workers have also used the OPC to track the time-evolution of late-stage *C. finmarchicus* C5 diel vertical migration in the lower Bay of Fundy (unpublished data). Dusk and dawn migrations to and from the surface by a segment of the *C. finmarchicus* C5 population were clearly distinguished in half-hourly casts conducted over a 28 hour period on two separate occasions. These observations were corroborated by concurrent, but much less frequent, MOCNESS net sampling. These studies indicate that the OPC can be effectively used to measure the distribution and abundance of *C. finmarchicus* C5 in a variety of applications. Given the importance of this species in the North Atlantic and the current questions about the ecology of the fifth copepodite resting stock, the OPC has much to offer as a rapid assessment tool in future *C. finmarchicus* research.

5.6. ACKNOWLEDGMENTS

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6. SUMMARY

North Atlantic right whale behavior, distribution and movements can be considered to be influenced by two processes: feeding and reproduction. This view is overly simplistic, but it serves as a convenient framework for interpreting the results presented here. Kenney et al. (1986) indicated that right whales must seek out and feed upon very dense aggregations of *C. finmarchicus* C5 to meet annual, maintenance metabolic requirements. The results of Chapter 2 corroborate these findings on a shorter time scale by suggesting that some right whales in the lower Bay of Fundy may need to forage for a significant portion of the day to meet daily, maintenance metabolic requirements. Mayo and Marx (1990) reported nearly continuous skim-feeding bouts of many hours in Cape Cod Bay. All of these findings suggest that right whales devote much of their time to searching for and feeding upon suitable prey patches. However, foraging is interrupted occasionally for socializing or sexual activity (Kraus and Hatch, 2001). Females may devote more time to this activity than males, since they are the focus of most observable social activity (termed surface active groups) in which individual males are comparatively ephemeral participants (Kraus and Hatch, 2001). At longer time scales, reproduction drives the migration of pregnant females to the southeastern U.S. calving grounds and the return of females, some escorting and nursing calves, to the "nursery" grounds in the lower Bay of Fundy and possibly elsewhere during the summer (Schaeff et al., 1993).

Throughout this summary, aspects of right whale behavior, distribution and movements will be considered largely in the context of feeding. In the sense that individual survival over short time scales (several years) is paramount to replacing oneself in the population via reproduction over time scales approaching a lifespan (decades), feeding is assumed to be the primary factor influencing right whale

behavior, distribution and movements. Reproductive motivations must, however, play a role and will therefore be considered when appropriate.

6.1. FACTORS INFLUENCING RIGHT WHALE FORAGING SUCCESS

The amount of prey consumed by a filter-feeding right whale is dependent upon a myriad of factors that affect (1) the productivity and survivorship of the prey, (2) its vertical and horizontal aggregation and (3) the foraging capabilities of the whale. Each of these are discussed below.

6.1.1. Productivity and survivorship of *Calanus finmarchicus*

Productivity of *C. finmarchicus* depends on the survivorship of adult males and females as well as factors that affect egg production rates such as temperature and food availability (Hirche et al., 1997). *C. finmarchicus* leave diapause in winter as adults, migrate to the surface and begin to feed and reproduce.

Conditions in winter, then, affect the productivity of these progenitors (dubbed the G_0 generation). Their offspring (the G_1 generation) may go on to spawn a second generation (G_2) and there may even be a third generation (G_3) in the Gulf of Maine and Scotian Shelf (Sameoto and Herman, 1990; Durbin et al., 2000).

Environmental factors affecting the production of *C. finmarchicus* are complex and probably include the strength of winter mixing, intensity of vernal warming, timing and strength of stratification and primary production rates. These factors, in turn, are all influenced by variability in large-scale ocean-atmosphere interactions such as the North Atlantic Oscillation (NAO). Thus, the abundance of *C. finmarchicus* encountered by a right whale is influenced, in part, by processes that are occurring

at seasonal or even annual time scales. These processes may promote conditions that are suitable for high *C. finmarchicus* productivity, but it is important to bear in mind that those conditions occur long before a copepod is consumed by a right whale. Because right whales target older stages of *C. finmarchicus*, there will always be a lag of ca. 5-10 weeks (Durbin et al., 2000) before a copepod reaches these older stages and is either energetically acceptable or can be efficiently filtered by a right whale. Since *C. finmarchicus* arrest their development after undertaking an ontogenetic downward migration and entering diapause, there may be an even longer time interval between the conditions that promoted the production of a copepod and its consumption by a right whale.

Advection ensures that the location at which a copepod was spawned will not be the same location at which it reaches an older stage and is available for consumption by a right whale. Therefore, conditions that promote high production of *C. finmarchicus* will be removed from where right whales feed not only in time, but in space as well. Thus, it is not surprising that the factors that are thought to affect *C. finmarchicus* productivity, such as surface chlorophyll concentration or temperature, were unrelated to the spatial variability in right whale occurrence (Chapter 3). Similarly, the South Channel Ocean Productivity Experiment (SCOPEX; Kenney and Wishner, 1995) found no evidence to suggest that *in-situ* secondary productivity was responsible for promoting the large aggregations of *C. finmarchicus* upon which right whales feed in the Great South Channel.

Conditions that promote the survivorship of *C. finmarchicus* during the period of growth and development will also be displaced from the actual consumption of those *C. finmarchicus* by right whales in both time and space. Survivorship is influenced by temperature and food availability during this time, but can be influenced by much more complex conditions that promote the abundance of predators. Once *C. finmarchicus* reaches stage 5 and enters diapause (when feeding ceases), survivorship is likely controlled by predation. Temperature

may also play a role in survivorship since metabolic rate is strongly influenced by temperature (Hirche, 1983) and *C. finmarchicus* has a limited store of energy for diapause. Thus, high temperatures may increase mortality due to depletion of oil reserves. Unlike the conditions that affect copepod production and survivorship during development, the conditions that promote survivorship in diapausing *C. finmarchicus* C5 are contemporaneous with right whale feeding. Therefore, some association between right whale spatial distribution and these conditions may be expected. Right whales equipped with satellite-monitored radio tags frequented areas with low bottom temperatures (Chapter 4), which suggests that right whales forage in these areas because *C. finmarchicus* C5 survivorship is higher (and thus abundance is higher) or because the rate of oil reserve depletion in *C. finmarchicus* C5 is lower in these regions (and thus these copepods have higher energetic content).

6.1.2. Prey aggregation

Prey aggregation is critical for successful filter feeding. Right whales depend on the behavior of *C. finmarchicus* and physical mechanisms to provide suitable concentrations on which to feed. Since *C. finmarchicus* cannot traverse any significant horizontal distances, aggregation of prey in the horizontal must be facilitated by physical processes. One such process is mesoscale, gyre-like circulation that captures and retains *C. finmarchicus*. Miller et al. (1998) suggested that this process may aggregate *C. finmarchicus* C5 preparing for diapause in the SCOPEX gyre in the northern part of the Great South Channel. Woodley and Gaskin (1996) suggest that the central gyre of Grand Manan Basin in the lower Bay of Fundy may aggregate *C. finmarchicus* there as well. Ocean fronts can also aggregate zooplankton if accompanied by changes in vertical swimming behavior.

Downwelling at the interface of a convergent front transports passive particles away from the surface expression of the front, but organisms that can resist this downwelling by swimming upward will aggregate there (Olson and Backus, 1985; Epstein and Beardsley, 2001). Vertical aggregation is much more dependent on copepod behavior, but may be facilitated by physical processes. For instance, skim-feeding by right whales in the late winter and spring is made possible by very high, near-surface concentrations of *C. finmarchicus*. This feeding behavior is typically observed on calm days. Mechanical mixing by the wind would certainly disrupt surface aggregations, but this does not explain why these aggregations form in still weather. Perhaps on calm spring days, insolation warms and thus isolates a shallow surface layer which, if it has sufficient nutrient concentration, can promote high primary productivity and attract *C. finmarchicus* to the surface to feed. During the summer and fall seasons, diapause in *C. finmarchicus* C5 is likely the primary, vertical aggregative mechanism, but this may be enhanced by temperature or salinity preferences by the copepods or avoidance of turbulent layers.

The results of Chapter 2 indicate that *C. finmarchicus* C5 in the lower Bay of Fundy and Roseway Basin avoid the turbulent bottom mixed layer and aggregate just above it. In 2001, zooplankton samples collected via MOCNESS in the lower Bay of Fundy below 100 m were dominated by *C. finmarchicus* C5. These animals were not very active and had well-developed oil sacs and empty guts (R.G. Campbell, unpublished data), which suggests that they were in diapause. While the factors influencing the selection of a resting depth by *C. finmarchicus* are unknown (particularly on the continental shelf), they may include temperature (Hirche, 1991), density (which influences copepod buoyancy; Visser and Jónasdóttir, 1999), predation pressure (Kaartvedt, 1996; Dale et al., 1999) or light level (Miller et al., 1991). It seems clear that *C. finmarchicus* C5 in the lower Bay of Fundy and Roseway Basin migrated as deep as possible without entering the turbulent bottom

mixed layer. Right whales take advantage of this behavior by concentrating their foraging effort just above the bottom mixed layer.

Unlike environmental factors that promote copepod productivity and survivorship during development, environmental factors that promote aggregation of prey are expected to have a significant influence on right whale spatial distribution. The results of Chapter 3 provide evidence of this. Higher sighting probabilities of right whales were associated with greater depth, which was suggestive of a circulatory aggregative mechanism. This is particularly true in the lower Bay of Fundy where a gyre over Grand Manan Basin may aggregate *C. finmarchicus* C5. In Roseway Basin, an increased abundance of fronts was accompanied by higher sighting rates of right whales in both space and time. There was little evidence of an association between the distribution of right whales equipped with satellite-monitored radio tags and either surface temperature gradient, surface chlorophyll gradient or ocean front probability (Chapter 4). In order of likelihood, this may indicate that (1) associations between right whales and ocean fronts only occur in particular areas (e.g., the southwestern Scotian Shelf), (2) the statistical methods employed for the analysis of satellite-monitored whale movements were inappropriate or imprecise or (3) the results of the regional habitat analysis for Roseway Basin in Chapter 3 were spurious. Both ocean fronts and closed circulation can aggregate prey and it is likely that certain regions are utilized by right whales because of the presence of one or the other mechanism. Different physical mechanisms may also promote horizontal aggregation of prey in some areas or at smaller spatial scales. These might include internal waves or Langmuir cells.

6.1.3. Foraging capabilities

Ingestion of prey is ultimately a function of a right whale's foraging capabilities, that is, its ability to find prey and feed efficiently. There are many hypotheses concerning how right whales go about locating suitable prey patches (reviewed by Kenney et al., 2001), but there is little evidence to elucidate how this is actually accomplished. One plausible hypothesis is that right whales learn where profitable feeding grounds are located through maternal "teaching" or individual experience. There is strong evidence that right whales exhibit similar regional site fidelity to that of their mothers (Schaeff et al., 1993; Malik et al., 1999). Furthermore, Mate et al. (1997) tracked a female equipped with a satellite-monitored radio tag that was accompanied by her calf from the lower Bay of Fundy to Cape Cod Bay, Nantucket Shoals, the northern mid-Atlantic Bight south of Long Island, New York and back again to the lower Bay of Fundy. These movements suggest that females bring their calves to alternative feeding grounds and thus teach their calves where to forage (Bruce R. Mate, personal communication). At spatial scales of several to tens of kilometers, right whales may rely on hydrographic or chemical cues (Kenney et al., 2001) or may even localize sounds produced occasionally by other feeding right whales (Watkins and Schevill, 1976) to find prey patches. At spatial scales of tens of meters, right whales must have sensory capabilities to detect prey concentrations, such as vision, sensory hairs or taste (Kenney et al., 2001). Observations of right whales foraging at depths that were likely devoid of light suggests that vision does not aid in locating prey (Chapter 2). Yet accurate and immediate selection of the depth of maximum *C. finmarchicus* C5 without any searching suggests that right whales have some mechanism to observe prey concentrations directly. Since *C. finmarchicus* C5 were not observed in the bottom mixed layer, the results of Chapter 2 indicate that right whales restrict their foraging to depths above this layer. Based on individual foraging experience, right

whales may be able to similarly exclude other strata in the water column (e.g., surface waters in the summer or fall when *C. finmarchicus* C5 abundance there is low) or even whole geographic regions from their foraging activities.

Once a prey patch is located, right whales can modify their foraging behavior to increase ingestion rates. This can be accomplished by increasing swim speeds and maximizing their time in the patch. Ingestion rate is proportional to swim speed when a right whale is filter-feeding in a patch of constant prey density, but increasing swim speed to increase ingestion has an associated cost. Hydrodynamic drag increases with the square of the swim speed (Costa and Williams, 1999), so the metabolic rate to support faster swimming also increases exponentially. Therefore, the energetic benefit of an increased ingestion rate must exceed the energetic cost of higher drag at faster swim speeds. The appropriate balance between these benefits and costs is likely realized at the observed feeding swim speeds of approximately 1.5 m s^{-1} (Watkins and Schevill, 1976; Mayo et al., 2001). During skim-feeding, right whales make adjustments in their movements to remain in those areas of the patch that have the highest prey concentrations (Watkins and Schevill, 1979; Mayo and Marx, 1990). Right whales do not need to leave the patch in order to breathe when skim feeding, whereas feeding at depth must be punctuated by respiration intervals. Therefore, efforts to maximize the time spent in the patch will not only involve sensory capabilities to detect the highest prey concentrations, but will also include aspects of diving behavior such as dive times, depth of feeding and descent and ascent rates. Chapter 2 indicated that ascent and descent rates were positively correlated with time within the patch (i.e., duration at depth) and Chapter 3 suggested that right whales seek areas where prey were shoal. For a constant total dive time (which is presumably fixed by physiology), faster descent and ascent speeds and shallower dive depths afford a right whale longer time in a prey patch and hence, higher ingestion rates.

6.2. IMPLICATIONS FOR DISTRIBUTION, MOVEMENTS AND PREY ABUNDANCE MEASUREMENTS

The factors that affect prey consumption are likely the primary influences of right whale distribution on the northern feeding grounds, but how do *C. finmarchicus* productivity, survivorship, horizontal and vertical aggregation and availability to surface-bound whales interact to determine right whale distribution both in space and time? Spatial variability in *C. finmarchicus* abundance varies by as much as 4-6 orders of magnitude during summer in the Gulf of Maine (Meise and O'Reilly, 1996). In comparison, interannual variability in the abundance of *C. finmarchicus* is low; annual *C. finmarchicus* abundance in the Gulf of Maine only varies by about 2 orders of magnitude (Meise-Munns et al., 1990; Conversi et al., 2001). As mentioned above, interannual variability in secondary production and survivorship are likely influenced by variability in complex atmosphere-ocean interactions such as the NAO (Fromentin and Planque, 1996; Conversi et al., 2001). These processes occur at spatial scales that are much larger than the Gulf of Maine and Scotian Shelf, so spatial variability in *C. finmarchicus* production and survivorship might actually be quite low. Therefore, the large, observed spatial variability in *C. finmarchicus* abundance is likely attributable to aggregative mechanisms and not spatial variability in secondary production or survivorship. I would suggest, then, that the large-scale spatial distribution of right whales is principally influenced by interannual and spatial variability in aggregative mechanisms.

High-use areas, such as Cape Cod Bay, the Great South Channel and the lower Bay of Fundy, are probably characterized by reliable physical mechanisms that aggregate prey every year. Therefore, right whales return to these areas annually. Circulation patterns provide an influx of late-stage *C. finmarchicus* (as indicated for the Great South Channel by Miller et al. [1998]), so prey abundance is probably independent of local secondary productivity. The timing of *C.*

finmarchicus development may determine if copepods are advected into these high-use areas at a stage that is appropriate for predation by right whales. For instance, Wishner et al. (1995) and Kenney (2001) suggest that in years of colder spring waters, *C. finmarchicus* development is delayed and regional currents advect them through the Great South Channel by the time they reach stages 4 or 5. This may explain why right whales are located on the eastern (downstream) side of the Great South Channel or along the northern flank of Georges Bank during late spring in some years (Kenney et al., 1995).

Aggregative mechanisms also have significant implications for relating right whale occurrence with measures of prey abundance made at regional or larger spatial scales. Consider the case where the total regional abundance of late-stage *C. finmarchicus* is high, but there is no aggregative mechanism. These copepods would not be aggregated in dense enough local concentrations for right whales to feed on them profitably. Since foraging conditions are poor, right whales would not remain in the area. Thus, right whale occurrence may not be associated with regional-scale measurements of prey abundance. To illustrate this, recall the results of the habitat study presented in Chapter 3. Right whale relative abundance increased from 1999 to 2001 in Roseway Basin, yet the regionally averaged, OPC-derived *C. finmarchicus* C5 abundance decreased over this same period. Moreover, the odds of sighting a right whale were over 9 times greater in the lower Bay of Fundy than in Roseway Basin during 2000, the same year that the regional average of OPC-derived *C. finmarchicus* C5 abundance in Roseway Basin was 8 times higher than that in the lower Bay of Fundy. The analyses of Chapter 3 indicated, albeit tenuously, that interannual variability in right whale occurrence in Roseway Basin was positively associated with SST gradient, a proxy for ocean fronts. Increased presence and strength of ocean fronts in Roseway Basin during 2001 was accompanied by a significant increase in the odds of sighting a right whale. Therefore, I suggest that, despite the relatively low regional abundance of *C.*

finmarchicus C5 during 2001, these ocean fronts aggregated *C. finmarchicus* C5 into dense concentrations at small spatial scales that could then be exploited by right whales.

As noted above, right whales likely abandon regions with low prey abundance on these smaller spatial scales. In years of low *C. finmarchicus* production or survivorship, right whales may even abandon areas with strong, reliable aggregative mechanisms, since lower abundances of prey will be depleted after some time there. Therefore, variability in aggregative mechanisms or *C. finmarchicus* production and survivorship can induce changes in right whale site fidelity and movements. However, site fidelity for reproductively active animals must also be influenced by breeding opportunities. It is unclear if high-use areas are visited because they provide reliable feeding conditions or because other animals also visit there and thus they provide reliable breeding opportunities. It seems likely that the former is the primary influence whereas the latter is an advantageous side-effect. But what happens in years when aggregative mechanisms fail or *C. finmarchicus* production is low? Whales must move more often to feed and may not encounter other animals as frequently. Not only will whales ingest less prey and store less fat in these years, but breeding may also be curtailed due to fewer encounters with other animals. Thus, reproductive success may be severely depressed by these environmental factors. Chapter 4 documents time periods when the residency of satellite-tagged whales in the lower Bay of Fundy was both low (1989-1991) and high (2000). Zooplankton samples collected near right whales suggest that 1989 may have been a year of higher *C. finmarchicus* abundance in this region compared to 2000 (Woodley and Gaskin, 1996; Chapter 3). Although the zooplankton sample sizes were quite small and sampling was not collocated with the satellite-tagged whales, these data suggest that some right whales remain in particular regions even when feeding conditions are sub-optimal to maximize their breeding opportunities. For instance, reproductively active males may remain in an

area regardless of the prey conditions for the opportunity to breed with females that visit the region. Males may be more tolerant of poor feeding conditions, since their reproductive capabilities are not diminished by low fat reserves. The sample sizes obtained in Chapter 4 made it difficult to confirm such demographic trends in site fidelity.

6.3. FUTURE WORK

This research has raised a number of issues that merit continued or new investigation. The work described in Chapter 2 suffers from our lack of understanding of right whale metabolic rates. If it were possible to directly measure metabolism in right whales, then a more accurate comparison of ingestion rates and metabolic rates could be made to address the hypothesis that right whales do not ingest enough food to successfully reproduce. Measuring metabolism in large whales appears impossible, since current techniques require manipulation of the animal. It may be possible, however, to directly measure *relative* metabolic rates. A heat flux sensor could be incorporated into the tag described in Chapter 2 (after Westgate et al., 2001), and by making a few assumptions, metabolic rate might be inferred from the resulting heat flux measurements. These assumptions are as follows: (1) core temperature remains constant, (2) total heat loss is proportional to metabolic rate, (3) the proportion of a whale's total heat loss given off by a discrete area of skin always remains constant and (4) resting metabolic rate is known or can be reasonably estimated. By assumptions 1-3, the variability in the heat flux measurement will be proportional to the variability in metabolic rate. Heat flux measurements averaged over different activities (e.g., foraging and resting) will then provide an estimate of relative metabolic rate (i.e., foraging relative to resting). Absolute metabolic rate during foraging (M_f) could be computed as follows:

$$M_f = \frac{F_f}{F_r} M_r$$

where F_f is the average heat flux during foraging, F_r is the average heat flux during resting and M_r is the known or estimated resting metabolic rate. These measurements, however, would require longer attachment durations than those achieved in Chapter 2 to fully capture the desired behaviors.

Comparable studies to those presented in Chapters 2 and 3 would be beneficial in other high-use areas. In particular, foraging ecology and habitat investigations in the two other feeding areas, Cape Cod Bay and the Great South Channel, would provide a better understanding of the physical mechanisms and aspects of copepod behavior that make *C. finmarchicus* available to right whales in a springtime high-use area. Surface processes and phytoplankton production and abundance will likely influence *C. finmarchicus* distribution, so different measurements and instrumentation may be required. The increased abundance of phytoplankton and small zooplankton may cause difficulties for an OPC, so different instrumentation for assessing prey distribution may be required, such as a video plankton recorder (VPR; Davis et al., 1992) or acoustic instruments. One interesting addition to such a study might be the recently installed CODAR array on Cape Cod which would provide synoptic measurements of surface currents over both of these proposed study areas. Surface aggregation of *C. finmarchicus* could then be investigated with respect to processes related to wind forcing, such as turbulent mixing, convergent fronts or Langmuir cells. Integrated foraging ecology and regional-scale habitat studies in Cape Cod Bay and the Great South Channel would allow direct comparison of diving behavior, foraging strategies and habitat requirements to observations obtained in the lower Bay of Fundy and Roseway Basin (Chapters 2 and 3).

Continued monitoring of regional-scale right whale occurrence and associated environmental variables in the lower Bay of Fundy and Roseway Basin would also be desirable to refine inferences about interannual variability. Recall that the 3-year duration of the study described in Chapter 3 was not ideal for detecting associations between interannual variability in right whale occurrence and the environmental variables. Several more years of surveys might, for instance, elucidate the relationship between right whale presence in Roseway Basin and the occurrence of cooler temperatures and higher SST gradients there. Alternatively, a retrospective study may be conducted with historical sightings and AVHRR data. Surveys have been conducted in Roseway Basin since 1983 (Kraus et al., 2001) and an examination of these data with corresponding remotely-sensed SST and SST gradient observations may provide independent confirmation of the temporal associations between right whales, SST and SST gradient identified in Chapter 3.

The difficulties in measuring mean currents in the lower Bay of Fundy were discussed in Chapter 3. In that study, it was difficult to infer that a gyre existed in Grand Manan Basin of the Lower Bay of Fundy from hydrographic measurements alone since the residual barotropic component of the currents was probably of similar magnitude to the density-driven component. Modern numerical ocean models have the capacity to provide these mean currents, given sufficiently accurate forcing fields. It would be extremely useful to know where in the Gulf of Maine and on the Scotian Shelf passively advected particles may be aggregated due to either convergence or closed circulation. A model of mean currents over particular seasons would provide the advective field into which particles could be introduced and tracked. This approach was used by Miller et al. (1998) in an individual-based model of *C. finmarchicus* distribution to determine the location of diapause-ready copepodites that were spawned in particular areas. The underlying physics of this model (Lynch et al., 1996) might be used in a similar fashion to identify other areas at other times of the year where passive particles would be concentrated. These

areas might then be presumed to have one of the characteristics of a right whale high-use area: an aggregative mechanism. This approach would be useful, for instance, to investigate the currents around Jefferys Ledge to determine if an aggregative mechanism is a persistent feature there. If so, this may explain why right whales use this area in the fall (Weinrich, 2000; Chapter 4).

An important drawback of the OPC calibration equation presented in Chapter 5 is that it is based on *C. finmarchicus* C5 abundance estimates that only range as high as 1621 copepods m^{-3} . The concentrations that right whales encounter while feeding are at least an order of magnitude above this value. In fact, all of the OPC-derived *C. finmarchicus* C5 abundance estimates presented in Chapter 2 are extrapolations from this calibration equation. It is nearly impossible to calibrate the OPC with traditional net samples at the smaller spatial scales resolvable by the OPC. Therefore, it would be helpful to collect collocated measurements with an OPC and other instrumentation designed to rapidly estimate *C. finmarchicus* C5 abundance at similar spatial scales as the OPC. One candidate for this intercomparison is a VPR which records digital images of a small volume of water and uses pattern recognition software to count and identify particles in the digital images. In the presence of feeding whales, the VPR could corroborate the “blind” OPC observations of high *C. finmarchicus* C5 abundance at the depth of feeding. Moreover, quantitative comparison between these two instruments would confirm the appropriateness of using the calibration equation determined in Chapter 5 for abundances outside the range of the calibration dataset.

Finally, significant methodological improvement in the statistical analysis of radio-tracked right whale movements with respect to environmental conditions is required. The novel methods presented in Chapter 4 are a good start, but could use refinement. The Monte Carlo approach was, in my opinion, a powerful technique to assign an accurate probability of obtaining the observed number of individuals or ARGOS-acquired locations in a particular area by chance. This approach provided

an answer to the very simple and intuitive question, “Could there have been as many (or as few) locations or individuals in this area if the tagged right whales simply wandered about at random?” The analysis accounts for all of the idiosyncrasies of the whale’s radio-tracked movements, such as the duration of the deployment and the whale’s speed of travel. Given these idiosyncrasies, it is sometimes difficult to tell just by looking at maps of ARGOS-acquired data whether a cluster of locations or individuals in a particular area is significant or not. The Monte Carlo techniques provided the statistical methodology to assess this significance directly. The technique presented in Chapter 4 for examining the distribution of environmental variables observed at the ARGOS-acquired locations was, however, not nearly as satisfying. In this case, the distribution of observed environmental variables must be compared to 10,000 similar distributions derived from Monte-Carlo-generated random tracks to determine if right whales are found in particular conditions more often than expected. The observed value of a statistic can easily be judged extreme when its sampling distribution is known (either via modeling or, as in Chapter 4, via Monte-Carlo methods). But how does one judge whether an observed *distribution* is extreme? My approach was to separately test the “extremeness” of the mean, standard deviation, skewness and kurtosis of the observed distribution (after Manly, 1997), as well as to classify the continuous environmental variables in discrete bins and test the observed number of locations and individuals in each of these bins. This was not particularly elegant nor was it, I suspect, the best approach. Considering the large volume of radio-tracked animal movement data in both the terrestrial and marine environments and the need for these types of analyses, further refinement or improvement of these methods would be quite useful.

6.4. LITERATURE CITED

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