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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