Using the Continuous Plankton Recorder to Investigate the Abandonment of the Roseway Basin Foraging Ground by the North Atlantic Right Whale (*Eubalaena glacialis*)

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ABSTRACT

North Atlantic right whales (*Eubalaena glacialis*) abandoned Roseway Basin, located off southeastern Nova Scotia, for a seven-year period (1993-1999). The objective of this study was to examine the availability of the right whale's main prey, *Calanus finmarchicus*, in Roseway Basin during the abandonment to determine if right whales left this region due to inadequate prey resources. Since we had no historical data on zooplankton abundances at depth on the Scotian Shelf, near-surface zooplankton abundance data from the Continuous Plankton Recorder were used to infer water column abundances. In addition, environmental parameters that are often correlated with high zooplankton concentrations were examined. The hypotheses tested were that changes in these parameters would be detectable between three time periods: pre-1993, 1993-1999, and post-1999. *Calanus finmarchicus* abundance was found to be lowest during 1993-1999, confirming that right whales were not foraging in Roseway Basin because of the near-absence of their main prey species. Decreased *in situ* salinity and density proved to be indicators of the changes in circulation in the 1990s that may have affected the advection of *C. finmarchicus* onto the Scotian Shelf.

INTRODUCTION

The North Atlantic right whale (*Eubalaena glacialis*) is one of the most endangered large whale species in the world (Kenney *et al.,* 1995; Clapham *et al.,* 1999; Kraus *et al.*, 2005). The western North Atlantic stock was estimated at 438 individuals in 2008 (NARWC, 2009; Pettis, 2009). They utilize four main feeding grounds around the Gulf of Maine (Winn *et al.*, 1986) (Fig. 1), although their patterns of seasonal movements are highly variable and there is a great deal of interannual variability of habitat use among individuals. Our study focused on the Roseway Basin foraging area in the coastal waters of Nova Scotia, which is primarily utilized by right whales during the late summer and early autumn.

The right whale is a baleen whale that feeds by "skimming," or swimming with the mouth open at or below the surface and allowing water to flow through the baleen filtering apparatus, trapping organisms too large to pass through the baleen. Observational data show that right whales in Roseway Basin forage primarily at depth; often very close to the ocean bottom (Winn *et al.*, 1986; Baumgartner and Mate, 2003). Although there is some variation in prey between feeding grounds in the North Atlantic (Pendleton *et al.*, 2009), in the Scotian Shelf region right whales have been observed feeding mostly on only older copepodid stages (copepodid stage 5 = CV) of *Calanus finmarchicus*

(Baumgartner *et al.*, 2007). It has been hypothesized that these late stage *C. finmarchicus* are preyed upon by right whales because of their high availability and large size in comparison to other species of copepods. Also, *Calanus* copepodids are often in diapause during the late summer and autumn. Diapausing copepods are rich in oil, yielding a higher caloric intake (Baumgartner *et al.*, 2003a), another potential reason for right whale feeding preferences.

The populations of *C. finmarchicus* on the Scotian Shelf must be sustained by either local reproduction or by advection (McLaren *et al.,* 2001). Head *et al.* (Head *et al.*, 1999) suggested that *C. finmarchicus* is advected onto the Scotian Shelf in the spring by the deep slope water. Plourde and Runge (Plourde and Runge, 1993) and McLaren *et al.* (McLaren *et al.*, 2001) suggested that the Scotian Shelf Current is the dominant supply for expatriate *C. finmarchicus* in the late summer. It is thought that dense aggregations of older copepodid stages of *C. finmarchicus* may be the most important component comprising right whale foraging 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; Baumgartner *et al.,* 2003b). The processes causing these aggregations are ambiguous, particularly in the Scotian Shelf region. Physical oceanographic parameters, meteorological measurements, and atmospheric indices are often used as proxies to investigate copepod distributions (Baumgartner *et al.,* 2003a; Greene *et al.,* 2003; DeLorenzo Costa *et al.*, 2006).

North Atlantic right whales largely abandoned the Roseway Basin feeding ground on the southeastern Scotian Shelf for a seven-year period from 1993 to 1999 (Brown *et al.,* 2001; IWC, 2001) (Table I). Our underlying hypothesis is that the whales abandoned this feeding ground because there was inadequate prey species composition and/or concentrations. During this same seven-year period, there was a large increase in the number of right whales observed in the lower Bay of Fundy feeding ground (Patrician, 2005). The North Atlantic right whale population suffered poor overall health condition (Pettis *et al.*, 2004) and low reproductive success (Kraus *et al.*, 2001, Kraus *et al.*, 2007) during the 1990s, suggestive of food stress. It has been speculated that the abandonment of Roseway Basin and the overcrowding of the Bay of Fundy may have contributed to these conditions.

We used the long-term zooplankton abundance data from the Continuous Plankton Recorder (CPR) to assess prey availability before, during and after this abandonment event. The CPR survey is an extensive global marine biological monitoring program managed by the Sir Alister Hardy Foundation for Ocean Sciences in Plymouth, UK. The CPR instrument is towed by merchant ships to monitor near-surface plankton. The CPR filters plankton from the water on a moving silk band over long distances (up to 500 nautical miles). The silk filter band is wound on rollers through the CPR and the plankton samples are preserved in formalin in a storage tank inside the internal mechanism (Hardy, 1956; SAHFOS, 2004; Richardson *et al.*, 2006). On return to the laboratory, the filter band is removed and divided into samples representing 10 nautical miles of towing.

The CPR provides only near-surface zooplankton data, however, right whales feed throughout the water column. Since we had no historical data for zooplankton concentrations in Scotian Shelf waters at depth, we relied on CPR data from the upper 10 m as an index of water column *C. finmarchicus* abundances in Roseway Basin. Pendleton *et al.* (2009) used CPR data to examine relationships between right whale distribution and copepod abundance in both Cape Cod Bay and Great South Channel. They showed that the near-surface numbers from the CPR are a reasonable estimate of the availability of prey for right whales (Pendleton *et al.,* 2009) and found a positive relationship between CPR measures and estimates from standard water-column net tows.

We examined a variety of factors—biotic (remotely sensed chlorophyll, *in situ* chlorophyll and phytoplankton color index) and abiotic (sea-surface temperature, frontal probability, *in situ* temperature, salinity and density, wind observations, the North Atlantic Oscillation and the Gulf Stream Index)—to determine their effects on zooplankton, emphasizing the ecological relationships between the environmental parameters and *C. finmarchicus* abundance. Therefore, the objectives of this study were to (*i*) examine the availability of *C. finmarchicus* in Roseway Basin before, during and after the seven-year abandonment period and (*ii*) examine the environmental parameters which may have affected the advection and/or aggregation of *C. finmarchicus*.

METHOD

The study area was defined to encompass the right whale feeding habitat in the waters surrounding southwestern Nova Scotia (Fig. 1). Although centered on Roseway Basin, it also included Browns Bank, Baccaro Bank, and portions of Roseway and LaHave Banks. The study area also extended into the Northeast Channel and included some deeper waters beyond the shelf break. It was also designed to include the Canadian Department of Fisheries and Oceans (DFO) right whale conservation area for Roseway Basin.

Various temporal scales were examined. Seasons were used to more closely analyze trends during the summer and autumn, when right whales are found in the Nova Scotian feeding grounds (Winn *et al.* 1986). Seasons were defined as: Winter (January–March), Spring (April–June), Summer (July–September), and Autumn (October–December). Data were also organized into time periods to examine differences between the period when the whales abandoned Roseway Basin and the periods before and after the abandonment. These periods were defined as "PRE" (1985–1992), "DURING" (1993–1999), and "POST" (2000 to the most current data available, which varied between datasets), respectively.

Calanus finmarchicus abundance (number of organisms/100 m^3) and Phytoplankton Color Index (PCI) data were obtained from the CPR dataset for the Roseway Basin study area from 1985 to 2004. Plankton off the eastern coast of North America and Canada are sampled by the CPR on a monthly basis by the NOAA National Marine Fisheries Service (NMFS) Laboratory in Narragansett, Rhode Island (Jossi *et al.,* 2003) (Fig. 1). Only a portion of Roseway Basin is sampled by the NMFS transect and the data in this study come from only the segment of the transect found within the Roseway Basin study area boundaries (Fig. 1). Based on mesh size used during sampling, two size classes of *Calanus* sp. are quantified: copepodid stages I-IV, for which no species identification is assigned, and copepodid stage V-VI, defined as *C. finmarchicus*. This study focused on the abundance of *C. finmarchicus* CV-VI, herein referred to, for simplicity, as *C. finmarchicus*. Samples are also examined for phytoplankton color and given a 'green-ness' value of 0 (no green-ness), 1 (very pale green), 2 (pale green), or 6.5 (green). The data used for this study were those from the transect seen within the box in Figure 1.

Remotely sensed data were collected from the Advanced Very High Resolution Radiometer (AVHRR) sensors on polar-orbiting satellites and processed into sea-surface temperature (SST) images. The AVHRR data had been processed and archived at the University of Rhode Island (URI) according to the methods of Cornillon *et al.* (Cornillon *et al.*, 1987). Processed AVHRR data (1.2 km resolution) from 1985 to 1999 were obtained from the Oceanographic Remote Sensing Laboratory at the University of Massachusetts at Dartmouth (Bisagni and Smith, 1998) and were processed using the Pathfinder algorithm (Vazquez *et al.*, 1995). Processed AVHRR data (1.25 km resolution) from 2000 to 2002 were obtained from URI (Yoder *et al*., 2002) and were processed using the multi-channel sea-surface temperature algorithm (Walton, 1988).

The probability of surface thermal fronts was determined by the application of an edge-detection algorithm on processed AVHRR SST data (Ullman and Cornillon, 1999). Monthly-averaged data, already run through the edge-detection algorithm, were obtained from URI for January 1985 to August 2003. Frontal probability was determined by dividing the number of times a pixel was on a front by the number of times a pixel was clear.

Remote-sensing data from the Sea-viewing, Wide Field-of-view Sensor (SeaWiFS) were used from September 1997 to August 2004. These data, at 1.4 km resolution, were obtained from URI. Chlorophyll-*a* values (mg/m^3) were calculated according to the URI standard SeaWiFS processing method (O'Reilly *et al*., 1998, 2000; Yoder *et al.*, 2002; Schollaert *et al.*, 2004). For January 1985 to June 1986, data from the Coastal Zone Color Scanner (CZCS), at 1.4 km resolution, were obtained from the NMFS Narragansett Laboratory. The CZCS data were converted so they could be compared directly to the SeaWiFS data (Gregg *et al.,* 2003).

Hydrographic data for Roseway Basin from 1985 to 2004 were collected from the Ocean Science hydrographic database, available from the Bedford Institute of Oceanography (BIO), Dartmouth, Nova Scotia (BIO, 2004). CTD profiles (temperature (°C), salinity (psu), and density (σ_t)) with depths ranging from 0 m to 600 m were obtained. Within the profiles, samples from individual depths had been binned into depth classes: every 10 m (+/- 5 m) from 0 to 50 m, every 25 m (+/- 10 m) from 75 to 300 m, and every 100 m (+/- 25 m) from 400 to 600 m. There were no sample data for intermediate depths between the depth classes.

For all in situ measurements, there was uneven weighting of the data throughout the profile. The majority of the study area consisted of shallow banks and basins which did not reach depths below 150 m. Therefore, there was a spatial bias in the number of profiles sampled that extended below 200 m. Also, these data were obtained in already-binned depth classes and the binning scheme included increasing gaps between those depth classes with increasing depth. This resulted in uneven weighting of the data included in average water column properties in the lower portion of the water column—the depths between the pycnocline and 100 m were more heavily weighted than depths below 100 m. Statistical analyses were run with all data and with all samples below 200 m removed.

The CTD profile data were also used to determine pycnocline intensities and depths. The density gradient between each successive pair of depths was determined as the difference between the sigma-t values divided by the difference in depth. The depth for each gradient value was assigned as the mid-point between the two successive depths. The maximum gradient value for each profile was identified. The magnitude of the maximum gradient was defined as "Pycnocline Intensity" (sigma-t units/100 m) and the depth corresponding to that gradient value was defined as "Pycnocline Depth" (m). If there were two or more identical maximum gradient values for one profile, the value at the shallowest depth was used.

An index of water column stability was determined using sigma-t values. Average "Pycnocline Depth" was used to define the upper and lower layers of the water column by area and season. The index value was defined as the average sigma-t of the lower layer minus the average sigma-t of the upper layer. The same average "Pycnocline Depth" was also used to define the upper and lower layers of the water column by area and season for *in situ* temperature, salinity and density analyses.

BIO also provided *in situ* chlorophyll data from their BioChem database—a collection of biology and chemistry data gathered from a number of DFO research institutions (Gregory and Narayanan, 2003). *In situ* chlorophyll data (µg/L) from 1985 to 2003 were extracted from this database for Roseway Basin.

Wind speed and direction at Yarmouth, Nova Scotia were obtained from the wind observation database maintained by Environment Canada and distributed by the Atlantic Zone Monitoring Program in DFO (AZMP, 2004). Daily and monthly mean wind speeds were computed directly from the hourly data, however, wind directions could not be directly averaged because they are circular data, not linear data. In order to calculate mean wind direction, the true eastward component (U) and true northward component (V) of wind speed were averaged separately, and mean wind direction was then trigonometrically calculated from mean U and mean V. Using this method, the computed mean wind direction is the compass direction that the wind is blowing towards, which is the opposite of the typical meteorological convention.

The NOAA Climate Prediction Center has a current database of the monthly North Atlantic Oscillation (NAO) index dating back to 1950 (CPC, 2004). Since the effects of NAO variability are most apparent throughout the winter, when the Icelandic Low and Azores High are strongest, the standard practice is to use the winter mean NAO (Hurrell, 1995). Winter NAO was calculated as the average of the monthly NAO values for the months of December (of the prior year), January, February, and March.

The Plymouth Marine Laboratory in Plymouth, England, has an extensive collection of Gulf Stream Index (GSI) data available as monthly time-series data from 1966 to 2003 (Taylor, 2004). Higher GSI values indicate the Gulf Stream location is farther northward, while lower values indicate the Gulf Stream location is farther southward. For this study, data from 1985 to 2003 were extracted.

A number of analyses were performed in order to investigate the data. For each dataset, the first step was to test for significant interannual variability using non-parametric analysis of variance (Kruskal-Wallis test), by month and for all months combined. Non-parametric analysis of variance was used because the data were not normally distributed. Absence of significant interannual variability eliminated that dataset from further analysis.

After the initial investigation of each dataset, the data were examined based on the three defined time periods of our study. Non-parametric ANOVA (Kruskal-Wallis test) was used to test for significant inter-period variability, by month and season, with a null hypothesis of no significant variability. The alternative hypothesis was that there was significant inter-period variability, with a prediction that the DURING period would have clearly different values from the PRE and POST periods, whose values would be similar.

RESULTS

C. finmarchicus abundance was lowest throughout the DURING period in summer and autumn (the seasons in which right whales inhabit the feeding grounds) (Table II). Average *C. finmarchicus* abundance throughout the DURING period in the summer was 1000 per m^3. This is extremely low when compared to the PRE and POST period mean abundances of 3800 per m^3 and 1900 per m^3, respectively. The same low abundances were seen throughout the DURING period for autumn. The mean abundance for the DURING period for autumn was only 110 per m^3, while the PRE and POST mean abundances were 1100 per m^3 and 180 per m^3, respectively.

Right whale sightings and SPUE (sightings per unit effort) in Roseway Basin dropped to zero in 1993 and remained at zero through the entire DURING period, except for two small deviations observed in 1995 and 1998 (Table I, Fig. 2). Right whales slowly began to return to the Roseway Basin feeding ground in 2000 and steadily increased in SPUE to 2004. Summer *C. finmarchicus* abundance closely shadowed this pattern, with peak POST period abundance in 2002 (Fig. 2). A non-parametric (Spearman) correlation analysis showed a significant correlation between SPUE and summer *C. finmarchicus* abundance (r^2=0.274, P=0.018). Autumn *C. finmarchicus* abundance, however, dropped off much earlier, in 1990, and remained low throughout the rest of the study (Fig. 2), and the correlation with SPUE was not statistically significant (r^2=0.125, P=0.125). These data suggest that it is the summer abundance of *C. finmarchicus* that is the most important cue for right whale foraging and residence in Roseway Basin.

The following parameters did not show statistically significant variability between the PRE, DURING and POST periods, and therefore were excluded from the rest of the analysis: sea-surface and *in situ* temperature, remotely-sensed and *in situ* chlorophyll, wind speed and direction, pycnocline depth, the North Atlantic Oscillation and the Gulf Stream Index. While pycnocline intensity did show significant variability between time periods, the results were not informative and therefore will also be excluded from further discussion. The rest of this analysis will focus on the potential effects of fronts, salinity and density on *C. finmarchicus* presence, aggregation and abundance.

PCI was used as an index of the amount of primary productivity ("green-ness") in the area at the time of copepod collection. Overall, the highest PCI was found throughout the DURING period ($\bar{X}$=0.7) when compared to the PRE and POST periods ($\bar{X}$=0.6 and $\bar{X}$=0.3, respectively), although the difference was only significant for all seasons combined (Table II). Even though the low mean PCI values ("very pale green") indicate the study area has generally low near-surface phytoplankton abundance, there was a statistically significant trend observable for the three time periods.

Overall, lower-salinity water was observed throughout the DURING period (Table II). There were no changes in any of the vertical profile analyses with or without samples below 200m—further evidence for the relatively low weighting of the deepest samples in the averages. The annual salinity measurements for each period were very close; therefore the results of the statistical analyses were not well illustrated in the vertical profile. There was a pivotal depth just below 100 m. Above this depth, the vertical profile showed the DURING period to be less saline than the PRE and POST periods. Below this depth, the PRE and DURING periods were more saline than the POST periods (Fig. 3). The surface layer demonstrated this trend the strongest with the top 20 m showing the greatest decrease in salinity throughout the DURING period ($\bar{X}$ = 31.49 psu) when compared to the PRE and POST periods ($\bar{X}$ = 31.72 psu and $\bar{X}$ = 31.82 psu, respectively).

The density of the water column was lowest throughout the DURING period for the upper portion of the water column (specifically 20-50 m) and spring appeared to be the season during which this trend was the most evident. The spring also demonstrated the clearest difference in water column stability (density difference between the upper and lower layers of the water column) in the DURING period ($\bar{X}$ = 1.01) when compared to the PRE and POST periods ($\bar{X}$ = 0.80 and $\bar{X}$ = 0.65, respectively). This low density and more stable water column, combined with the low salinity seen throughout the DURING period in the upper water column, is evidence to support a change in water-mass structure with a less saline, less dense water mass intruding at the surface throughout the DURING period.

Overall frontal probability was highest throughout the DURING period ($\bar{X}$ = 12.08%) when compared to the PRE and POST periods ($\bar{X}$ = 10.58% and $\bar{X}$ = 8.91%, respectively) (Table II) with exceptionally high values during 1995 and 1996 (>16%). Upon further investigation, the winter, spring and autumn seasons all had significantly higher frontal probabilities throughout the DURING period ($\bar{X}$ = 16.41%, $\bar{X}$ = 9.10% and $\bar{X}$ = 14.82%, respectively) when compared to the PRE and POST period.

DISCUSSION

Our underlying hypothesis was that western North Atlantic right whales abandoned the Roseway Basin feeding ground because prey resources were inadequate for successful right whale foraging. The zooplankton abundance data obtained from the CPR support this hypothesis. *Calanus finmarchicus* abundance was lowest throughout the summer and autumn months in the DURING period (Fig. 2). Although CPR data represent a measure of near-surface zooplankton because the instrument only samples the upper 10 meters of the water column (Richardson *et al.*, 2006), any sampling bias would have been identical across the entire period of the study. This suggests that CPR data may be used as an indicator to detect trends in zooplankton abundance throughout the water column. The conclusions of Pendleton *et al.* (2009) also supported the use of the CPR data as a proxy for water column abundance.

The decrease in *C. finmarchicus* abundance throughout the DURING period has been observed in the Gulf of Maine as well, as part of a 'community shift' of zooplankton throughout the 1990s (Pershing *et al.,* 2005; Greene and Pershing, 2007). There was a dramatic decrease in the abundance of older-stage *C. finmarchicus*, while smaller copepod species such as *Centropages*, *Oithona*, *Pseudocalanus*, *Metridia*, and *Calanus* copepodids (CI-IV) increased dramatically. This 'community shift' was correlated with several changes in recruitment patterns of fish stocks in the Gulf of Maine, suggesting that changes in the composition of the zooplankton community may be indicators of broad-scale processes (Pershing *et al.,* 2005).

Similar changes in fish stocks were also observed on the eastern (Frank, 2003) and western (Shackell and Frank, 2007; Shackell *et al.*, 2009) Scotian Shelf, where there was a shift in dominance from groundfish to smaller pelagic species. Increased predation on *C. finmarchicus*, as a result of this structural change in the fish community, could have also contributed to the low abundance of *C. finmarchicus* on the Scotian Shelf during this time. Since pelagic fish species prey on *C. finmarchicus* throughout their entire life cycle, while groundfish only prey on copepods during early juvenile stages of the life cycle (Bigelow and Schroeder, 1953), this shift in the structure of the fish community could also have led to an increase in predation on *C. finmarchicus* throughout the 1990s. Greene and Pershing (Greene and Pershing, 2007) similarly hypothesized that the decrease in *C. finmarchicus* CV and VI in the Gulf of Maine during the 1990s was a result of increased predation by herring, while small copepods increased due to bottom-up processes.

Of all the environmental and atmospheric parameters explored, *in situ* salinity and density provided the most information about the physical processes that may have affected *C. finmarchicus* abundance throughout the DURING period in Roseway Basin. A low-salinity (and low-density) anomaly was observed in the mid-1990s for the Gulf of Maine, Georges Bank, and the Mid-Atlantic Bight (Smith *et al.,* 2001; Drinkwater and Gilbert, 2004; Mountain, 2004; Greene and Pershing, 2007). Our findings are consistent with the observed anomaly, with the mean salinity values being lowest throughout the DURING period. This anomaly was caused, at least in part, by an increase in the inflow of low-salinity surface water from the Scotian Shelf to the Gulf of Maine (Mountain, 2004), derived from increased flow of fresher water from the Arctic Ocean to the Labrador Sea and downstream (Greene and Pershing, 2007). Scotian Shelf water (SSW), also referred to as the Nova Scotian Current, is relatively cold and low-salinity water that enters the region at the surface around Cape Sable (Smith, 1983). Slope water (SLW) is relatively warm and more saline water that enters the region at depth, especially through the Northeast Channel (Ramp *et al.,* 1985). The normal inflow of these waters into the Gulf of Maine is approximately a 2:1 ratio (SLW:SSW) (Mountain, 2004). While the total inflow of water into the region remained the same throughout the mid-1990s, there was a significant increase in the inflow of SSW and a decrease in the inflow of SLW into the region (Mountain, 2004), changing the ratio to approximately 1:2 (SLW:SSW) in the Gulf of Maine. This change in circulation was also seen in our *in situ* density data, with a decreased density throughout the DURING period for the upper layer. Frank (Frank, 2003) also observed this low-salinity anomaly for the eastern Scotian Shelf, attributing the change to upstream sources from the Grand Banks and beyond. Smith *et al.* (Smith *et al.*, 2001) and Drinkwater *et al.* (Drinkwater *et al.*, 2003) similarly found increased freshwater on the Labrador Shelf.

This low-salinity anomaly indicates a change in circulation patterns, as observed by Mountain (Mountain, 2004). Since *C. finmarchicus* is an expatriate species and must be advected onto the Scotian Shelf from external oceanic sources (Greene and Pershing, 2000; MERCINA, 2003, 2004) it can be assumed that a change in circulation may have affected the advection or aggregation of *C. finmarchicus* into Roseway Basin, resulting in the low abundance of *C. finmarchicus* seen throughout the DURING period (Fig. 2). In has been hypothesized that *C. finmarchicus* enters the Scotian Shelf in the spring in the SLW (Head *et al.,* 1999) and enters the region in the late summer in the SSW (Plourde and Runge, 1993; McLaren *et al.,* 2001). If this is the case, then the population of diapausing *C. finmarchicus* on which right whales are foraging enters the Scotian Shelf in the spring in the slope water. The decrease in the inflow of SLW throughout the 1990s would explain the decrease in abundance of *C. finmarchicus* observed throughout the DURING period.

Lastly, frontal probability was observed to have the highest mean value throughout the DURING period, when right whale and *C. finmarchicus* abundance were lowest. This appears, at first, to be inconsistent with the findings of Baumgartner *et al.* (Baumgartner *et al.*, 2003b), who showed that high SST gradients were associated with high right whale abundances. However, they worked at a much smaller spatial scale than our study; therefore, the results of the two studies are not directly comparable. Although right whales were located near the strongest fronts within a localized area

(Baumgartner *et al.*, 2003b), this does not necessarily predict that increased right whale presence is correlated with higher frontal probability over a broader region. While ocean fronts may be involved in the aggregation process of *C. finmarchicus*, this can only occur if the copepods are relatively abundant and actively being advected into the area. Our results suggest that the changes in circulation in the 1990s were responsible for both increased occurrence of fronts and decreased *C. finmarchicus* abundance. The increase in frontal probability may have been due to the increase in surface Scotian Shelf water in the region, causing greater dynamic interactions between surface currents, tides, and bathymetry.

The abandonment of Roseway Basin had detrimental effects on the North Atlantic right whale population. While there was a decrease in right whale abundance in Roseway Basin, there was an increase in the number of whales in the Bay of Fundy during those same years. The mean number of photo-identified right whales in the Bay of Fundy in the PRE period was 57 individuals (ranging from 31-74) while the mean for the DURING period was 174 individuals (ranging from 133-215) (Patrician, 2005). And this increase was drastic, with 72 individuals in the Bay of Fundy in 1992 and 148 individuals in 1993, the first year of the Roseway Basin abandonment (Patrician, 2005). This led to a greater number of whales competing for the same prey resource. A visual assessment of the health of the population concluded that the poor health condition of the right whales in the Bay of Fundy may have been due, at least in part, to starvation (Pettis *et al.*, 2004). It is likely that *C. finmarchicus* in the Bay of Fundy was not abundant enough to sustain the metabolic requirements of the increased number of foraging whales. Low prey availability may also explain the low reproductive success observed during the mid- to late 1990s, when there was a decrease in the numbers of calves born and an increase in the calving interval from 3-4 yr to 5-6 yr (Kraus *et al.*, 2001, Kenney, 2007, Kraus *et al.*, 2007).

Our findings support the hypothesis that right whales abandoned the Roseway Basin feeding ground because of inadequate prey resources. The long-term CPR data were invaluable in this analysis. The observed low-salinity (low-density) anomaly of the 1990s likely contributed, at least in part, to the low *C. finmarchicus* abundances observed in the study area throughout the DURING period by reducing the advection of *Calanus* into the region. The community shift observed in fish stocks, from groundfish to smaller pelagic species, may have led to increased predation on larger *C. finmarchicus*, also contributing to the reduced abundances. The small-scale processes responsible for creating the dense zooplankton aggregations upon which right whales feed are as yet poorly understood. At a broader scale, however, the factors underlying regional-scale zooplankton abundances appear to be a complex amalgam of top-down and bottom-up processes.

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TABLE AND FIGURE LEGENDS

Fig. 1. There are four main right whale feeding grounds around the Gulf of Maine—Cape Cod Bay, Great South Channel, the Scotian Shelf (Roseway Basin) and the lower Bay of Fundy. The Roseway Basin study area, designated by the box, was designed to include the right whale critical habitat area (small trapezoid; defined by DFO) and the surrounding waters. The general track of the NMFS CPR transect is shown by the heavy dashed line and only data from the segment of the transect found within the boundaries of the Roseway Basin study area was used in this study.

Table I: Total survey effort (km), sightings and numbers of whales sighted on Roseway Basin during the months of July through October from 1987 to 2004. Effort is the length of trackline surveyed during that year. Sightings are single observations of one or more whales. Sightings Per Unit Effort (SPUE, whales/1000 km) is the number of whales divided by effort (following Kenney and Winn, 1986; Winn *et al.*, 1986; Kenney, 1990; Hain *et al.*, 1992; Shoop and Kenney, 1992). ID is the number of confirmed photo-identified whales for each year (Kraus *et al.*, 1986). The shaded rows represent the years when right whales abandoned Roseway Basin.

Table II: Summary of all parameters that followed the predicted pattern of the study (the DURING period being statistically different than the PRE and POST periods). The results shown are based on a non-parametric Kruskal-Wallis ANOVA. Tests where the results were not statistically significant are not included.

Fig. 2. Annual North Atlantic right whale sightings per unit effort (SPUE) (solid line) compared to mean summer (solid bars) and autumn (open bars) *C. finmarchicus* abundance in the Roseway Basin study area. Low *C. finmarchicus* abundances for both seasons were found during the time right whales abandoned this feeding ground.

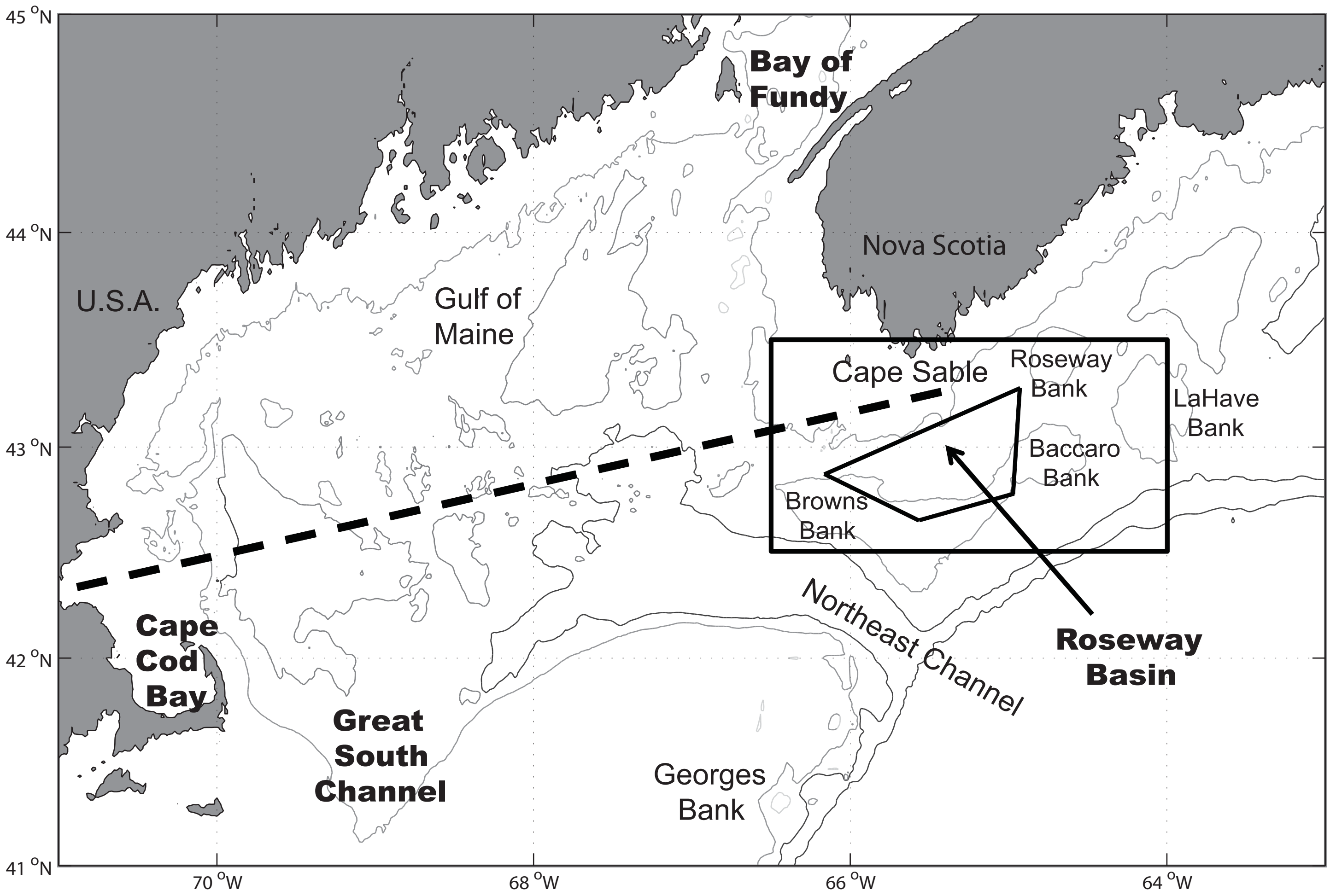
Fig. 3. Average annual vertical profiles of *in situ* salinity and density for the Roseway Basin study area, as defined by the three time periods of the study: PRE (1985–1992), DURING (1993–1999) and POST (2000–2004). Both *in situ* measurements showed a trend of lower values throughout the DURING period when compared to the PRE and POST periods in the upper layer of the water column.

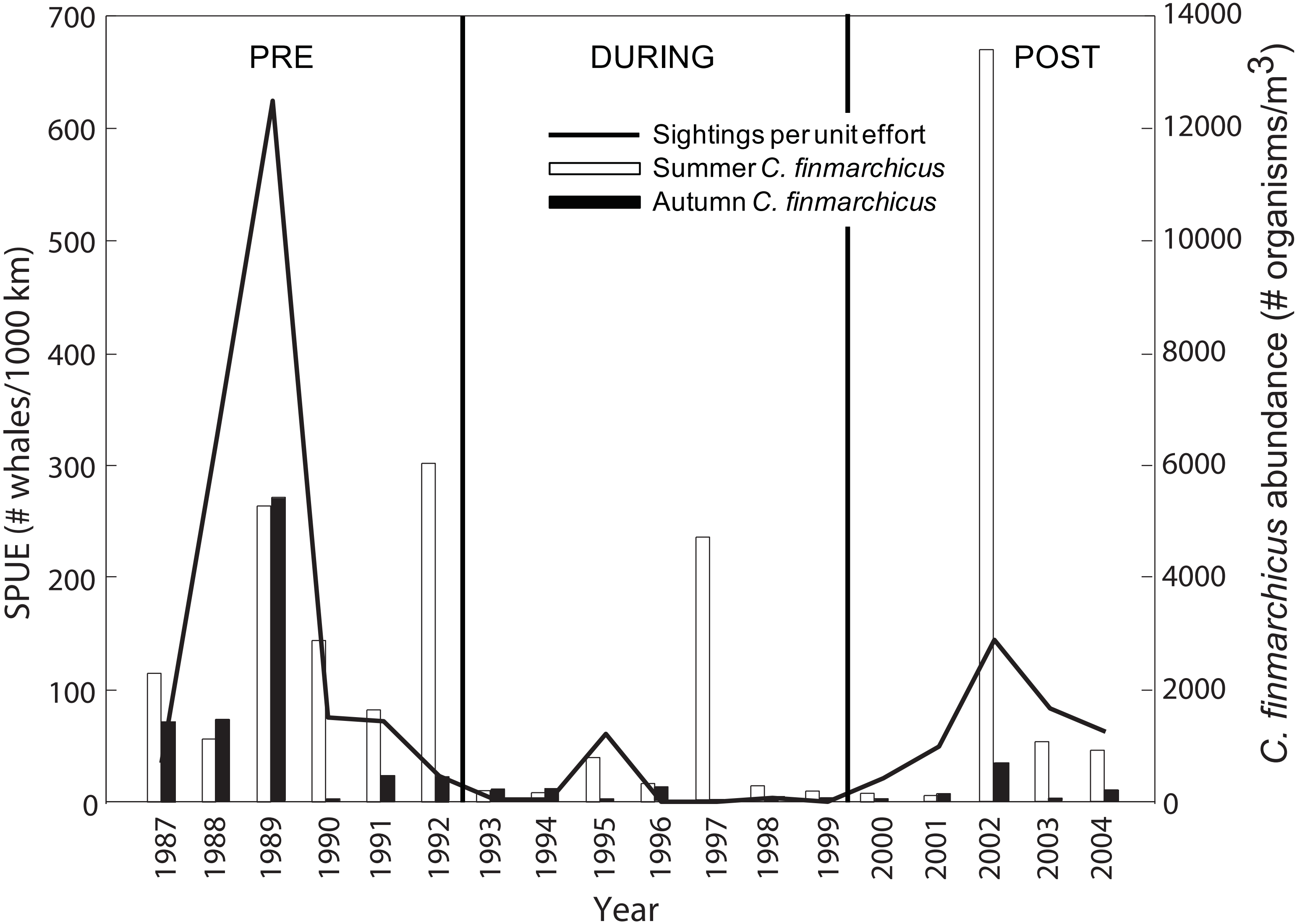
Table I: North Atlantic Right Whale Sighting Summary

Year	Effort	Sightings	Whales	Mean SPUE	SE of SPUE	ID
1987	2092.4	62	148	36.477	13.015	82
1988	1345.0	129	244	326.614	189.997	118
1989	1267.6	122	259	624.565	522.858	116
1990	522.0	42	74	76.647	34.198	47
1991	1487.5	86	170	73.315	19.362	91
1992	1391.4	29	39	24.728	8.069	17
1993	158.9	0	0	0.000	0.000	0
1994	962.2	0	0	0.000	0.000	0
1995	779.7	4	5	62.268	58.499	7
1996	299.0	0	0	0.000	0.000	0
1997	1842.7	0	0	0.000	0.000	4
1998	1106.0	1	1	1.335	1.335	4
1999	998.0	0	0	0.000	0.000	0
2000	2343.6	16	35	22.695	9.078	14
2001	1359.8	14	24	50.892	31.691	6
2002	483.5	32	48	145.706	58.948	42
2003	308.5	17	54	84.896	41.979	20
2004	1044.2	32	129	63.982	26.598	69

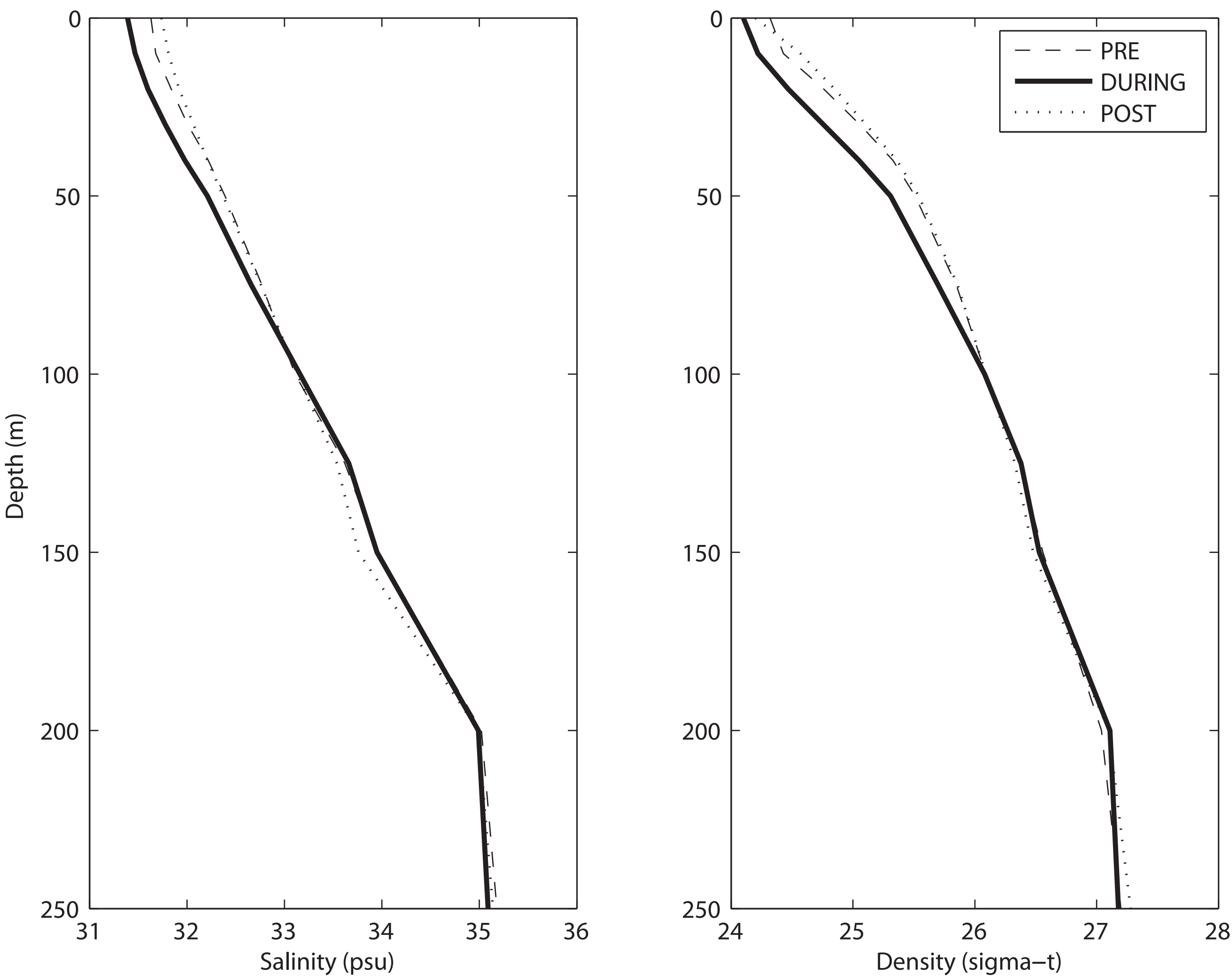
Table II: Significant Habitat Parameters

Dataset	Season	Depth (m)		PRE	DURING	POST	P	X^2
C. finmarchicus	Summer	N/A	$\overline{X}$	3834.1	1013.7	1895.9	<0.001	15.148
			n	24	19	10		
	Autumn	N/A	$\overline{X}$	1124.1	107.5	179.3	0.027	7.218
			n	21	11	7		
PCI	All	N/A	$\overline{X}$	0.6	0.7	0.3	0.009	9.503
			n	91	68	47		
In situ Salinity	All	All	$\overline{X}$	31.74	31.53	31.87	0.044	6.238
			n	36	38	25		
	All	0	$\overline{X}$	31.63	31.39	31.74	0.028	7.180
			n	37	38	25		
	All	10	$\overline{X}$	31.68	31.47	31.81	0.038	6.527
			n	29	38	25		
	All	20	$\overline{X}$	31.84	31.60	31.92	0.036	6.671
			n	29	38	25		
In situ Density	All	20	$\overline{X}$	24.76	24.47	24.85	0.024	7.479
			n	29	38	25		
	All	30	$\overline{X}$	25.06	24.76	25.11	0.003	11.706
			n	30	38	25		
	All	40	$\overline{X}$	25.33	25.05	25.36	0.002	12.661
			n	28	38	25		
	All	50	$\overline{X}$	25.51	25.31	25.54	0.017	8.123
			n	28	37	25		
	Spring	30	$\overline{X}$	25.44	25.08	25.29	0.008	9.582
			n	8	8	7		
	Spring	40	$\overline{X}$	25.60	25.20	25.38	0.011	8.955
			n	8	8	7		
	Summer	40	$\overline{X}$	25.56	25.30	25.50	0.035	6.176
			n	8	13	9		
	Spring	50	$\overline{X}$	25.74	25.3	25.46	0.021	7.754
			n	8	8	7		
	Spring	75	$\overline{X}$	25.97	25.63	25.72	0.047	6.117
			n	9	7	7		
Frontal Probability	Winter	N/A	$\overline{X}$	13.74	16.41	13.13	0.035	6.715
			n	24	21	12		
	Spring	N/A	$\overline{X}$	8.38	9.10	6.46	0.002	12.807
			n	24	21	12		
	Autumn	N/A	$\overline{X}$	13.45	14.82	8.54	0.029	7.101
			n	24	21	9		


45 °N
44 °N
43 °N
42 °N
41 °N
70 °W
68 °W
66 °W
64 °W
Bay of Fundy
Nova Scotia
U.S.A.
Gulf of Maine
Cape Sable
Roseway Bank
LaHave Bank
Baccaro Bank
Browns Bank
Northeast Channel
Roseway Basin
Cape Cod Bay
Great South Channel
Georges Bank



PRE
DURING
POST
Sightings per unit effort
Summer C. finmarchicus
Autumn C. finmarchicus
SPUE (# whales/1000 km)
C. finmarchicus abundance (# organisms/m3)
Year
0
100
200
300
400
500
600
700
0
2000
4000
6000
8000
10000
12000
14000
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004



Depth (m)
0
50
100
150
200
250
31
32
33
34
35
36
Salinity (psu)
24
25
26
27
28
Density (sigma−t)
PRE
DURING
POST