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Oceanographic connectivity between right whale critical habitats in Canada and its influence on whale abundance indices during 1987–2009

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ABSTRACT

The Roseway and Grand Manan basins on the Canadian Atlantic coast are neighboring late-summer critical feeding habitats for endangered North Atlantic right whales. Although in late summer these habitats regularly contain thick aggregations of right whale food – the copepod *Calanus* spp. – right whales periodically abandon one or both habitats in the same year. The causes of abandonments, their relationship to food supply, and the locations of whales during abandonment periods are unclear. The goals of this study were to explain variation in right whale abundance indices from a habitat perspective, and to determine whether or not oceanographic variation in the habitats influences occupancy. Four indices of whale abundance and habitat occupancy, including sightings per unit effort (SPUE), photographic sightings of known individuals, population size and habitat transition probabilities, were analyzed in relation to unique datasets of *Calanus* concentration and water mass characteristics in each basin over the period 1987 through 2009. *Calanus* concentration, water mass sources and various hydrographic properties each varied coherently between basins. *Calanus* concentration showed an increasing trend over time in each habitat, although a short-lived reduction in *Calanus* may have caused right whales to abandon Roseway Basin during the mid-1990s. Food supply explained variation in right whale sightings and population size in Roseway Basin, but not in Grand Manan Basin, suggesting that the Grand Manan Basin has important habitat characteristics in addition to food supply. Changes in the distribution of whale abundance indices during years when oceanographic conditions were associated with reduced food supply in the Scotia-Fundy region suggest that other suitable feeding habitats may not have existed during such years and resulted in negative effects on whale health and reproduction.

1. Introduction

The North Atlantic right whale (*Eubalaena glacialis*) is an endangered species that migrates to the Canadian eastern continental shelf to feed during summer (June through October). Grand Manan Basin in the Bay of Fundy and Roseway Basin on the Scotian Shelf are areas of whale aggregation that are federally-designated by Canada as 'critical habitat' (Brown et al., 2014) because they contain a rich supply of whale food; the *Calanus* spp. copepods. In preparation for the onset of winter, *Calanus* attain their annual maximum content of energy-rich lipid, enter diapause (hibernation) and sink into highly concentrated layers at depths near 100 m. These layers are an energetically valuable resource to right whales and other zooplankton predators (Baumgartner et al., 2003a,b; Davies et al., 2014; Michaud and Taggart, 2007, 2011; Murison and Gaskin, 1989; Woodley and Gaskin, 1996). The basins, with their energy-rich food supply, play a significant role in right whale ecology; e.g., Grand Manan is a nursery habitat where calves and cows can efficiently boost their energy reserves (Knowlton et al., 2000; Malik et al., 1999), and each habitat provides an energetic boon that helps sustain the whales through winter (Weisbrod et al., 2000). The habitats are also relevant to conservation monitoring teams who rely on the consistent and often highly concentrated whale residency to estimate population dynamics, demography (Brown et al., 2001), and health (Pettis et al., 2004) and to respond to fishing-gear entanglements (Knowlton et al., 2012) and vessel strikes (Silber et al., 2012).

The number of right whales observed in each basin in each year is variable (Hamilton et al., 2007). Right whales are thought to have virtually abandoned Roseway Basin and the nearby Great South Channel for several years during the mid-1990s, as did sei whales, another copepod predator (Brown et al., 2001; Hamilton et al., 2007), and surveys in 2013 documented the lowest number of right whales in Grand Manan since surveys began in the 1980s (Brown, Dr. M.W. pers. comm. Research Faculty, New England Aquarium. 1 Central Wharf, Boston MA, 02110, USA). The abandonment of critical feeding habitats, presumably due to a paucity of food, represents two serious conservation concerns; first because food supply is linked to variation in reproductive rate (Fujiwara and

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Caswell, 2001; Meyer-Gutbrod and Greene, 2014) and second because conservation measures implemented in the critical habitats (Lagueux et al., 2011; van der Hoop et al., 2014; Vanderlaan et al., 2008) will not protect whales if the whales are to be found elsewhere. There are few insights into where the whales go when known critical habitat is abandoned; for example whether they disperse to other Scotia-Fundy and Gulf of Maine feeding regions or migrate to other unknown habitats elsewhere. Grand Manan and Roseway are each within a few days swimming for a whale, and photo-identification and demographic evidence shows that during the apparent abandonment of Roseway in the 1990s, many whales normally observed in Roseway were instead observed in Grand Manan (Hamilton et al., 2007). In 2013, the year of fewest whale observations on record in Grand Manan, observations were at typical levels in Roseway, but the demographics were more representative of whales normally observed in Grand Manan (i.e., many cow-calf pairs, Brown, M.W., pers. comm.). It is hypothesized that some abandoning whales may migrate northward in search of alternate feeding habitats because the whales have been sporadically observed on the Scotian Shelf (Mitchell et al., 1986), in the Gulf of St. Lawrence, on the Newfoundland and Labrador shelves and in waters south of Greenland and Iceland (Knowlton et al., 1992; Lien et al., 1989); each of these areas are within the historic migratory range of the species (Reeves et al., 1978). Alternate nursery areas outside the Bay of Fundy must exist since approximately 39% of identified calves born are never sighted in Grand Manan, and finding the locations of these other nursery areas remains a conservation objective (Malik et al., 1999). The extent to which the two known Canadian late-summer critical feeding habitats may co-vary in quality and/or act as supporting habitats when other areas lack sufficient food has not been adequately addressed, and almost nothing is known about right whale aggregations in more northerly regions.

Several studies have hypothesized that the abandonment of Roseway and the Great South Channel, and concurrent decline in calving rates during the 1990s, were caused by declines in the abundance of *Calanus* sp. in the Gulf of Maine and Scotian Shelf waters (Greene and Pershing, 2007; Greene et al., 2008; Greene et al., 2013; Meyer-Gutbrod and Greene, 2014; Patrician and Kenney, 2010). Much of the late-summer diapausing copepod populations in Grand Manan and Roseway are not produced locally, but rather are advected into the basins by continental shelf and slope circulation, both before and after diapause has been initiated (Davies et al., 2014; Michaud and Taggart, 2007). During the 1990s, declines in semi-quantitative indices of *Calanus* abundance are hypothesized to have resulted from changes in large-scale circulation that reduced the advection of *Calanus* source waters into the region (Greene et al., 2013). Patrician and Kenney (2010) addressed this hypothesis by using Continuous Plankton Recorder (CPR) data collected in the surface layer southwest of Roseway Basin as an index of *Calanus finmarchicus* abundance before, during, and after the abandonment by right whales. They concluded that average near-surface *C. finmarchicus* abundance was lower during the abandonment period than either before or after. They attributed variation in surface-layer density, as well as variation in *C. finmarchicus* abundance, to a climate-associated water mass "regime shift" in the late-1980s caused by a low salinity water mass pulse from the Arctic that reduced phytoplankton and zooplankton productivity in the Gulf of Maine. This pulse was followed by a large drop in the North Atlantic Oscillation (NAO) which caused the transport of the cold, fresh water by the Nova Scotia Coastal Current to increase and the on-shelf transport of warm-salty Slope Water, the major supplier of copepods to the Shelf region in spring and summer, to decrease (Greene et al., 2013; Meyer-Gutbrod and Greene, 2014). The paucity of in situ biological data (i.e., diapausing copepods at depth) was a noted limitation of the Patrician and Kenney (2010) study because processes that advect and accumulate diapausing copepods at depths where right whales feed during late-summer lead to uncertainties in predicting at-depth concentrations based on surface-layer properties. Further, a region-wide decline in *Calanus* abundance and whale calving suggests that during the 1990s no suitable feeding habitats existed elsewhere (except Grand Manan) for the whales that abandoned Roseway. The large numbers of whales in Grand Manan during the 1990s suggest that this region may have provided sufficient food in the face of larger scale declines in *Calanus* elsewhere.

Given the variations summarized above, we here examine a suite of 22-year historical datasets of right whale observations, *Calanus* concentrations and water mass characteristics collected at depth in both the Grand Manan and Roseway basins with the goal of explaining interannual, decadal and between-habitat variation among four indices of right whale abundance and occupancy: sightings per unit effort, number of photo-identified individuals, statistically-derived populations estimates and transition probabilities (migration of individuals) among habitats. We address four questions: (1) How did whale observations, population estimates and habitat residency change in the Scotia-Fundy region during the abandonment of Roseway Basin in the mid-1990s? (2) Can interannual and decadal variation in whale observations in Grand Manan and (or) Roseway be explained by variation in prey concentration at depth? (3) Was the abandonment of Roseway Basin related to decreases in prey concentration at depth in Roseway while Grand Manan acted as a supporting habitat? (4) Can variation in *Calanus* source-water masses explain variation in *Calanus* concentration in either Basin?

2. Methods

2.1. Right whale observational time series

To quantify interannual variation in right whale abundance in the Grand Manan and Roseway feeding habitats, we compared two annual indices: sightings per unit effort (SPUE; number of whale sighted per 1000 km of survey track) provided by the North Atlantic Right Whale Consortium (NARWC, 2008), and number of photo-identified individuals (ID) from Hamilton et al. (2007) and Vanderlaan (2010). The SPUE and ID methodologies and quality control are provided in Brown et al. (2007) and summarized here. Survey platforms were vessels and aircraft following systematic survey lines and deviating only to collect IDs and biopsy samples. Observers used standardized methods with vessels traveling at ~12 knots (22 km h^{-1}) along typically N–S survey lines with an ~4 nautical mile, nm, (7.4 km) spacing. Data were considered valid only when visibility was ≥2 nm (3.7 km) and sea state <4 Beaufort scale. Aircraft followed survey lines at ~100 knots (185 km h^{-1}) at ~230 m altitude along E–W survey lines spaced at ~5 nm (9.3 km). All observed whales were counted and geo-referenced. SPUE data were provided for the period of 1987 through 2009 as cell-specific observations and effort estimates across the standard NARWC 20 × 20-cell (Grand Manan; total area = 2520 nm^2; 8643 km^2) and 25 × 20-cell (Roseway; total area = 3300 nm^2; 11,319 km^2) grids with each cell defined by 3′ N latitude and 3′ W longitude (Fig. 1). There were no surveys in Roseway during 1993, 2007 and 2008. We used all ID data collected during formal and opportunistic surveys over the period 1987 through 2005 (Hamilton et al., 2007) that were validated using the NARWC comprehensive catalog of all known right whale individuals (Hamilton et al., 2007; Kraus et al., 1986).

In 2007 and 2008 we collected right whale SPUE data in Roseway Basin either on dedicated transects or opportunistically while completing a comprehensive prey-field survey (prey-field analysis in Davies et al., 2014). SPUE estimates in each year were derived using the above NARWC protocol except the vessel traveled at ~3 to 8 knots, not along N–S transects, that were of limited extent (80 km in 2007 and 168 km in 2008). Forty-two sightings in 2007 and one sighting in 2008, corrected for effort, are included in our analyses, and should be interpreted with caution (likely under-estimates) due to the low number of dedicated observers (usually one). Annual SPUE estimates collected during August and September (late-summer) for each survey grid-cell were log-transformed to homogenize variance and then averaged across all surveyed grid-cells. In 2006 six grid-cells in Grand

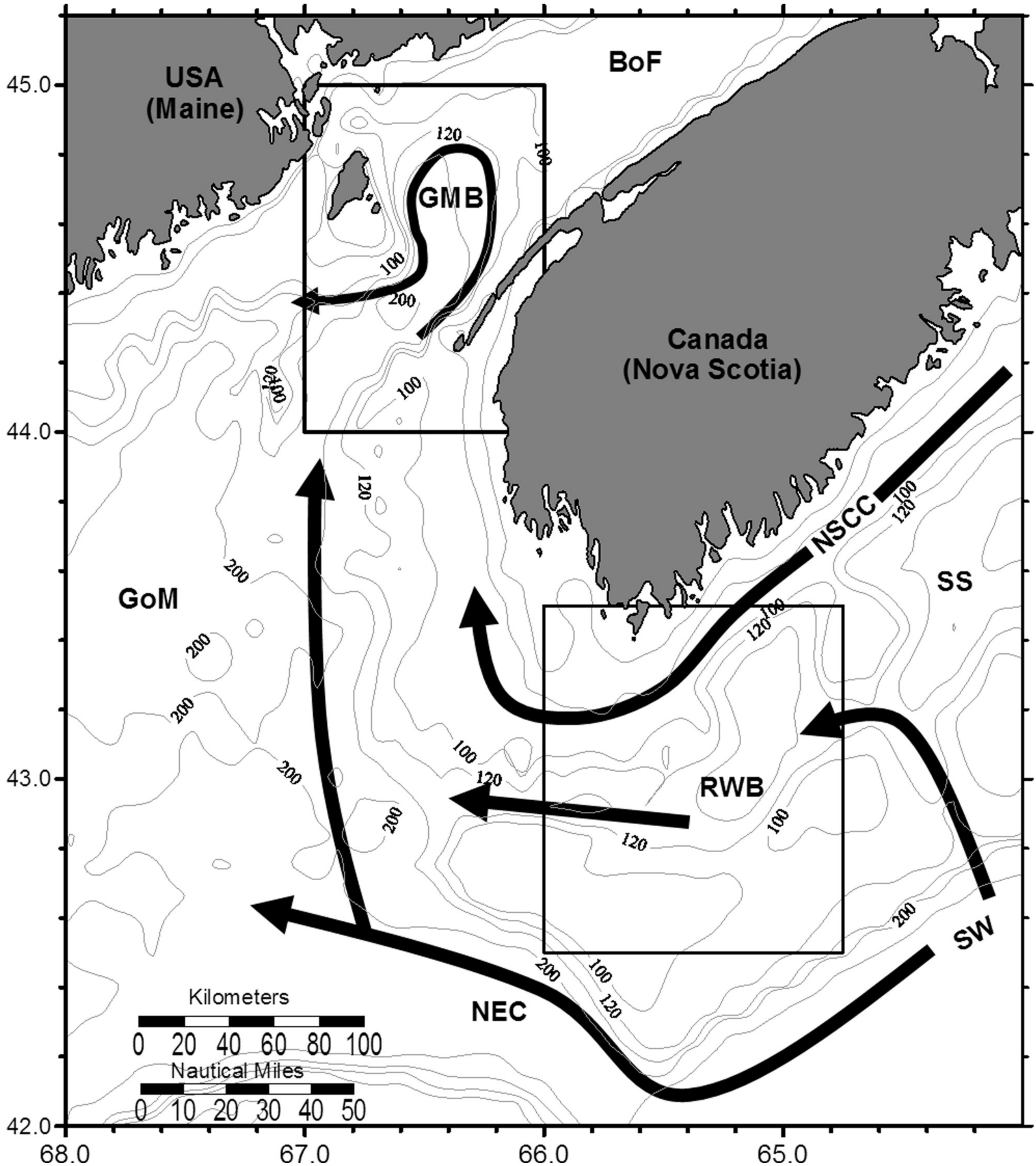

Fig. 1. Bathymetric (m) chart illustrating the data collection domains (black rectangles) in Grand Manan Basin (GMB) located in the Bay of Fundy (BoF), and Roseway Basin (RWB) located on the Scotian Shelf (SS). Habitat data collected deeper than the 100 m isobath in Roseway and the 120 m isobaths in Grand Manan Basin within these domains were used in this study. Arrows depict generalized circulation patterns of Slope Water (SW) moving along the Scotian Slope (SL) and into the Gulf of Maine (GoM) through the Northeast Channel (NEC), and the Nova Scotia Coastal Current (NSCC) moving along the SS.

Manan had anomalously high effort (650 to 960 km range) relative to the entire data set (3081 surveyed grid-cells) and were 20 fold greater than the inter-quartile range. Thus, the SPUE estimates for these cells were replaced by the overall grid-cell average (outliers excluded) of 41.2 whales per 1000 km, following Vanderlaan et al. (2008).

SPUE and ID indices were used in this study because each is an imperfect measure of whale abundance and each has different limitations when making comparisons between habitats and among years. ID data are biased as no meaningful estimate of effort is possible. There is no estimate of spatial or temporal variance within a year, and differences among years cannot be tested (Brillant et al., 2015). While SPUE includes effort and provides a variance, large uncertainties can accrue due to multiple sightings of the same whales. Further, survey effort not only varies among years and between habitats, particularly in Roseway Basin (Vanderlaan, 2010), it also tends to be concentrated where the whales are ‘expected’ to be observed.

2.2. Right whale population size and transition probabilities

Variation in right whale population estimates and residency across the Scotia-Fundy region were assessed by statistically estimating population size and individual transition probabilities from photo-identification data. These indices were estimated among habitats during August through October using the SOCPROG model (ver. 2.5), which performs statistical analyses on the mark-recapture ID data to estimate population parameters within the 'Movement' module (Whitehead, 2009). Such estimates for right whale photo-identification data were first published by Vanderlaan (2010) and Brillant et al. (2015). We completed three analyses; before (1988–1992), during (1993–1999) and after (2000–2005) the apparent abandonment of Roseway. Transition probabilities were estimated using the 'lagged identification rate' which in our case is the probability that an individual ID'd in either Roseway or Grand Manan would be later ID'd again in Roseway or Grand Manan or 'elsewhere', the latter being any region outside the two habitats. We used a 30-day lag to calculate the monthly transition probabilities based on the assumption that a whale ID'd in any region could reach any other region within this interval; i.e., full interchange between the habitats and (or) elsewhere. If a whale was not ID'd again after 60 days, it was judged to remain 'elsewhere'. We assumed a closed population where observations of the ID'd animals are independent and thus the lagged identification rate is the inverse of the population size. Standard errors were estimated using non-parametric bootstrap techniques (re-sampling with replacement, n = 10,000). The result was a 3 × 3 matrix where the diagonal represents the probability of a whale remaining in the same habitat after 30 days, and the off-diagonal entries represent the probability of transitioning to another habitat within 30 days.

Table 1
Late-summer (Aug through Oct) right whale population (Popn.) estimates and monthly transition (to, from) probabilities (+/− one standard error) among the Grand Manan and Roseway basins (see Fig. 1 for regional boundaries) and 'other' regions for each of: 1988 through 1992 when occupancy in Roseway Basin was higher than in Grand Manan, 1993 through 1999 when whales virtually abandoned Roseway, and 2000 through 2005 when the whales returned to Roseway. All estimates were derived from the 'Movement' module of SOCPROG (Whitehead, 2009).

(A) 1988–1992: Occupancy higher in Roseway Basin than Grand Manan Basin				
To area				
From area		Grand Manan	Roseway	Elsewhere
	Grand Manan	0.827 (0.108)	0.042 (0.016)	0.130 (0.107)
	Roseway	0.018 (0.007)	0.982 (0.086)	0.000 (0.086)
	Elsewhere	0.184 (0.201)	0.000 (0.185)	0.816 (0.271)
	Popn:	55 (14.9)	126 (20.9)	39 (25.6)
(B) 1993–1999: Abandonment of Roseway Basin				
To area				
From area		Grand Manan	Roseway	Other
	Grand Manan	0.974 (0.032)	0.025 (0.022)	0.001 (0.010)
	Roseway	0.195 (0.137)	0.605 (0.163)	0.199 (0.194)
	Elsewhere	0.007 (0.113)	0.021 (0.183)	0.972 (0.216)
	Popn:	177 (7.6)	23 (22.3)	58 (29.1)
(C) 2000–2005: Occupancy higher in Grand Manan Basin than Roseway Basin				
To area				
From area		Grand Manan	Roseway	Other
	Grand Manan	0.928 (0.036)	0.071 (0.036)	0.000 (0.006)
	Roseway	0.072 (0.077)	0.707 (0.163)	0.221 (0.143)
	Elsewhere	0.047 (0.040)	0.031 (0.087)	0.922 (0.096)
	Popn:	125 (8.6)	44 (27.2)	125 (42.4)

2.3. In situ Calanus concentration time series

To estimate how much of the interannual variation in whale occupancy was explained by food concentration we used in-situ concentration estimates of right whale food; diapausing *C. finmarchicus* copepodite stage-5 (hereafter C5) and *Calanus hyperboreus* copepodite stage-4 (hereafter C4) collected at depth (>100 m depth) in Grand Manan and Roseway during 1980 through 2009. The food data were based on a dataset we compiled from in-situ zooplankton samples collected in the basins before, during and after the Roseway abandonment period. We extended the *Calanus* time series to the 7 years that precede the right whale time series to better describe habitat conditions prior to abandonment. Data were gathered from five sources representing plankton collections within the boundaries of the 100 m isobath in Roseway and 120 m isobath in Grand Manan. A summary of the data sources, sampling gear and year and month of collections is provided in Suppl. Table 1 along with a description of collection details, sampling protocols and data treatment used to develop the time series of annual *Calanus* concentration, at depth, in each Basin.

2.4. Physical oceanographic time series

Comparisons of the above zooplankton time series with hydrographic data were made to explore the relationships between whale food and water masses within and between the two habitats. Temperature, salinity and density profiles collected within the Roseway and Grand Manan basins (Fig. 1) were extracted from the Fisheries and Ocean Canada (DFO) Hydrographic Climate Database[1] maintained at the Bedford Institute of Oceanography in Dartmouth, NS. Profiles were binned at 1 m depth resolution and encompassed late summer in each of 1980 through 2009 (Suppl. Tables 2 & 3). The data were screened for duplicates, density inversions, extreme values, and impossible depths. Additional CTD profiles were collected by Dalhousie Oceanography in Roseway during 2007 through 2009 and in Grand Manan during 2002 using a SeaBird SBE-25 CTD. Deep-water time series were created by calculating the average temperature (T, °C), salinity (S, PSU) and density (D, sigma-t, ρ(S,T)-1000 kg m^{-3}) below 100 m from each profile and then by calculating the average T, S and D (± 1 SE) over all profiles within each year in each Basin. No data were available for 1981 and 1985 in Roseway Basin, and for several years in Grand Manan (Suppl. Tables 2 & 3).

Interannual variation in the presence of different water masses in Grand Manan and Roseway was estimated by quantifying the relative contributions of potential *Calanus* source waters within each basin, each year. To achieve this, the hydrographic data (as above) were extracted among all hydrographic areal polygons (Petrie et al., 1996) containing the Nova Scotia Coastal Current (polygon SS14), Slope Water (SS34), and Northeast Channel Water (SS29). Each represents a potential source water to each basin. Data were extracted for late-summer each year and then averaged over a 100 to maximum 200 m depth range. As three source-water masses could contribute to each Basin (see results) it was possible to calculate the relative proportion that each contributed annually to each Basin by using the T–S signature and solving the following set of linear equations:

$$aT_{source1} + bT_{source2} + cT_{source3} = T_{deep\_basin} \quad (4)$$

$$aS_{source1} + bS_{source2} + cS_{source3} = S_{deep\_basin} \quad (5)$$

$$a + b + c = 1 \quad (6)$$

where a, b and c are the desired proportions, and subscripts represent each of the source and Basin water masses.

2.5. Statistical analyses

Interannual variation in right whale SPUE was assessed within each habitat using an unbalanced Welch ANOVA (Legendre and Borcard, 2008), with Games–Howell post-hoc pair-wise comparisons. Linear trends in the *Calanus* concentration time series were defined statistically in each habitat using analysis of covariance (ANCOVA) with 'year' as the

[1] http://www.mar.dfo-mpo.gc.ca/science/ocean/database/doc2006/clim2006app.html.

continuous independent variable and 'habitat' (Grand Manan or Roseway) the discrete independent variable. Correlations between habitats and all variables (SPUE, ID, *Calanus* concentration and hydrography) were assessed using Pearson's correlation coefficient (r), where the biological variables were log-transformed. Variation in *Calanus* concentration was grouped among sets of years using Principal Components Analysis (PCA). Within each habitat, the dependence of annual right whale observations on *Calanus* concentration was assessed using linear regression, where the biological variables were log-transformed. The dependence of *Calanus* on hydrographic variables and source water mass proportions were assessed within each habitat using stepwise multiple linear regression. Model selection was based on multivariate linear regression employing criteria to maximize explained variance (r^2), and maintain significant ($P \sim 0.05$) F-values for the model and the contributing variables. A total of 12 possible independent hydrographic variables were used as predictors in each habitat.

3. Results

3.1. Right whale observations, transition probabilities and population size estimates before, during and after Roseway abandonment

Over the 33-year series the annual average SPUE varied between 20 and 264 sightings per 1000 km in Grand Manan Basin, and between 0 and 202 in Roseway (Fig. 2A, B). The maximum number of whales ID'd within a year in Roseway was approximately half the maximum in Grand Manan, and there were five years in the 1990s when no whales were photo-identified in Roseway. Annual SPUE and the total number of whales ID'd were strongly correlated in Roseway ($r = 0.88$, $P < 0.001$) with relatively high index values pre-1993, at or near zero values over 1993 through 1999, and subsequently high values with the exception of 2005 and 2008 when available abundance indices were as low as in the mid-1990s (Fig. 2B). In contrast, whales were observed and ID'd every year in Grand Manan, though the interannual variation in inferred residency is ambiguous given that the SPUE and ID indices were not correlated (Fig. 2A). Each index showed a strong increase in Grand Manan in 1993; the year the whales presumably abandoned Roseway. Thereafter the SPUE index decreased back to pre-1993 levels with some indication of an increase starting around 2005.

The annual number of ID'd whales was inversely correlated between habitats ($r = -0.68$, $P < 0.003$, Fig. 2C) over the entire series. Assuming that the index is directly comparable between basins, this result may indicate that there were years when one basin was preferentially occupied by the whales relative to the other. When the index was subdivided into three periods, there were more whales in Roseway than in Grand Manan during 1988–1991, many more in Grand Manan than Roseway during 1992–1999, and post-1999 the index began to increase in Roseway while declining in Grand Manan. Similarly, the population estimates for the two basins and elsewhere (Table 1), based on IDs, indicated that the Roseway estimates were inversely related to the Grand

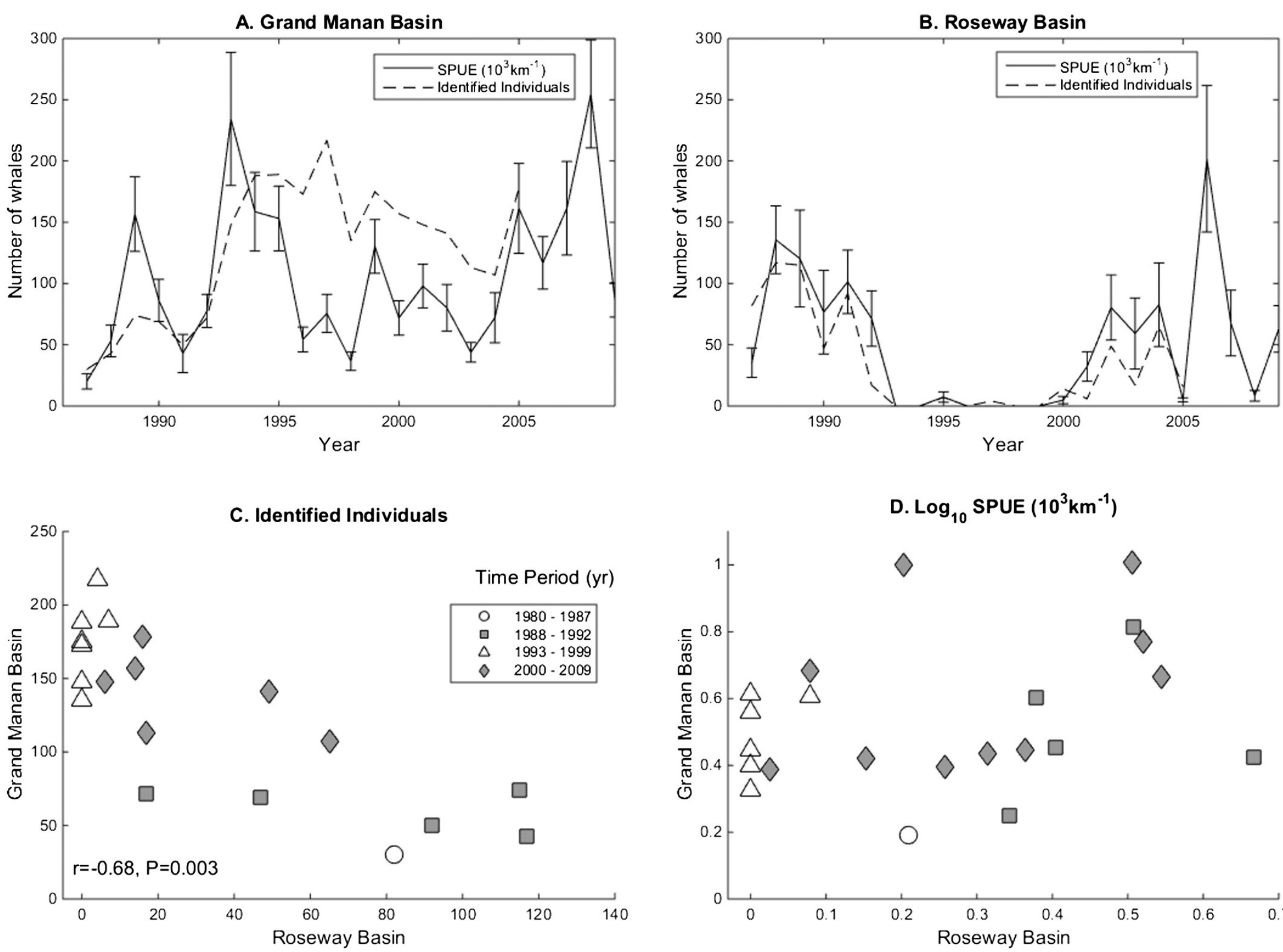

Fig. 2. Comparisons of inter-annual variation in late summer (Aug–Sep) average right whale sightings per unit effort (SPUE, sightings per 1000 km, 1987–2009) and photo-identified individuals (1987–2005, from Vanderlaan, 2010) between the Roseway and Grand Manan basin critical habitats. Data are compared as time series (A, B) and as correlation between habitats (C, D). Each datum represents a single year, and in (C, D) data are aggregated among 4 periods based on variation in the abundance of whale food in Roseway Basin: 1980–1987 (open circles, low food); 1988–1992 (filled squares, high food); 1993–1999 (open triangles, low food); 2000–2009 (closed diamonds, high food).

Manan and 'elsewhere' estimates among all three periods (Table 1A, B, C). Further, prior to the Roseway abandonment period, a 2- to 3-fold larger population (~126 whales) resided in Roseway relative to the other two regions (Table 1A). During the Roseway abandonment period, Grand Manan contained the highest population estimate of ~177 whales (Table 1B) while subsequently both Grand Manan and elsewhere shared equally high estimates (~125 whales) while those for Roseway (~44 whales) were moderate (Table 1C).

Although there was a significant correlation in the ID index between the two basins, there was no such correlation between the SPUE indices (Fig. 2D). Since SPUE and ID were well correlated in Roseway, we surmised that the difference in correlations pointed to different temporal patterns in the two indices in Grand Manan. Using the population size and transition estimates, we asked how do we explain that after 1993 the annual number of ID'd whales in Grand Manan remained high while the average SPUE returned to its lower pre-1993 levels (Fig. 2A)? We initially reasoned that the discrepancy could occur if many different individuals entered Grand Manan but the residence time of each was short, producing high turnover within Grand Manan while the average number of whales (i.e., average SPUE) at any given time remained low. However, during the abandonment period, the increased population estimate in Grand Manan was not associated with increased transitions to Roseway or 'elsewhere' (Table 1B). Right whales residing in both Grand Manan and 'elsewhere' during late-summer showed very high fidelity for those regions over 30 days in all three periods (0.827 to 0.974), whereas in Roseway fidelity varied from 0.605 during abandonment (Table 1B) to 0.982 when the population in Roseway was high (Table 1A).

3.2. Does Calanus concentration explain variation in whale occupancy?

Annual average *Calanus* concentrations in each Basin varied between 40 and 1927 m^{-3} during 1980 through 2009 (Fig. 3A). The ANCOVA between the two series revealed an overall positive trend that was not different between the basins (Table 2, Fig. 3A). During 1993 through 1999, the period of Roseway abandonment, the residuals for each Basin were negative, whereas from 2000 through 2009, almost all residuals were positive (Fig. 3A). The annual *Calanus* concentrations between habitats were marginally positively correlated ($r = 0.52$, $P = 0.046$), and two distinct relationships operating at different scales were apparent (Fig. 3B). At the larger of the two scales, PCA isolated two groups along the 1st PC that accounted for 80% of the variance. The two groups are the 'high prey' group ([*Calanus*] order 1000 m^{-3}) containing the 1989 and 1999 through 2004 estimates, and the 'low prey' group ([*Calanus*] order 100 m^{-3}) encompassing the 1981, 1983 1987, 1994, 1996 and 1998 estimates. Within each group strong negative correlations existed between the two basins ('low prey', $r = -0.813$, $P = 0.049$; 'high prey', $r = -0.906$, $P = 0.005$).

Calanus concentration significantly explained 30 to 50% of the interannual variation in the whale abundance indices in Roseway Basin, but not significantly so in Grand Manan. In Roseway Basin, both indices increased with increasing *Calanus* concentration among years (Fig. 3C, D), although the relationship between *Calanus* and SPUE was best described by a linear model ($r^2 = 0.46$), while that with ID'd whales was best described by a quadratic ($r^2 = 0.32$); perhaps indicative of a carrying capacity. Right whales occupied Roseway during the period when *Calanus* concentration was high and were virtually absent when *Calanus* concentration was low during 1993 through 1999. In contrast, *Calanus* concentration did not explain a significant degree of variation in either of the whale abundance indices in Grand Manan (Fig. 3E, F) although the relationship with SPUE was marginal ($P = 0.056$, Fig. 3E), suggesting that the prey field may play a role in influencing whale abundance and (or) occupancy in Grand Manan. When the right whale transition probabilities and population size estimates were compared with the 'high' and 'low' *Calanus* estimates before (high), during (low) and after (high) the Roseway abandonment, they were qualitatively correlated. During 1988–1992, high *Calanus* concentrations in Roseway coincided with a high whale population (~126) and a high transition probability (0.982) into the Basin (Table 1A). The 'low prey' period of the mid-1990s coincided with virtual abandonment of the habitat with a whale population estimate of ~23 whales that were much more likely (~0.40) to depart Roseway than to remain relative to the probability (~0.02) for the previous period (Table 1B). From year 2000 onward, the population estimate in Roseway Basin was lower than expected (44 individuals) given the consistently high *Calanus* concentrations, though the probability of remaining resident (~0.71) was higher than that (~0.61) of the previous period (Table 1C, Fig. 3A). It is not possible to draw a meaningful comparison between the low population abundance of right whales in the Grand Manan Basin and *Calanus* concentration during the pre-abandonment period due to sparse (i.e., 2) *Calanus* estimates. However, the data do demonstrate that during the Roseway abandonment, the high whale population size in Grand Manan (~177) and the correspondingly high residency probability (0.974) coincided with low prey concentration and the *Calanus* concentrations in Grand Manan were as low or lower than in Roseway (Fig. 3A, B). From 2000 through 2005, *Calanus* concentration, SPUE, ID and whale population size estimates were all elevated in Grand Manan Basin.

3.3. Can Calanus variation be explained by the transport of water masses?

Annual temperature and salinity estimates of deep (>100 m) waters were each correlated between the two basins (Fig. 4A, B, Suppl. Fig. 3). Salinity was approximately of the same magnitude in each basin whereas water mass temperature was consistently warmer in Grand Manan by up to 3 °C, causing the deep waters of Grand Manan Basin to be, on average, less dense than Roseway (Fig. 4C). Three water masses of differing origin (Nova Scotia Coastal Current — NSCC, Slope Water — SW, and Upper Layer Roseway Water — ULRW) contributed to three water mass end-members (Basin Water — BW; intermediate Basin Water — iBW; and modified Basin Water, mBW) that characterized the deep waters of Roseway (Fig. 5A). The NSCC, a cold and (relatively) salty (average $T = 2.8$ °C and $S = 33.4$) water mass, was the major source of the BW end-member. SW (average $T = 8.7$ °C and $S = 34.8$), originating over the continental slope, was the major source of the warmer, saltier mBW end-member. The third end-member, iBW (Fig. 5A), appeared to be a mixture of the denser NSCC and SW source water masses. The third source water (ULRW, average $T = 7$ °C and $S = 32.1$) originated in the low-density shallow layer overlaying the deep basin water, and likely contributed to the deep-water mass through vertical mixing. The largest interannual variation in the deep-water hydrography of Roseway occurred in a direction parallel to the mBW and BW end-member mixing line (Fig. 5A). Within any given year, more ULRW modified the deep layer hydrographic signature in Roseway toward the warm-fresh side of the mixing line, while mixing between the NSCC and SW sources modified the hydrographic signature toward the cold-salty side of the mixing line.

Three source water masses also contributed to the deep-water end-members in Grand Manan Basin; SW, Upper Layer Fundy Water (ULFW), and western Scotian Shelf water represented by Roseway Basin (RWB) water (Fig. 5A). We concluded that Roseway Basin was a source of water to Grand Manan, or at least a good proxy, for three reasons: the water mass characteristics in each basin were correlated (Fig. 4A, B), the two basin-water-masses were closer to each other on the T–S diagram than any external source water (Fig. 5A), and Roseway lies upstream of Grand Manan (Fig. 1). The NSCC was a less significant source water to Grand Manan because the NSCC water originates well upstream of Roseway Basin in the Gulf of St. Lawrence (Fig. 1. Fig. 5A), and no new influxes of NSCC water occur between Roseway and Grand Manan. Thus the signature of NSCC in Grand Manan Basin was reflected only by the Roseway Basin source water (Fig. 5A). Unlike NSCC water, SW did enter the Grand Manan Basin region southwest and downstream of Roseway through the Northeast Channel (Fig. 1,

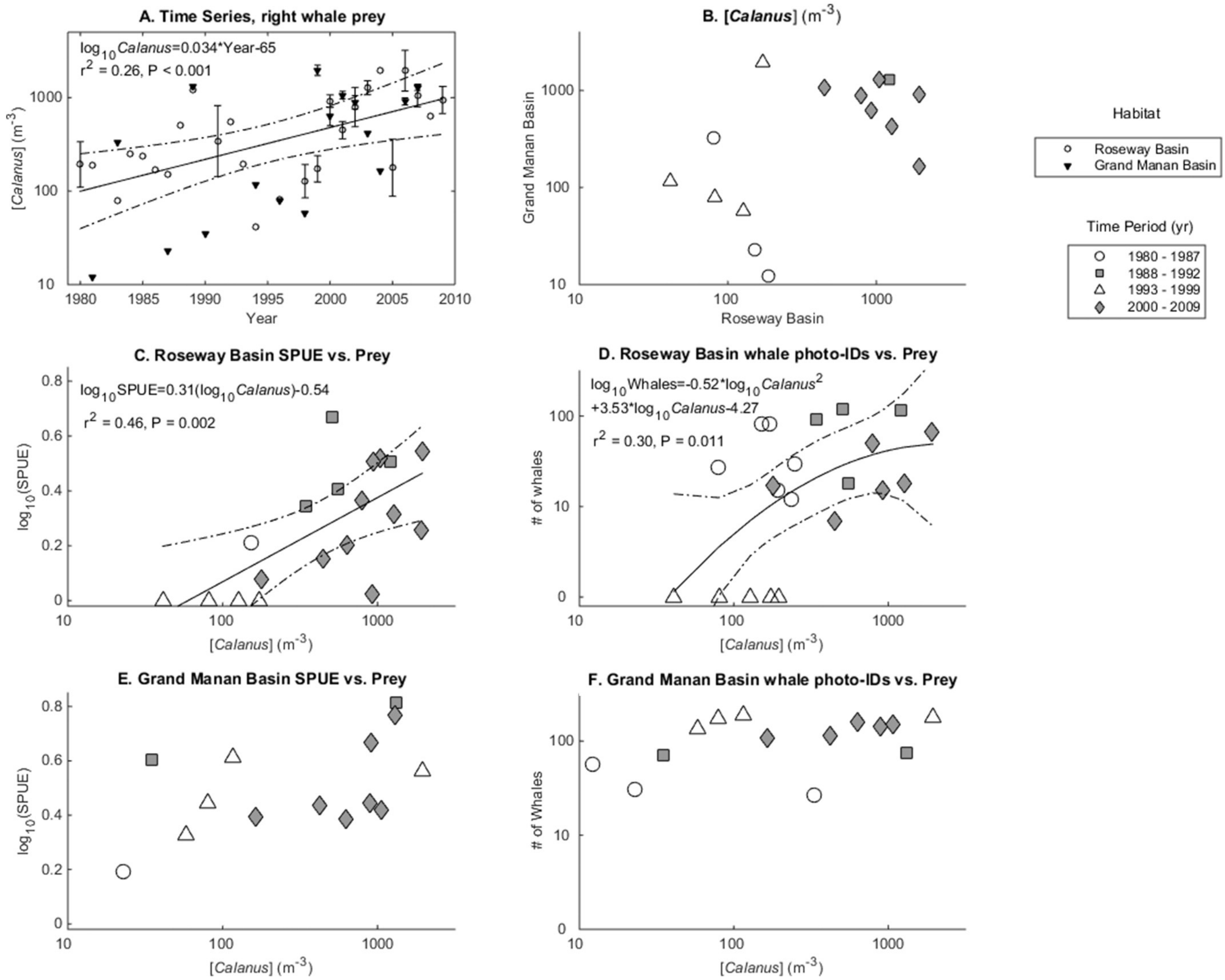

Fig. 3. Interannual variations in average *Calanus* spp. concentration (m^{-3}) in the Grand Manan and Roseway basins compared (A) as time series within each Basin and (B) between basins, (C, E) to right whale sightings per unit effort (SPUE, sightings per 1000 km) within each habitat, and with (D, F) the number of photo-identified right whales (# of whales) within each habitat. Scatter-grams in C–D show regression models (solid line) only when significant. Each datum represents a single year in A, and 4 periods in B–F where data were aggregated based on variation in the abundance of whale food in Roseway Basin: 1980–1987 (open circles, low prey); 1988–1992 (filled squares, high prey); 1993–1999 (open triangles, low prey); 2000–2009 (closed diamonds, high prey).

Fig. 5A). Strong tidal currents and vertical mixing in the Bay of Fundy made ULFW a significant water mass source.

Multiple regression analysis for assessing the dependence of *Calanus* concentrations in Roseway on water mass hydrographic properties,

Table 2
Statistical summary of analysis of covariance for diapausing *Calanus* concentration (m^{-3}) estimates with effects of year (continuous variable) and Grand Manan and Roseway basins (discrete factor).

Source	Deg. of freedom	Adj. sum sq.	Adj. mean sq.	F-value	P-value
Regression	3	4.33	1.44	6.54	0.001
Year	1	2.67	2.67	12.09	0.001
Habitat	1	0.44	0.44	1.98	0.17
Year × habitat	1	0.43	0.43	1.96	0.17
Error	38	8.38	0.22		
Total	41	12.72			
Model term	**Coef**	**SE**	**T-value**	**P-value**	**VIF**
Constant	−65.4	17.3	−3.79	0.001	
Year	0.034	0.009	3.93	<0.001	1
r^2	0.28				

including proportions of each source water mass (Suppl. Fig. 4A), produced only one significant ($P = 0.016$) model, essentially a bivariate linear regression; water mass density (Fig. 4G) explained 24% of the variation with concentration increasing with increasing water density. The lowest density waters occurred during the mid-1990s (26 to 26.3, sigma-t), and density increased after 2000 (26.1 to 26.8, sigma-t). The same analysis for Grand Manan, including proportions of each source water mass (Suppl. Fig. 4B), also produced only one significant ($P = 0.031$) model; water mass temperature (Fig. 4H) explained 36% of the variation with concentration increasing with increasing temperature. In neither habitat was *Calanus* concentration significantly influenced by any other hydrographic variable (Fig. 4D, E, I, J) or source water (Fig. 5B, C).

4. Discussion

The motivation for this study was to determine whether interannual variation in right whale abundance indices in known Canadian critical habitats could be explained by variation their food source. Our results demonstrate that the abandonment of Roseway Basin by right whales

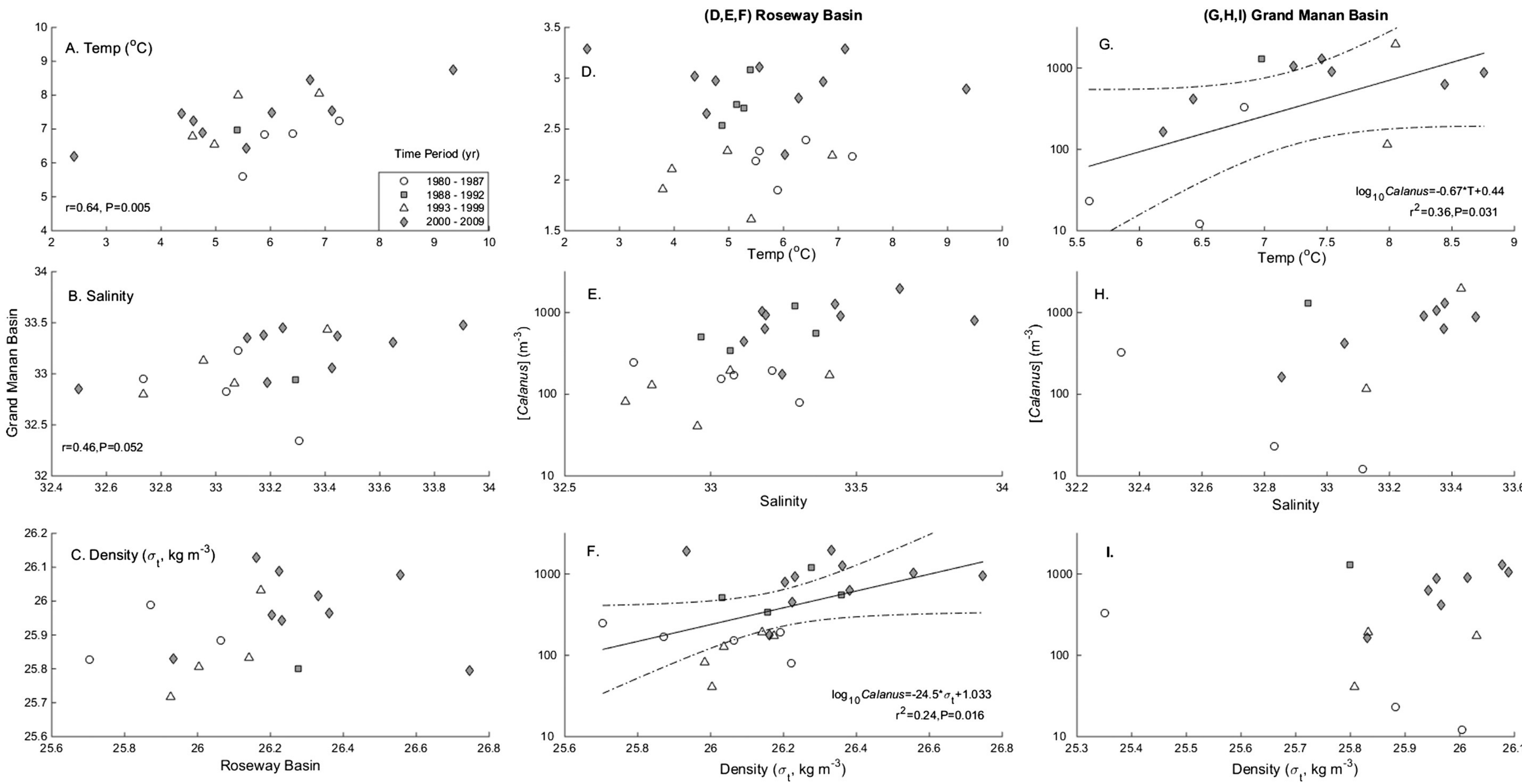

Fig. 4. (A–C) Between-basin comparisons of Roseway and Grand Manan in terms of water mass temperature (A), salinity (B) and density (C), where Pearson's correlation coefficients (r) are provided only where significant (P). (D–I) *Calanus* spp. concentration (m^{-3}) at depths >100 m in relation to water mass properties in Roseway Basin (D–F) and Grand Manan Basin (G–I) where regression models (solid line) and coefficients of determination (r^2) are provided only when significant (P). Each datum represents a single year, each symbolically noted according to 4 periods based on variation in the abundance of whale food in Roseway Basin: 1980–1987 (open circles, low food); 1988–1992 (filled squares, high food); 1993–1999 (open triangles, low food); 2000–2009 (closed diamonds, high food).

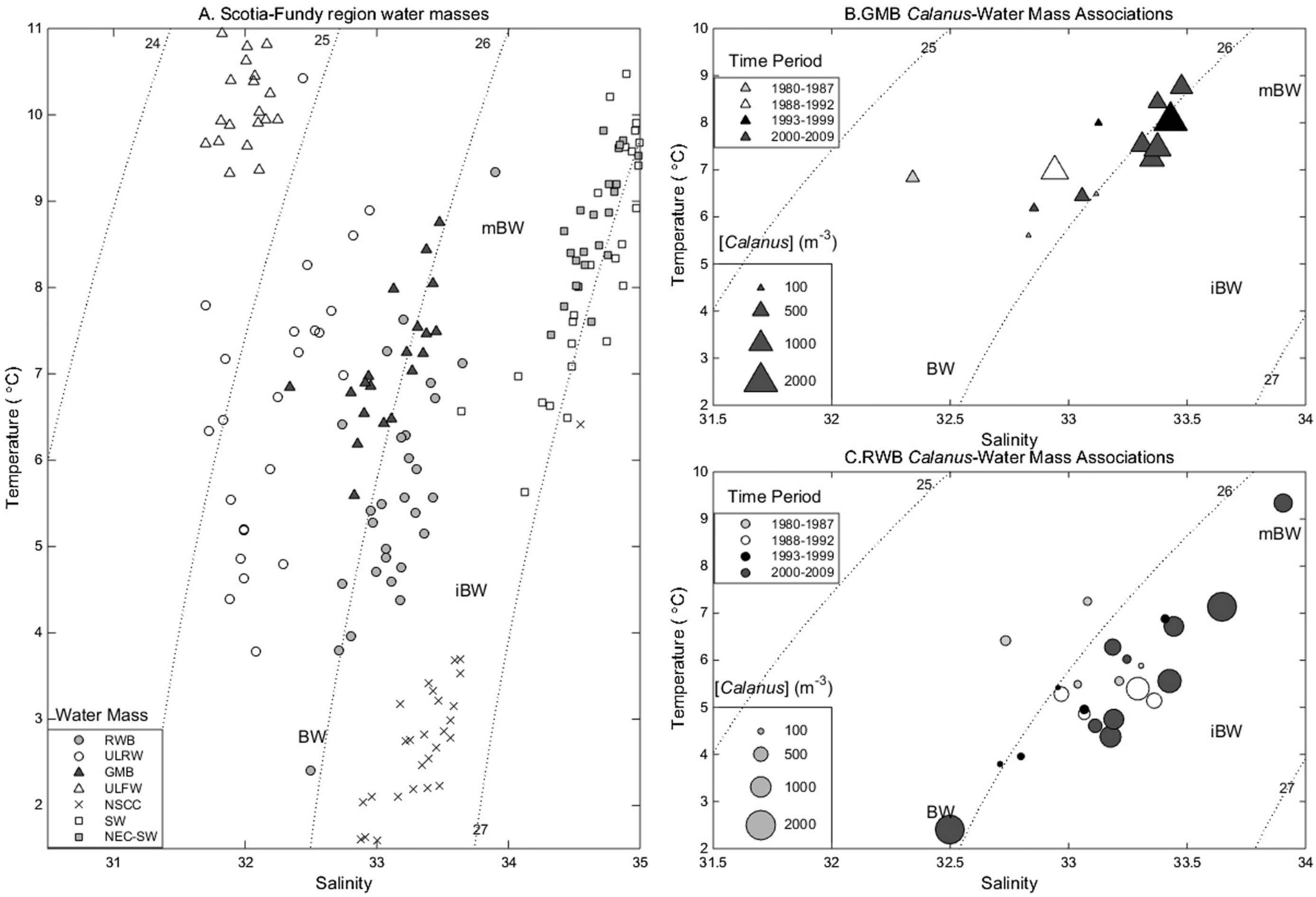

Fig. 5. T–S diagrams illustrating (A) Scotia-Fundy average annual deep-water temperature and salinity below 100 m in Grand Manan Basin (GMB, filled triangles) and Roseway Basin (RWB, filled circles), and within the 25–50 m depth stratum in Grand Manan (ULFW; open triangles) and Roseway (ULRW; open circles), and in comparison with the properties of their potential source water masses: the Nova Scotia Coastal Current (NSCC >100 m; crossed symbols), Slope Water (slope >100 m; open squares), and the Northeast Channel slope water (NEC >100 m), where each datum represents a single each year from 1980 through 2009 with dotted lines showing 24 to 27 sigma-t isopycnals, and average annual late-summer deep-water temperature and salinity below 100 m in (B) Grand Manan (GMB) and (C) Roseway (RWB) in relation to water-mass-specific *Calanus* spp. concentrations (m^{-3}) are represented by expanding-symbol marker size, with dotted lines showing the 25 and 26 sigma-t isopycnals. Approximate densities of the Roseway and Grand Manan water mass end-members (mBW, iBW, BW) in T–S space are illustrated in each panel (see text for details).

during the 1990s was likely due, in part, to a significant reduction in the concentration of diapausing *Calanus*. A similar pattern was identified with surface sampling of zooplankton across the western Scotian Shelf region during the same period (Patrician and Kenney, 2010). The deep water *Calanus* series examined here was positively related to water mass density. Patrician and Kenney (2010) interpreted the regional reduction of surface *Calanus* during the mid-1990s to inter-decadal variation in the transport of a low salinity, low density water mass from the Arctic into the Shelf region, coupled with a strongly negative phase of the North Atlantic Oscillation, which impacted both external sources and local production of *Calanus* throughout the western Scotian Shelf and Gulf of Maine region (Greene and Pershing, 2007; Greene et al., 2008; Greene et al., 2013; Meyer-Gutbrod and Greene, 2014; Patrician and Kenney, 2010). Our results are in general agreement with this interpretation; i.e, low density water intrusion was associated with low *Calanus* abundance.

While a low-density-water signal was apparent in our study, we did not identify a separate end-member signature that distinguished a fresh Arctic water mass at depths >100 m in Roseway Basin. The water mass properties in Roseway Basin in any given year were always described by a mixture of the NSCC and SW sources, both of which were more saline and dense than Roseway Basin water at depth, and ULRW which was always less saline and dense than Roseway Basin water at depth. This suggests that the Arctic water mass was already well-mixed with the various temperate source water masses by the time it arrived in the Roseway region, and so much so that its expression in the end member hydrographic properties was, at best, weak compared to the local source waters. Similarly, water mass fluctuations measured in three deep basins in the Gulf of Maine during the mid-1990s were caused by variable mixing ratios between the two local source waters (SW and NSCC water) rather than a change in the character of the SW end member, and a low salinity contribution was present in both source waters (Smith et al., 2001). Thus, ocean basin-scale forcing of water mass advection, rather than local forcing, may be the dominant driver of interannual variation in regional *Calanus* supply to the western Scotian Shelf.

This study demonstrated that *Calanus* supply and abundance were drivers of interannual right whale occupancy in Roseway Basin, however the same may not be true for Grand Manan Basin. This conclusion is based on the observation that Grand Manan Basin suffered reduced *Calanus* concentrations during the mid-1990s coincident with reductions measured in Roseway Basin, whereas all whale abundance indices were relatively high in Grand Manan Basin during the 1990s. Further, over the entire time series, the maximum number of whales photographed in Grand Manan was higher than in Roseway, indicating that Grand Manan has a higher carrying capacity despite average food concentrations and total habitat area being similar between basins (Fig. 1). Interannual variation in SPUE and IDs was lower in Grand Manan than Roseway and therefore more stable from year to year in terms of right whale occupancy. Finally, neither SPUE nor IDs were statistically related to variation in *Calanus* concentration in Grand Manan Basin over the time series.

One interpretation of this pattern is that properties other than food supply may draw right whales to Grand Manan Basin. The Basin is a known nursery habitat, occupied by up to 59% of calves and disproportionately more adult females than males (Malik et al., 1999). Lower variability in annual identification frequencies of adult females indicates higher fidelity to the Basin than males, particularly during years when they are pregnant or resting from a previous pregnancy (Brown et al., 2001). Grand Manan is surrounded on three sides by land and may offer protection to calves in addition to food supply, and the nursing cows that return there each year appear not to occupy other feeding grounds, e.g., Roseway, or others if they exist. Some have speculated that habitat occupancy by adult females may be due to a dietary requirement difference relative to males or juveniles due to a higher energy demand when rearing offspring (Lockyer, 1984), or avoidance of areas where other whales aggregate, especially those where there is a high percentage of males (Brown et al., 2001).

A second interpretation is that despite reductions in *Calanus* in Grand Manan during the mid-1990s, alternative food sources existed in the habitat, such as other copepod species that may bloom in the absence of *Calanus* aggregations. This interpretation seems less likely, although the possibility cannot be ruled out. Several studies assessing right whales and their food base have taken place in the Basin over 3 decades, and each has demonstrated a strong spatial and temporal association between right whales and *C. finmarchicus* stage-C5 (e.g., Murison and Gaskin, 1989; Baumgartner et al., 2003a, b; Michaud and Taggart, 2007, 2011), whereas the distributions of conspecific whale species that feed on other zooplankton and fish were different from right whale distributions (Woodley and Gaskin, 1996). Up to 96% of the total biomass and energy of zooplankton in the Basin region is consistently comprised of *C. finmarchicus* stage C5, with smaller numbers of other, smaller copepod species (Michaud and Taggart, 2007, 2011; Murison and Gaskin, 1989). The right whale annual migration takes them into the Basin during late-summer, which coincides with the maximum in high energy *C. finmarchicus* stage-C5 concentration at depths exceeding 100 m. Although small copepods can dominate the mesozooplankton abundance in surface waters, their biomass and energy is much lower than *C. finmarchicus*, primarily due to their smaller size (Michaud and Taggart, 2007). Copepod biomass is generally significantly greater near feeding right whales, whereas no such correlation is found between euphausiids and right whales, suggesting that right whales seek patches of high copepod density but not high euphausiid density, even in locations where euphausiid biomass can be very high (Baumgartner et al., 2003a; Murison and Gaskin, 1989; Watkins and Schevill, 1979), and right whales have in the past departed the Bay of Fundy during a period when euphausiid biomass was increasing to a seasonal maximum (Murison and Gaskin, 1989). Euphausiids have been found in the stomachs of right whales in other areas, although they usually accompany copepods (Buchet, 1985 as cited in Murison and Gaskin, 1989).

During the mid-1990s, right whale food in the late-summer critical habitats declined, yet the total right whale population size during this period was as high as in the 2000s when food concentration was high. Whale food in the springtime habitats in the Gulf of Maine also declined during the mid-1990s (Greene et al., 2003), indicating that food was limited in the known habitats during the entire feeding season each year. Perhaps high right whale population size during a region-wide food shortage resulted in the whales maintaining their residency within the region, rather than searching for other potential feeding habitats elsewhere. Right whales also suffered overall reduced health and calving rates during the mid-1990s which may indicate that all known feeding habitats were limited (Kraus et al., 2007; Meyer-Gutbrod and Greene, 2014). Sporadic sightings indicate that alternate right whale aggregation areas must exist in the Gulf of Maine (Brillant et al., 2015), on the Scotian Shelf (Mellinger et al., 2007; Mitchell et al., 1986), in the Gulf of St. Lawrence (Hamilton et al., 2007) and likely elsewhere, though few surveys take place in the latter two regions. Right whales are highly mobile, with the swimming ability to travel 10s of kilometers per day (Baumgartner and Mate, 2005; Brillant et al., 2015) such that when food declines in one habitat, they can easily migrate to others within a feeding season. It seems that during the 1990s suitable feeding habitats were limited and this has serious implications for the whales in the future, since many of the above variations were linked to decadal-scale climate oscillations that are likely to return in the future (Greene et al., 2013; Meyer-Gutbrod and Greene, 2014). We can hypothesize about the above observations: (1) un-surveyed right whale aggregation areas exist elsewhere in the NW Atlantic but they may not be reliable or critical contributors to right whale energetic requirement; or (2) reliable or critical feeding habitats do exist elsewhere, but they too suffer the same and apparently climate-linked reductions in food supply as in the known critical habitats. The latter hypothesis seems plausible for the western Scotian Shelf region and other locations in the Gulf of Maine. Overall, there has been a general trend of increase in diapausing *Calanus* concentration over 29 years in both Roseway and Grand Manan Basins (Fig. 3) and this helps to explain the return of right whales to Roseway Basin, increasing calving rates, and improved health of the population since the turn of the millennium. As we were unable to identify any hydrographic or water mass properties to suggest that the increase in *Calanus* is due to an increased presence of external copepod source waters, perhaps there has been an overall increase in regional diapausing *Calanus* production, though with high annual and seemingly decadal variation.

Clearly, much of the variation in each of the whale population abundance indices we examined, and their habitats, remains unexplained by the suite of variables we assessed. Despite the fact that the data we compiled are the most extensive (time) and comprehensive (variables) available for the Grand Manan and Roseway basins, low sampling effort and irresolvable biases were limiting. In particular, coherency among all abundance indices and all habitat metrics within a year was never achieved. Collaborative and comparable sampling schemes that include whale observations and habitat measurements collected together within and among habitats are clearly a priority for future research where and whenever possible. Further, we hope to contribute to the advancement of survey effort by highlighting one potential bias in right whale observation data and their associated indices; strong inconsistency in the interannual variation between sightings per unit effort (SPUE) and the number of photographically-identified (ID) individuals in Grand Manan Basin that could not be attributed to ecological mechanisms. It is possible that the relation is masked by inter-annual variation in surveys relative to whale occupancy, and (or) inter-annual variation in repeated migration into and out of the Basin. This may occur due to effort biases, particularly since effort associated with ID is not easily estimable (Brillant et al., 2015). It is assumed that, at least since 1994, adequate effort in the known critical habitats has been sufficient to identify all individuals in the population (Hamilton et al., 2007). If valid, then the negative correlation between the ID estimates between Roseway and Grand Manan Basin may be robust. However, we could not envision or demonstrate any underlying mechanism in the habitat variables that could validate the negative correlation; all the habitat variables indicate that food availability and oceanographic properties between the two habitats are positively correlated. We conclude that it is important to treat this negative correlation in the ID index between Roseway and Grand Manan with caution, and design hypotheses, survey schemes and improved analytical techniques in the near future that can help explain this phenomenon. We hope that this research will help guide future data collection efforts where the seasonal, spatial and interannual variation in these biological and oceanographic variables and mechanisms can be explored simultaneously.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jmarsys.2015.05.005.

References

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

Baumgartner, M.F., Cole, T.V.N., Clapham, P.J., Mate, B.R., 2003a. North Atlantic right whale habitat in the lower Bay of Fundy and on the southwest Scotian Shelf during 1999–2001. Mar. Ecol. Prog. Ser. 264, 137–154.

Baumgartner, M.F., Cole, T.V.N., Campbell, R.G., Teegarden, G.J., Durbin, E.G., 2003b. Associations between North Atlantic right whales and their prey, *Calanus finmarchicus*, over diel and tidal time scales. Mar. Ecol. Prog. Ser. 264, 155–166.

Brillant, S.W., Vanderlaan, A.S.M., Rangeley, R.W., Taggart, C.T., 2015. Quantitative estimates of the movement and distribution of North Atlantic right whales along the northeast coast of North America. Endanger. Species Res. 27, 141–154.

Brown, M.W., Brault, S., Hamilton, P.K., Kenney, R.D., Knowlton, A.R., Marx, M.K., Mayo, C.A., Slay, C.K., Kraus, S.D., 2001. Sighting heterogeneity of right whales in the western North Atlantic 1980–1992. J. Cetacean Res. Manag. Spec. Issue 2, 245–250.

Brown, M.W., Kraus, S.C., Slay, C.K., Garrison, L.P., 2007. Survey for discovery, science, and management. In: Kraus, S.D., Rolland, R.M. (Eds.), The urban whale: North Atlantic right whales at the crossroads. Harvard University Press, Cambridge, MA, pp. 105–137.

Brown, M.W., Fenton, D., Smedbol, K., Merriman, C., Robichaud-Leblanc, K., Conway, J.D., 2014. Fisheries and oceans Canada. Recovery Strategy for the North Atlantic Right Whale (*Eubalaena glacialis*) in Atlantic Canadian Waters [Final]Species at Risk Act Recovery Strategy SeriesFisheries and Oceans Canada (vi + 66p.).

Buchet, G., 1985. De la baleine des Basques dans les eaux islanaises et de l'aspect des grands cetaces a la mer. Mem. Soc. Zool. Fr. 8, 229–231.

Davies, K.T.A., Taggart, C.T., Smedbol, R.K., 2014. Water mass structure defines the diapausing copepod distribution in a right whale habitat on the Scotian Shelf. Mar. Ecol. Prog. Ser. 497, 69–85.

Fujiwara, M., Caswell, H., 2001. Demography of the endangered North Atlantic right whale. Nature 414, 537–541.

Greene, C.H., Pershing, A.J., Kenney, R.D., Jossi, J.W., 2003. Impact of climate variability on the recovery of endangered North Atlantic right whales. Oceanography. 16, 96–101.

Greene, C.H., Pershing, A.J., 2007. Climate drives sea change. Science 315, 1,084–1,085.

Greene, C.H., Pershing, A.J., Cronin, T., Ceci, N., 2008. Arctic climate change and its impacts on the ecology of the North Atlantic. Ecology 89, S24–S38.

Greene, C.H., Meyer-Gutbrod, E., Monger, B.C., McGarry, L.P., Pershing, A.J., Belkin, I.M., Fratantoni, P.S., Mountain, D.G., Pickart, R.S., Proshutinsky, A., Ji, R., Bisagni, J.J., Hakkinen, S.M.A., Haidvogel, D.B., Wang, J., Head, E., Smith, P., Reid, P.C., Conversi, A., 2013. Remote climate forcing of decadal-scale regime shifts in Northwest Atlantic shelf ecosystems. Limnol. Oceanogr. 58, 803–816.

Hamilton, P.K., Knowlton, A.R., Marx, M.K., 2007. Right whales tell their own stories: the photoidentification catalogue. In: Kraus, S.D., Rolland, R. (Eds.), The Urban Whale: North Atlantic Right Whales at the Crossroads. Harvard University Press, pp. 75–104 (543 p.).

Knowlton, A.R., Sigurjonsson, J., Ciano, J.N., Kraus, S.D., 1992. Long distance movements of North Atlantic right whales (*Eubalaena glacialis*). Mar Mammal. Sci 8, 397–405.

Knowlton, A., Hamilton, P., Kraus, S., Brown, M., 2000. Right whale research and conservation efforts in the lower Bay of Fundy. Technical Report Available from New England Aquarium, Central Wharf, Boston, MA 02110.

Knowlton, A.R., Hamilton, P.K., Marx, M.K., Pettis, H.M., Kraus, S.D., 2012. Monitoring North Atlantic right whale (*Eubalaena glacialis*) entanglement rates: a 30 yr retrospective. Mar. Ecol. Prog. Ser. 466, 293–302.

Kraus, S.D., Moore, K.E., Price, C.A., Crone, M.J., Watkins, W.A., Winn, H.E., 1986. The use of photographs to identify individual North Atlantic right whales (*Eubalaena glacialis*). Rep. Int. Whaling Comm. 10 (Spec. Issue), 145–151.

Kraus, S.D., Pace, R.M., Frasier, T.R., 2007. High investment, low return: the strange case of reproduction in *Eubalaena glacialis*. In: Kraus, S.D., Rolland, R. (Eds.), The Urban Whale: North Atlantic Right Whales at the Crossroads. Harvard University Press, pp. 172–199 (543 p.).

Lagueux, K., Zani, M., Knowlton, A., 2011. Response by vessel operators to protection measures for right whales *Eubalaena glacialis* in the southeast US calving ground. Endanger. Species Res. 14, 69–77.

Legendre, P., Borcard, D., 2008. Statistical comparison of univariate tests of homogeneity of variances. J. Stat. Comput. Simul. 514, 1–22.

Lien, J., Sears, R., Stenson, G.B., Jones, P.W., Wi, I.H., 1989. Right whale, *Eubalaena glacialis*, sightings in waters off Newfoundland and Labrador and the Gulf of St. Lawrence, 1978–1987. Can. Field-Nat. 103, 91–93.

Lockyer, C., 1984. Review of baleen whale (*Mysticeti*) reproduction and implications for management. Rep. Int. Whaling Comm. 6 (Spec. Issue), 27–50.

Malik, S., Brown, M.W., Kraus, S.D., Knowlton, A.R., Hamilton, P.K., White, B.N., 1999. Assessment of mitochondrial DNA structuring and nursery use in the North Atlantic right whale (*Eubalaena glacialis*). Can. J. Zool. 77, 1217–1222.

Mellinger, D.K., Nieukirk, S.L., Matsumoto, H., Heimlich, S.L., Dziak, R.P., Haxel, J., Fowler, M., 2007. Seasonal occurrence of North Atlantic right whale (*Eubalaena glacialis*) vocalizations at two sites on the Scotian Shelf. Mar. Mammal Sci. 23 (4), 856–867.

Meyer-Gutbrod, E.L., Greene, C.H., 2014. Climate-associated regime shifts drive decadal scale variability in recovery of North Atlantic right whale population. Oceanography 27 (3). http://dx.doi.org/10.5670/oceanog.2014.64.

Michaud, J., Taggart, C.T., 2007. Lipid and gross energy content of North Atlantic right whale food, *Calanus finmarchicus*, in the Bay of Fundy. Endanger. Species Res. 3, 77–94.

Michaud, J., Taggart, C.T., 2011. Spatial variation in right whale food, *Calanus finmarchicus*, in the Bay of Fundy. Endanger. Species Res. 15, 179–194.

Mitchell, E., Kozicki, V.M., Reeves, R.R., 1986. Sightings of right whales, *Eubalaena glacialis*, on the Scotian Shelf, 1966–1972. Rep. Int. Whaling Comm. 10 (Spec. Issue), 83–107.

Murison, L.D., Gaskin, D.E., 1989. The distribution of right whales and zooplankton in the Bay of Fundy, Canada. Can. J. Zool. 67, 1411–1420.

NARWC (North Atlantic Right Whale Consortium), 2008. North Atlantic Right Whale Consortium Sightings Database. New England Aquarium, Boston, MA.

Patrician, M.R., Kenney, R.D., 2010. Using the continuous plankton recorder to investigate the absence of North Atlantic right whales (*Eubalaena glacialis*) from the Roseway Basin. J. Plankton Res. 32, 1685–1695.

Petrie, B., Drinkwater, K., Gregory, D., Pettipas, R., Sandstrom, A., 1996. Temperature and salinity atlas for the Scotian Shelf and the Gulf of Maine. Can. Tech. Rep. Hydrogr. Ocean Sci. 171 398p.

Pettis, H.M., Rolland, R.M., Hamilton, P.K., Brault, S., Knowlton, A.R., Kraus, S.D., 2004. Visual health assessment of North Atlantic right whales (*Eubalaena glacialis*) using photographs. Can. J. Zool. 82, 8–19.

Reeves, R.R., Mead, J.G., Katona, S., 1978. The right whale, *Eubalaena glacialis*, in the western North Atlantic. Rep. Int. Whaling Comm. 28, 303–312.

Silber, G.K., Vanderlaan, A.S.M., Tejedor Arceredillo, A., Johnson, L., Taggart, C.T., Brown, M.W., Bettridge, S., Sagarminaga, R., 2012. The role of the International Maritime Organization in reducing vessel threat to whales: process, options, action and effectiveness. Mar. Policy 36, 1221–1233.

Smith, P.C., Houghton, R.W., Fairbanks, R.G., Mountain, D.G., 2001. Interannual variability of boundary fluxes and water mass properties in the Gulf of Maine and on Georges Bank: 1993–1997. Deep-Sea Res. II 48, 37–70.

van der Hoop, J.M., Vanderlaan, A.S.M., Cole, T.V.N., Henry, A.G., Hall, L., Mase-Guthrie, B., Wimmer, T., Moore, M.J., 2014. Vessel strikes to large whales before and after the 2008 ship strike rule. Conserv. Lett. http://dx.doi.org/10.1111/conl.1210: 1-9.

Vanderlaan, A.S.M., 2010. Estimating Risk to the North Atlantic right whale (*Eubalaena glacialis*) From Ocean-going Vessels and Fishing Gear PhD Thesis, Dalhousie University, Halifax, NS Canada (176p.).

Vanderlaan, A.S.M., Taggart, C.T., Serdynska, A.R., Kenney, R.D., Brown, M.W., 2008. Reducing the risk of lethal encounters: vessels and right whales in the Bay of Fundy and on the Scotian Shelf. Endanger. Species Res. 4, 283–297.

Watkins, W.A., Schevill, W.E., 1979. Aerial observation of feeding behavior in four baleen whales: *Eubalaena glacialis*, *Balaenoptera borealis*, *Megaptera novaeangliae*, and *Balaenoptera physalus*. J. Mammal. 60, 155–163.

Weisbrod, A.V., Shea, D., Moore, M.J., Stegeman, J.J., 2000. Organochlorine exposure and bioaccumulation in the endangered North Atlantic right whale (*Eubalaena glacialis*) population. Environ. Technol. Chem. 19, 654–666.

Whitehead, H., 2009. SOCPROG programs: analysing animal social structures. Behav. Ecol. Sociobiol. 63, 765–778.

Woodley, T.H., Gaskin, D.E., 1996. Environmental characteristics of North Atlantic right and fin whale habitat in the lower Bay of Fundy, Canada. Can. J. Zool. 74, 75–84.