MODELS OF NORTH ATLANTIC RIGHT WHALE HABITAT: TOOLS FOR SCIENCE AND CONSERVATION

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MODELS OF NORTH ATLANTIC RIGHT WHALE HABITAT: TOOLS FOR SCIENCE AND CONSERVATION

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Intense whaling nearly abolished the North Atlantic right whale (*Eubalaena glacialis*) population. Present day threats to the species are collisions with vessels, entanglement in fishing gear, and environmental variability. In this body of work we quantify the relationship between right whales and their prey, rice-grain sized crustaceans called copepods, and employ a spatial model to predict the potential distribution of right whales on a weekly basis.

Time series datasets of right whale abundance and copepod concentration were analyzed to quantify the relationship between right whales and their prey. We found significant relationships between right whales and copepods in Cape Cod Bay and the Great South Channel. These results tell us that accurate regional-scale models of copepod concentration can be used to infer the time and location of good right whale feeding conditions.

The environmental niche of right whales was characterized using modeled prey abundance, sea surface temperature, chlorophyll concentration and bathymetry. With environmental data for the time and location of each right whale occurrence between 2002 and 2006, we trained and tested a model to predict right whale habitat suitability on a weekly basis. The accuracy of predictions was good, and the feasibility of our approach was verified. Results suggest that right whale habitat preferences are dynamic and that the distribution of prey is an important to the distribution of whales.

We built an operational forecasting model of right whale habitat suitability in Cape Cod Bay, and used it to make weekly predictions for the year 2009. Modeled concentration of two right whale prey taxa (*C. finmarchicus* and *Pseudocalanus* spp.) sea surface temperature, chlorophyll and bathymetry were used as predictor variables. Predictions were verified with occurrences of right whales in Cape Cod Bay from 2009. Model output was used to assess the utility of moving shipping routes in Cape Cod Bay. The model was then projected, beyond the model-training region, into Massachusetts Bay. Results suggested that altering of shipping lanes in Cape Cod Bay is unlikely to reduce the risk of ship-strikes. A significant positive relationship was found between predicted habitat suitability and the number of acoustic detections of right whales in Massachusetts Bay. We conclude that our modeling approach could be used to: 1) issue weekly forecasts of right whale habitat quality, 2) assess conservation actions, 3) guide survey effort in other regions, and ultimately to reduce human-caused risk to the right whales.

BIOGRAPHICAL SKETCH

Daniel Edward Pendleton was born in Saint Paul, Minnesota, on May 2, 1974. As the oldest of six kids, Dan learned to set a good example for others. His parents taught him that he could be whatever he wanted to be ... even an astronaut. Dan earned his B.S. degree in 1999 from Minnesota State University at Mankato, with a major in mathematics and a minor in statistics. After graduation and much contemplation while on the Superior Hiking Trail, Dan decided to apply his mathematics degree to environmental science. In 2001 Dan began a M.S. program in Crop and Soil Science at Cornell University. The choice of agriculturally oriented research was inspired by discussions with Raazesh Sainudiin, Dan's best friend, about the most effective ways to change the world. Life with a Master of Science degree was interesting, but not interesting enough to keep Dan from returning to Cornell for a Ph.D., which happened in January, 2005. Shortly after returning to Ithaca, Dan met Ms. Claudia Tomsa, and the two of them became "Dan & Claudia". The pair have had many wonderful adventures so far and look forward to many more.

Dedicated to the memory of the late Larry M. Pearson, professor of statistics at Minnesota State University, Mankato.

ACKNOWLEDGEMENTS

None of this work would have been possible without the guidance of my advisors, Andrew Pershing and Patrick Sullivan. Andy immersed me in the world of ocean science. The field was new to me when I joined his lab. He took me to scientific meetings, introduced me to interesting people, and made sure that all of my academic needs were met. Pat always made time to see me, always with a smile, and always with a challenge to look at things from a different angle. I could not have asked for more supportive and inspiring mentors.

The New England Aquarium right whale research team contributed greatly to my education. They trained me in field methods of right whale photo identification, instilled in me the perspective of a marine field biologist, and became my close friends. Thanks for your help, Philip, Amy, Bill, Yan, Scott, Ros, Moe, Jerry, Marylin, Monica, Jon, Candice, Cyndi, and all the others I met at The Whale House.

Steven Phillips and Richard Pearson were a major catalyst in bringing together the work for chapters three and four. Their five day course through the American Museum of Natural History gave me a wealth of knowledge in the field of species distribution modeling. They continued to help me develop by welcoming me into their discussion groups at the Museum

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CHAPTER 1

INTRODUCTION

North Atlantic right whales (*Eubalaena glacialis*) take their name from being the right whale to hunt. A millennium ago, their range spanned the width of Atlantic ocean – from the southeastern coast of the United States to the Gulf of Saint Lawrence in the west, and from the northwest coast of Africa to northern most coast of Norway in the east. By the mid-1700s the North Atlantic right whale population was severely depleted, and by the mid-1800s there were so few animals left that they were no longer the target of whaling expeditions (Reeves *et al.*, 2007). Today, the primary range of North Atlantic right whales is restricted to the coastal waters of the United States and Canada, from northern Florida to the Bay of Fundy. Approximately 400 individual whales remain.

There are four main hypotheses for the lack of recovery of North Atlantic right whales: 1) collisions with vessels (Knowlton and Kraus, 2001), 2) entanglements with fishing gear (Knowlton and Kraus, 2001), 3) increased levels of anthropogenic ocean noise which may hamper communication and reproduction (Parks and Clark, 2007; Clark *et al.*, 2007), and 4) changes in the distribution and abundance of copepods, the rice-grain sized organisms that right whales rely upon for sustenance (Kenney *et al.*, 2001; Greene and Pershing, 2004).

The Endangered Species Act (ESA) gave the National Marine Fisheries Service the authority to develop and implement recovery plans for endangered marine species. The recovery strategy outlined in the most recent North Atlantic right whale recovery plan (NMFS, 2005) identifies the need to "reduce or eliminate deaths and injuries from anthropogenic activities, namely shipping and commercial fishing" as the most significant need for recovery of the species. Since the ESA was enacted in 1973 many protective measures have been taken, although most did not begin until the 1990s. In 1993, the Cape Cod Bay, Great South Channel, and Southeast U.S. right whale critical habitats were established. In 1996, vessels were prohibited from approaching within 500 yards of a right whale in U.S. waters. In 1999, the Mandatory Ship Reporting system was implemented, requiring vessels in right whale habitat to report their position in exchange for information on recent right whale sightings and how to avoid the animals. In 2002, fishing activities were restricted in Seasonal Area Management (SAM) zones, with boundaries defined by areas with "annual predictable presence of right whales", and in Dynamic Area Management (DAM) zones, with boundaries defined by current aggregations of right whales. SAMs provided a basic level of protection, but zone boundaries did not vary from year to year. DAMs, which imposed gear modifications (a burden to fishermen), allowed a rapid response to aggregations of right whales that deviate from the typical distribution defined by SAMs. Restrictions on fishing and shipping activities come at a high economic cost, so there is a desire to implement restrictions within the smallest possible spatial and temporal boundaries. Inadequate knowledge about right whale distributions has led to the implementation of restriction over large spatial and temporal boundaries.

None of the enacted measures to date rely on right whale distributional patterns that are dynamic at the spatial and temporal scales at which right whales function. Furthermore, current protective measures do not rely on a mechanistic understanding of why whales aggregate in some areas and not others. A better understanding of the reasons for right whale occurrence could be used to inform conservation actions, especially as ocean conditions and whale populations change in the coming century

The body of work presented here addresses this deficit in two ways. First, by quantifying the relationship between right whales and their prey. And second, by generating dynamic forecasts of right whale habitat that will take us beyond the relatively static management rules implemented to date. This latter piece was accomplished using a combination of models that exploit the relationship between right whales and their prey.

The impetus for this work was that a better understanding of the drivers of the distribution of right whales, combined with predictive models, could help inform conservation actions. Furthermore, any management plan will be more effective if the temporal and spatial scale of conservation actions is on par with the temporal and spatial scale of events being managed for (e.g., aggregations of right whales in shipping lanes).

We found that mean copepod concentrations in Cape Cod Bay and Great South Channel right whale critical habitats are informative when analyzed at the temporal scale of one to three months – roughly the scale at which the Seasonal Area Management plan was designed to have an effect. We found that modeling of right whale habitat on a weekly time scale is feasible, and we applied a right whale habitat model to make weekly predictions about the conditions in Cape Cod Bay during the year 2009. To assess the ability of the model to guide survey effort beyond the model-training region, we projected the Cape Cod Bay model into Massachusetts Bay and verified results with acoustic detections in that region. To assess the ability of the model to inform a current management issue, we used the predictions to assess the utility of moving shipping routes in Cape Cod Bay for the purpose of reducing vessel transit through high quality right whale habitat. The timing of vessel transit in Cape Cod Bay was found to be more important than the path of transit.

Right whale movements in Gulf of Maine feeding grounds are tied to the appearance of dense aggregations of copepods (Kenney *et al.*, 1986; Wishner *et al.*, 1995). Chapter two (Pendleton *et al.*, 2009) explores the hypothesis that the distribution of right whales is driven by the distribution of copepods and it assess the utility of coarse-scale sampling programs for right whale management. We compared the concentration of copepods, the primary prey of right whales, from vessel-based zooplankton surveys with the abundance of right whales derived from aerial surveys. We found significant relationships between the concentration of copepods and right whale abundance in critical habitats at monthly and seasonal timescales. In the Cape Cod Bay critical habitat right whales appeared to respond strongly to *Pseudocalanus* spp. and *Centropages* spp., and in the Great South Channel critical habitat right whales appeared to respond strongly to *Calanus finmarchicus*. These results suggest that 1) a high background concentration of copepods is a prerequisite for the formation of the ultra-dense patches of copepods necessary to trigger right whale feeding activity, 2) the distribution of right whales is strongly influenced by the distribution of their prey, 3) the environmental preferences of right whales changes from one season and/or habitat to the next, and 4) regional-scale predictions of copepod abundance can provide useful information on when and where good feeding conditions will occur.

The key result from chapter two is that the background copepod concentrations are an important indicator of the number of right whales. Pershing *et al.* (2009b) and Pershing *et al.* (2009a) described a model capable of estimating background concentrations of copepods and identified simple relationships between modeled copepod concentration and the number of right whales in the

Great South Channel. The objective of chapter three was to generate estimates of right whale habitat suitability with a spatial resolution sufficient to be of use to resource managers. Toward this end, we tested a system to model right whale habitat suitability on a weekly time scale. Two hypotheses were tested: H_1) that prey is an important predictor of right whale habitat suitability, and H_2) that right whale preferences are dynamic. Significant improvements in model predictive capacity were found when prey was included as a predictor variable in models of the spring season, but not of the winter season. With respect to H_2, we observed a increased importance of prey and decreased importance of sea surface temperature the year progressed from winter to spring. This suggests that environmental habitat preferences of right whales change on a seasonal basis.

Building on chapter three, we developed a high resolution right whale habitat model for Cape Cod Bay, and used this model to forecast right whale movements during winter and spring 2009. The results presented in chapter four suggest that the model predictions are reliable, that the model could be used to forecast habitat suitability in other regions, and that it could be used to support conservation actions. We examined the impact of moving shipping lanes to reduce potential whale-vessel encounters. The time of vessel transit appeared to have a greater impact than the location of vessel transit. Projecting the model into Massachusetts Bay, we were able to explain the variability in the number of right whale acoustic detections. This work provides proof-of-concept that a system could be implemented to forecast right whale habitat suitability, and that forecasts or nowcasts could be used to issue alerts during times when the environment is suitable for right whale aggregation.

The approach outlined in this dissertation: generating realtime and forecasted predictions of habitat, based upon realtime and forecasted estimates of prey abundance and other environmental data, has the potential to transform the way we manage endangered species - moving from a static view of the species' distribution to one that changes on intra- and inter-annual timescales. One way to improve the forecasts from chapter four would be to include right whale occurrences from the year of prediction in the training dataset. This would help to sensitize the model to the peculiarities of right whale environmental preference in the year being predicted. Deeper ecological questions could be addressed by training models with demographic subsets of species occurrence data. There is potential to apply these approaches in other regions and for other target species. Finally, by manipulating the modeled environment, one could study the effects of climate change on endangered species.

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CHAPTER 2

REGIONAL-MEAN COPEPOD CONCENTRATION INDICATES RELATIVE ABUNDANCE OF NORTH ATLANTIC RIGHT WHALES

2.1 Abstract

Management plans to reduce human-caused deaths of North Atlantic right whales (*Eubalaena glacialis*) depend, in part, on knowing when and where right whales are likely to be found. Local environmental conditions that influence movements of feeding right whales, such as ultra- dense copepod patches, are unpredictable and ephemeral. We examined the utility of using the regional-scale mean copepod concentration as an indicator of the abundance of right whales in 2 critical habitats off the northeastern coast of the United States: Cape Cod Bay and Great South Channel. Right whales are usually found in Cape Cod Bay during the late winter and early spring, and in the Great South Channel during the late spring and early summer. We found a significant positive relationship between mean concentration of the copepod *Calanus finmarchicus* in the western Gulf of Maine and the frequency of right whale sightings in the Great South Channel. In Cape Cod Bay we found a significant positive relationship between the mean concentration of other copepods (largely *Pseudocalanus* spp. and *Centropages* spp.) and the frequency of right whale sightings. This information could be used to further our understanding of the environmental factors that drive seasonal movement and aggregation of right whales in the Gulf of Maine, and it offers a tool to resource managers and modelers who seek to predict the movements of right whales based upon the concentration of copepods.

2.2 Introduction

North Atlantic right whales *Eubalaena glacialis* migrate seasonally through the coastal shelf waters along the eastern coast of the USA and Canada, from southeastern Florida to the Bay of Fundy and Scotian Shelf (Winn *et al.*, 1986). They are one of the most endangered cetacean populations (Clapham *et al.*, 1999) and have been protected under the US Endangered Species Act since 1973. Collisions with ships and entanglement in fishing gear are the 2 primary causes of injury and mortality of right whales attributable to human activity. The development, implementation and effectiveness of management strategies to eliminate anthropogenic mortality depend on knowing when and where right whales are likely to occur. Therefore, knowing how environmental factors influence movements of right whales would inform decision making.

Changes in temperature, salinity, circulation and plankton abundance in the Northwest Atlantic have been linked to large-scale changes in the ocean and atmosphere (Durbin *et al.*, 2000; Greene and Pershing, 2000; MERCINA, 2001; Pershing *et al.*, 2005). The variability in abundance of the primary prey of right whales, the copepod *Calanus finmarchicus*, in the Gulf of Maine explains a large proportion of the variability in the number of right whale births (Greene and Pershing, 2004). On a finer scale, changes in circulation influence where whales feed (Kenney *et al.*, 1995). Given this, a better understanding of physical and biological oceanographic processes can aid conservation.

Direct observations of right whales feeding on dense aggregations of *Calanus finmarchicus* have been documented in several studies (Watkins and Schevill, 1976; Wishner *et al.*, 1988; Mayo and Marx, 1990; Beardsley *et al.*, 1996), and indirect evidence of right whales feeding at depth on this copepod has been inferred from simultaneous surface observations, water-column sampling (Murison and Gaskin, 1989) and dive records (Baumgartner and Mate, 2003). The diet of right whales, however, is not monospecific; it includes mesozooplankton such as *Pseudocalanus* spp., *Centropages* spp., larval barnacles and possibly euphausiids (Watkins and Schevill, 1976; Murison and Gaskin, 1989; Mayo and Marx, 1990).

A leading hypothesis to explain right whale movement posits that whales forage nomadically, moving through the Gulf of Maine and adjoining areas in response to changes in the zooplankton prey resource (Gaskin, 1982; Kenney *et al.*, 2001). Standard zooplankton sampling programs do a good job of measuring copepod concentrations at the regional-scale (10 to 100s of kilometers), but they do not adequately resolve the ultra-dense concentrations of copepods, at the scale of 1 to 10s of meters, that right whales feed upon (Kenney *et al.*, 1986b). Baumgartner *et al.* (2007) suggested that the regional-scale copepod concentration is not proportional to right whale abundance. In the present study we tested the hypothesis that regional-scale mean copepod concentration is an indicator of the number of right whales in a region and, by implication, the number and quality of ultra-dense copepod patches that right whales are known to consume. Our hypothesis stems from a simple conceptual model: if no copepods are present in a region, no copepod patches will form. If many copepods are present in a region, many patches will form.

Herein we report on a comparison of datasets representing the densities of copepods and sighting frequencies of right whales in 2 US right whale critical habitats: Cape Cod Bay, a shallow coastal bay that is protected by land on 3 sides, and the Great South Channel, a region at the southern end of the Gulf of Maine between Cape Cod and Georges Bank (Figure 2.1). Knowing the degree of association between the regional-scale mean copepod concentration and right whale abundance could offer managers a tool for assessing the likelihood of right whale occurrence. This information could also guide inferences drawn from model simulations of regional-scale copepod concentration (e.g. Lynch *et al.* (1998)).

2.3 Materials and Methods

We focused on 2 right whale critical habitats: Cape Cod Bay and the Great South Channel. In each habitat area we compared the mean copepod concentration with an effort-corrected index of right whale abundance, sightings per unit effort (SPUE). Copepod measurements came from 3 sources: the Gulf of Maine continuous plankton recorder (CPR), vessel-based net sampling in Cape Cod Bay by the Provincetown Center for Coastal Studies (PCCS), and vessel-based net sampling in the Great South Channel by the National Marine Fisheries Services (NMFS) Marine Resources Monitoring, Assessment and Prediction program (MARMAP). Right whale SPUE values were computed from survey data in the North Atlantic Right Whale Consortium (NARWC) database.

2.3.1 Copepod sampling

The CPR is an instrument that is towed behind ships of opportunity at a depth of about 10 m (Warner and Hays, 1994). Organisms are captured on a continuous silk mesh as seawater passes through the instrument body. The Gulf of Maine CPR survey collects samples along a transect from Boston, Massachusetts to Yarmouth, Nova Scotia (Jossi and Goulet, 1993). We analyzed copepod samples from 2 segments or tracts of the CPR transect, upstream of our study regions (Figure 2.1). *Calanus finmarchicus* progress through 13 stages: egg, 6 naupliar stages and 5 copepodid stages (C1 – C5) before reaching adulthood (C6). Stage C5 – C6 *C. finmarchicus* and other copepods (C6 *Pseudocalanus* spp. and *Centropages typicus*) from the CPR tract in Massachusetts Bay and the western Gulf of Maine were used in our analysis of Cape Cod Bay and the Great South Channel, respectively. Because the CPR is towed without respect to time of day at a constant depth, diel vertical migration could bias estimates of *C. finmarchicus* concentration. To test for this we performed an unpaired t-test on $\log_{10}(x + 1)$ - transformed, day versus night, data (Kane, 2005). No significant difference was found ($p = 0.34$) indicating that diel vertical migration would not adversely impact our results.

Copepod samples were collected by the Provincetown Center for Coastal Studies (PCCS) within Cape Cod Bay approximately weekly from late December to late May from 1999 to 2006. On each cruise 8 to 10 fixed stations were sampled; however, weather conditions sometimes reduced the number of stations visited. All sampling took place during daylight hours. Occasionally, sampling cruises were conducted at other times of the year. Typically, at each station a 30 cm diameter, 333 μm mesh net was towed at a depth of about 1 m and at a speed of 1.5 m s1 for 5 min, following the methods of Mayo *et al.* (2004). The 333 μm mesh size was chosen to mimic the particle capture properties of right whale baleen (Mayo *et al.*, 2001). From this dataset we defined 2 quantities: (1) the concentration of *Calanus finmarchicus*, and (2) the concentration of other copepods. Strictly, this second quantity represents the mean concentration of all organisms captured that were not *C. finmarchicus*, but it is primarily comprised of *Pseudocalanus* spp. and *Centropages* spp. (Mayo *et al.*, 2004). Beginning in 2003, surface tows were augmented with oblique tows. To test for potential bias introduced by surface-only sampling, we compared mean concentrations from surface and oblique tows within 28 d intervals (as was done for our interannual analysis, see below) from 2003 to 2006. There was a significant linear relationship between *C. finmarchicus* measured by oblique versus surface tows ($r^2 = 0.88, p < 0.001$), and between other copepods measured by oblique versus surface tows ($r^2 = 0.59, p < 0.001$). These statistics indicated that the vertical distribution of copepods would not impact our results. We elected to use the surface rather than the oblique tow dataset because it spanned 8 yr (1999–2006) rather than 4 yr.

During the MARMAP program (Sibunka and Silverman, 1984, 1989; Meise and OReilly, 1996) zooplankton were collected in the Gulf of Maine by double oblique tows with a 333 μm mesh net attached to a bongo sampler (Posgay and Marak, 1980). Tows were made from the surface to 5 m above the bottom and back to the surface, but did not exceed a depth of 200 m. For the purposes of the present study, we defined Great South Channel to include the Great South Channel right whale critical habitat expanded uniformly by 30%. The vertices of this polygon are 40°50.8′N, 69°07.2′W; 41°44.5′N, 69°51.8′W; 42°19.0′N, 68°26.9′W; 41°37.4′N, 68°03.5′W (Figure 2.1). We extracted archived MARMAP C5-6 *Calanus finmarchicus* data collected within the Great South Channel for use in the present study.

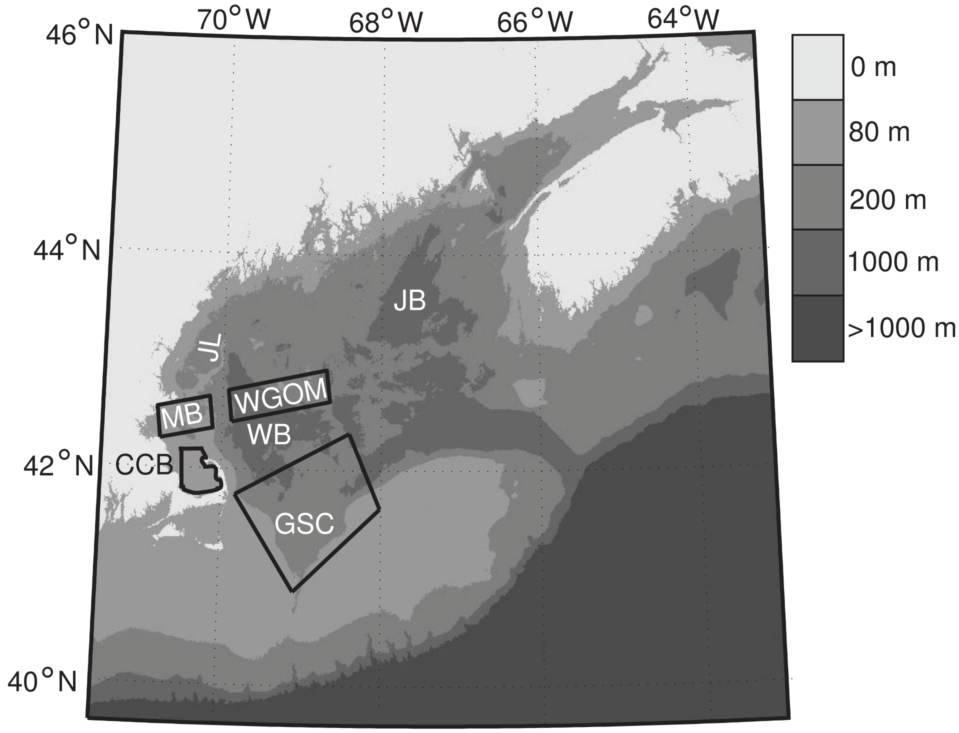

Figure 2.1: The Gulf of Maine, the northeastern coast of the USA and the southeastern coast of Canada. Bathymetric contours at 0, 80, 200 and 1000 m are depicted with shading. Cape Cod Bay (CCB) right whale critical habitat and the Great South Channel (GSC) right whale critical habitat expanded by 30% are outlined, as are the Massachusetts Bay (MB) and the western Gulf of Maine (WGOM) sections of the Gulf of Maine continuous plankton recorder (CPR) survey. JL: Jeffreys Ledge; JB: Jordan Basin; WB: Wilkinson Basin. All 1999–2006 CPR samples came from the MB and WGOM regions. A few samples prior to 1999 were collected as far north as 43°8.2′N and as far south as 42°14.3′N

2.3.2 Right whales

All analyses were accomplished using data extracted from the NARWC database (Kenney, 2001; Right Whale Consortium. North Atlantic Right Whale Consortium Sightings Database 08/23/2007. New England Aquarium, 2007). Included in our dataset is survey and right whale sighting information from numerous programs. The sources were the Cetacean and Turtle Assessment Program (CETAP) from 1978 to 1982 (CETAP, 1982), a set of contract surveys by the University of Rhode Island (URI) from 1984 to 1993 (Winn *et al.*, 1985; Kenney *et al.*, 1986a; Kenney and Winn, 1986a, 1987; Kenney, 2001), the South Channel Ocean Productivity Experiment (SCOPEX) program from 1988 to 1989 (Kenney and Wishner, 1995), aerial right whale surveys by the NMFS Northeast Regional Office and Northeast Fisheries Science Center (NEFSC) from 1998 to 2006 (Cole *et al.*, 2007), aerial surveys conducted by PCCS from 1998 to 2006 (Brown *et al.*, 2007), other aerial and shipboard surveys by NMFS between 1991 and 2002, and smaller survey datasets contributed by several NARWC member organizations (PCCS, New England Aquarium, International Fund for Animal Welfare, Whale Center of New England, and Associated Scientists at Woods Hole).

The dataset we used included 2 data types. First, line-transect aerial surveys were conducted as part of CETAP, SCOPEX and URIs Great South Channel studies to derive estimates of density and abundance of species within defined areas (which differed within and between programs). These surveys were conducted under rigorous criteria by highly trained observers from one of 2 aircraft, and were designed to represent statistically random samples of the area. Second, platforms-of-opportunity (POP) surveys were those where the observers collected complete records of aircraft or ship tracks and associated sighting conditions, but where the surveys were not sufficiently standardized to use for line-transect methods. Data from line-transect surveys conducted by NEFSC are archived in the NARWC database in the POP format.

The pattern of survey coverage (or effort) can bias the interpretation of raw sighting data. One method to overcome this potential bias is to quantify sighting effort, and then to correct sighting frequencies for differences in effort, producing an index termed sightings per unit effort (SPUE). The units are numbers of whales sighted per unit length of survey track. To standardize the SPUE data even further, the data may be limited to only a subset of the survey tracklines which meet some defined criteria for acceptability (see below). If the SPUE values are computed for consistent spatial units, they can be mapped to show effort corrected distribution patterns. SPUE values also can be statistically compared across areas, seasons, years, etc. Development of this method began during CETAP (1982), and it has been used in a variety of analyses (Kenney and Winn, 1986b; Winn *et al.*, 1986; Kenney, 1990; Hain *et al.*, 1992; Shoop and Kenney, 1992; Kraus *et al.*, 1993; of the Navy), 2005; Pittman *et al.*, 2006).

All available line transect aerial and POP aerial and shipboard survey data from 1999 to 2006 from the region encompassing Cape Cod Bay, and from 1978 to 2006 from the region encompassing the Great South Channel, were extracted from the NARWC database and combined to quantify sampling effort and derive right whale SPUE values. Only trackline segments completed with at least one observer on watch, clear visibility of at least 2 nautical miles (3.7 km), sea state of Beaufort 3 or lower, and altitude of less than 366 m (1200 ft) for aerial surveys were included as acceptable effort. The entire area was partitioned spatially into a grid of cells measuring 5 minutes of latitude (9.3 km) by 5 minutes of longitude (6.8 – 7.0 km) and temporally by 14 d periods.

Effort was quantified as the length of survey track completed within the spatial and temporal confines of the grid cells. All acceptable effort within each grid cell and time period was summed. Grid cells in which there was less than 2.5 km of survey track completed were excluded from our analysis as inadequately sampled. Similarly, only right whales sighted during acceptable effort were included and summed within each cell and period. The effort threshold value of 2.5 km was chosen after experimenting with several threshold values between 0 and 6.8 km (the east – west distance across a 5 x 5 minute cell). This threshold appeared to remove the most outliers without drastically reducing the number of records available for analysis. Finally, the number of animals sighted was divided by effort to generate the SPUE index, in units of animals sighted per 1000 km of valid effort. In the text of this manuscript we refer to right whale SPUE. In the figures and where numeric values are cited, we used right whales per 1000 km or whales per 1000 km.

We selected geographical subsets of the SPUE dataset for our analysis. For Cape Cod Bay our data included the area enclosed by Cape Cod Bay to the northern extent of the Cape Cod Bay right whale critical habitat (defined by the inner coastline of the Bay and 42°04.8′N, 70°10.0′W; 42°12.0′N, 70°15.0′W; 42°12.0′N, 70°30.0′W; 41°46.8′N, 70°30.0′W) (Figure 2.1). For the Great South Channel the SPUE data subset consisted of the area within a 30% uniform dilation of the Great South Channel right whale critical habitat (described above).

2.3.3 Data analysis

Copepod concentration and right whale SPUE values reported in the present study represent the mean concentration, or SPUE value, within each habitat area over the specified time interval. Copepod concentrations were log-transformed prior to analysis and are reported as $\log_{10}(no.\ ind.\ m^3 + 1)$.

We first analyzed seasonally expected changes in copepod concentration and right whale SPUE in each habitat area by computing climatological time series of copepod concentration and right whale SPUE values. A climatology is a 1-yr time series that is produced by averaging all measurements within predefined intervals of time across all years. The resultant time series represents conditions in a typical year. In the present study we used 14 d intervals to compute climatological values. Thus, each point in the climatology represents the mean copepod concentration or right whale SPUE value within the habitat area and within each 14 d period. Climatologies were computed from each dataset using data from the following years: (1) CPR-derived *Calanus finmarchicus* and other copepods from 1961 to 2006, (2) MARMAP-derived *C. finmarchicus* from 1977 to 1997, (3) PCCS-derived *C. finmarchicus* and other copepods from 1999 to 2006, and (4) NARWC right whale SPUE from 1999 to 2006 and 1978 to 2006 in Cape Cod Bay and the Great South Channel, respectively (Table 2.1).

Table 2.1: *Calanus finmarchicus*, other copepods (*Pseudocalanus* spp. and *Centropages* spp.) and *Eubalaena glacialis*. Number (n) of copepod net tows and right whale sightings per unit effort (SPUE) data records analyzed and years spanned by each dataset. na: Not applicable; MARMAP: Marine Resource Monitoring, Assessment, and Protection program; CPR: continuous plankton recorder

	Climatological analysis		Interannual analysis	
	n	Year	n	Year
Cape Cod Bay				
Right whale SPUE	3147	1999 – 2006	3147	1999 – 2006
Calanus finmarchicus	1420	1999 – 2006	1420	1999 – 2006
Other copepods	1420	1999 – 2006	1420	1999 – 2006
Great South Channel				
Right whale SPUE	12364	1978 – 2006	6366	1999 – 2006
Calanus finmarchicus (MARMAP)	995	1977 – 1997	na	na
Calanus finmarchicus (CPR)	1148	1961 – 2006	247	1996 – 2006
Other copepods (CPR)	1148	1961 – 2006	247	1996 – 2006

Next, we analyzed interannual changes in mean copepod concentration and right whale SPUE in each habitat area. The time frame for this analysis (1999 to 2006) was chosen to coincide with increased data collection efforts that began in 1999 and have been sustained.

In Cape Cod Bay we restricted our interannual comparison to the first 5 mo of each year, the time period of consistent sampling by PCCS. Yearly time series of *Calanus finmarchicus*, other copepods and right whale SPUE were computed using 14 d periods. For our statistical analysis, linear regression was used to determine if there was a significant relationship between mean copepod concentration and right whale SPUE within 28 d periods. This longer time period was used because timing of copepod sampling and right whale surveys was not synchronized, and some 14 d periods contained relatively small amounts of data.

For our interannual comparison of *Calanus finmarchicus* concentration and right whale SPUE in the Great South Channel habitat area, we plotted yearly time series of CPR-derived *C. finmarchicus* and other copepod concentration from the western Gulf of Maine using 56 d periods (2 consecutive 28 d periods), and yearly time series of right whale SPUE using 28 d periods. The 56 d time period was necessary because there are only few records each month from the CPR. For our statistical analysis, linear regression was used to determine if there was a significant relationship between mean *C. finmarchicus* and other copepod concentration and mean right whale SPUE within trimesters from 1999 to 2006. Trimesters were defined by the following intervals: 1 January–22 April (trimester 1, 112 d and 113 d during leap years), 23 April–12 August (trimester 2, 112 d), and 13 August–31 December (trimester 3, 141 d). Trimester 3 is longer than trimesters 1 and 2 because a year cannot be equally divided into the 28 d periods that we found necessary to standardize our analysis. We performed an identical 1999 to 2006 trimester analysis between CPR-derived *C. finmarchicus* concentration from Massachusetts Bay and right whale SPUE from the Great South Channel.

The temporal resolution of MARMAP sampling after 1987 was too sparse to use in our interannual analysis. Fortunately, the western Gulf of Maine tract of the CPR is directly upstream of the Great South Channel, and the regions are oceanographically connected by geographic proximity and local circulation patterns (Chen *et al.*, 1995). We found a significant correlation ($r^2 = 0.26, p < 0.001, n = 63$) between CPR and MARMAP-derived *Calanus finmarchicus* concentration from corresponding trimesters. For these reasons we feel justified using *C. finmarchicus* measurements from the western Gulf of Maine tract of the CPR as a proxy for the *C. finmarchicus* measurements in the Great South Channel.

The copepod sampling methodology was consistent within each region. Therefore, comparison of relative copepod concentrations within a region and across time is appropriate, but direct comparison of values between regions is not. Right whale SPUE values for both regions came from the same database, but we caution readers against making direct comparisons of SPUE values between regions.

Due to the small number of data points used in the linear regressions, correlation coefficients and statistical significance were sensitive to each data point. For this reason, we consider relationships with p-values near 0.15 to be meaningful; however, our criteria for statistical significance is $p < 0.05$.

2.4 Results

2.4.1 Cape Cod Bay: climatological patterns

Climatological *Calanus finmarchicus* concentration in Cape Cod Bay (Figure 2.2a) rises from a very low concentration in January to a local maximum of $10^{2.4}$ $ind.\ m^3$ at the end of April. *C. finmarchicus* concentration during May and June varies in excess of one order of magnitude. Maximum *C. finmarchicus* concentration of 10^3 $ind.\ m^3$ is reached in late June. From mid-July to early September *C. finmarchicus* concentration is less than $10^{0.5}$ $ind.\ m^3$, on par with the concentration measured during January. From October to mid-November there is an increase in *C. finmarchicus* concentration of almost 1.5 orders of magnitude. The concentration in December is less than $10^{0.2}$ $ind.\ m^3$ and is on par with the January concentration. There are no *C. finmarchicus* or other copepod measurements available in early July, mid- September or late November.

Unlike *Calanus finmarchicus*, the mean concentration of other copepods in January is near the maximum yearly value. The only other time that concentration exceeds 10^3 $ind.\ m^3$ is during December. From January to May the concentration of other copepods declines steadily, by almost an order of magnitude, from $10^{3.1}$ to $10^{2.2}$ $ind.\ m^3$. The concentration then increases and remains relatively high ($> 10^2$ $ind.\ m^3$) from June through August, when the concentration appears to decline substantially before rebounding to levels in excess of 10^2 $ind.\ m^3$.

The CPR measurements of *Calanus finmarchicus* (Figure 2.2b) from the Massachusetts Bay tract of the CPR, north of Cape Cod Bay, are generally higher than the measurements of *C. finmarchicus* within Cape Cod Bay, though a di-

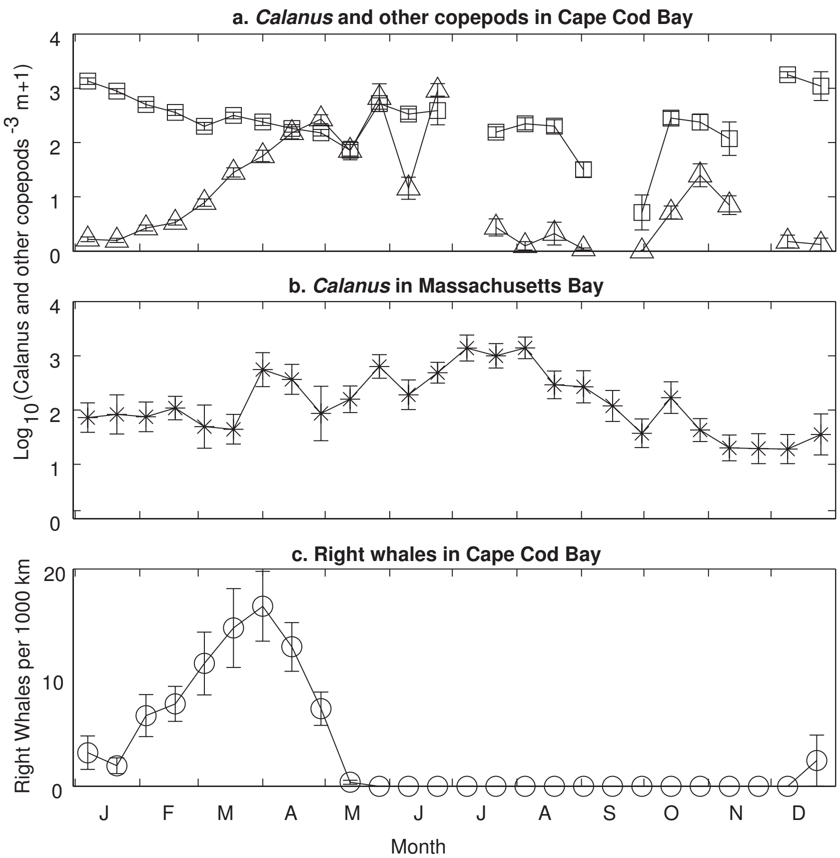

Figure 2.2: *Calanus finmarchicus*, other copepods (*Pseudocalanus* spp. and *Centropages* spp.) and *Eubalaena glacialis*. Climatological time series of (a) *C. finmarchicus* (△) and other copepods (□) from surface tows in Cape Cod Bay (1999 – 2006), (b) *C. finmarchicus* (∗) from the Massachusetts Bay tract of the CPR (1961–2006), and (c) right whale SPUE (whales per 1000 km of survey effort) (◯) in Cape Cod Bay (1999 – 2006). Each point represents the mean ± 1 SE for a 14 d period

rect comparison of concentrations from the CPR and net tows is problematic. Massachusetts Bay CPR *C. finmarchicus* concentration does not fall below $10^{1.3}$ *ind*. m^3, and only exceeds 10^3 *ind*. m^3 during 2 periods, early July and early August. The maximum springtime *C. finmarchicus* concentration occurs at the beginning of April. Subsequent to this, *C. finmarchicus* concentration rises and falls in a pattern reminiscent of, but less pronounced than, *C. finmarchicus* in

Cape Cod Bay (Figure 2.2a). From this point on in Massachusetts Bay, *C. finmarchicus* concentration declines steadily, with the exception of a brief increase in concentration during October. During November and December the concentration is relatively constant.

Right whale SPUE is near zero whales per 1000 km in January (Figure 2.2c), but increases to its maximum value of 16.5 whales per 1000 km in early April. Right whale SPUE then decreases nearly twice as fast as it increased. Right whale SPUE is at or near zero whales per 1000 km from late June to early December.

The rise and fall in right whale SPUE is not reflected in copepod data, however there are some similarities. *Calanus finmarchicus* concentration and right whale SPUE measured inside Cape Cod Bay both rise rapidly for about the first 3 mo of the year. In early April right whale SPUE declines rapidly, while *C. finmarchicus* concentration continues to rise. The concentration of other copepods declines throughout the entire rise and fall in right whale SPUE, January through May. In mid May, the concentration of other copepods and right whale SPUE are at their minimum values for the first 5 mo of the year. The springtime local maximum in *C. finmarchicus* concentration from the Massachusetts Bay tract of the CPR co-occurs with the yearly right whale SPUE maximum.

2.4.2 Great South Channel: climatological patterns

In the Great South Channel, MARMAP-derived *Calanus finmarchicus* concentration increases steadily from January through March (Figure 2.3a). There is an abrupt increase in *C. finmarchicus* concentration during April, after which the concentration remains high until mid-June. The maximum concentration ($10^{2.6}$ $ind.\ m^3$) occurs in mid-May. After late June, *C. finmarchicus* concentration falls back to pre-April levels. Following this reduction, there is subtle evidence of a second high concentration period during August and September. The *C. finmarchicus* concentration from mid-October through December is relatively low.

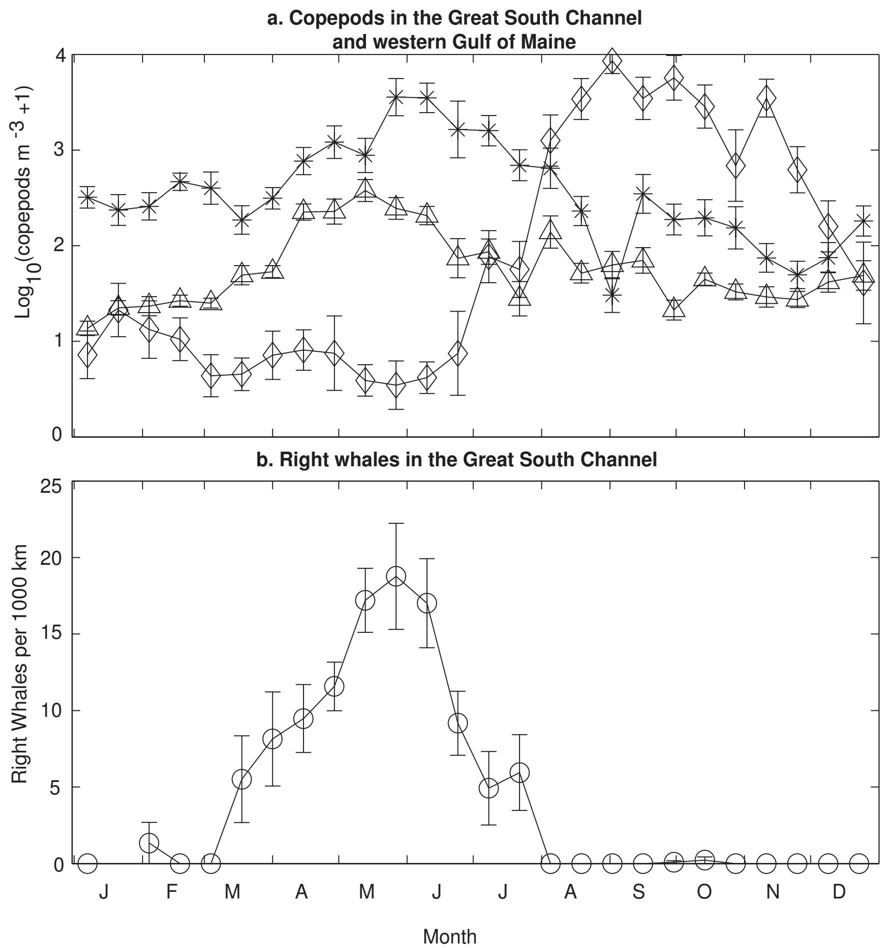

Figure 2.3: *Calanus finmarchicus*, other copepods (*Pseudocalanus* spp. and *Centropages* spp.) and *Eubalaena glacialis*. Climatological time series of (a) *Calanus* (∗) and other copepods (◊) from the western Gulf of Maine tract of the CPR (1961 – 2006), and *Calanus* (△) from the Marine Resources Monitoring, Assessment and Prediction (MARMAP) program in the Great South Channel (1977 – 1997), and (b) right whale SPUE (whales per 1000 km of survey effort) (○) in the Great South Channel (1978 – 2006). Each point represents the mean ± 1 SE for a 14 d period

From January to late March the CPR-derived *Calanus finmarchicus* concentration is relatively constant, with slight increases in concentration during late February and early March. The mean value during this period is $10^{2.5}$ $ind.\ m^3$. *C. finmarchicus* concentration then increases gradually to the maximum value of $10^{3.6}$ $ind.\ m^3$ in late May. This high concentration is sustained for about one month. There is a steady decline in concentration from mid-June to the end of August, when the minimum yearly concentration of $10^{1.5}$ $ind.\ m^3$ is reached. *C. finmarchicus* concentration quickly rebounds to values on par with those exhibited in mid-August, but then declines and is relatively low throughout November and December.

The concentration of other copepods from the CPR (Figure 2.3a) is inverted from that of *Calanus finmarchicus* it is relatively low for the first half of the year, and relatively high for the latter half of the year. A similar pattern was noted by Pershing *et al.* (2005) . The concentration declines from mid-January through February, and until mid-June a relatively low level is sustained ($mean\ =\ 10^{0.7}$ $ind.\ m^3$). The concentration then rises rapidly, 3 orders of magnitude over 2 mo, to the yearly maximum of $10^{3.9}$ $ind.\ m^3$, and remains high until a rapid decline begins in November.

The MARMAP and western Gulf of Maine CPR climatological *Calanus finmarchicus* time series show similar patterns in abundance through time. The CPR *C. finmarchicus* concentration appears to lag behind that of MARMAP by 2 to 4 wk. Both time series show a prominent and a subtle high-concentration period: a prominent peak occurs in early May and in the first half of June, and a less obvious peak occurs in late July and in mid-September, for the MARMAP and CPR time series, respectively. Additionally, the CPR time series shows a subtle peak in late February and early March that cannot be seen in the MARMAP time series.

As in Cape Cod Bay, right whale SPUE in the Great South Channel is seasonal (Figure 2.3b). During January and February right whales are sighted very infrequently in the habitat area, indicated by near zero SPUE values. In March, right whale SPUE begins to steadily increase, and during the 14 d period in early May there is a 67% increase in SPUE. The highest SPUE value of the year (18.8 whales per 1000 km) occurs in late May. This maximum value co-occurs with the maximum CPR *Calanus finmarchicus* concentration, and occurs 2 wk after the maximum MARMAP *C. finmarchicus* concentration. Right whale SPUE decreases from mid-June through July, and from early August to the end of the year SPUE is at or near zero whales per 1000 km.

There is a strong positive relationship between the climatological time series of *Calanus finmarchicus* and right whale SPUE during the right whale season of March through July in the Great South Channel (Figure 2.4). During this time period, the relationship between MARMAP *C. finmarchicus* concentration and right whale SPUE is significant ($r^2 = 0.65, p < 0.01$), while the relationship between climatological CPR *C. finmarchicus* concentration and right whale SPUE is weaker ($r^2 = 0.40, p = 0.05$). These relationships, along with the correlation between MARMAP and CPR *C. finmarchicus* concentrations (see above), support the use of mean *C. finmarchicus* concentration from the western Gulf of Maine tract of the CPR as a proxy for mean *C. finmarchicus* concentration in the Great South Channel.

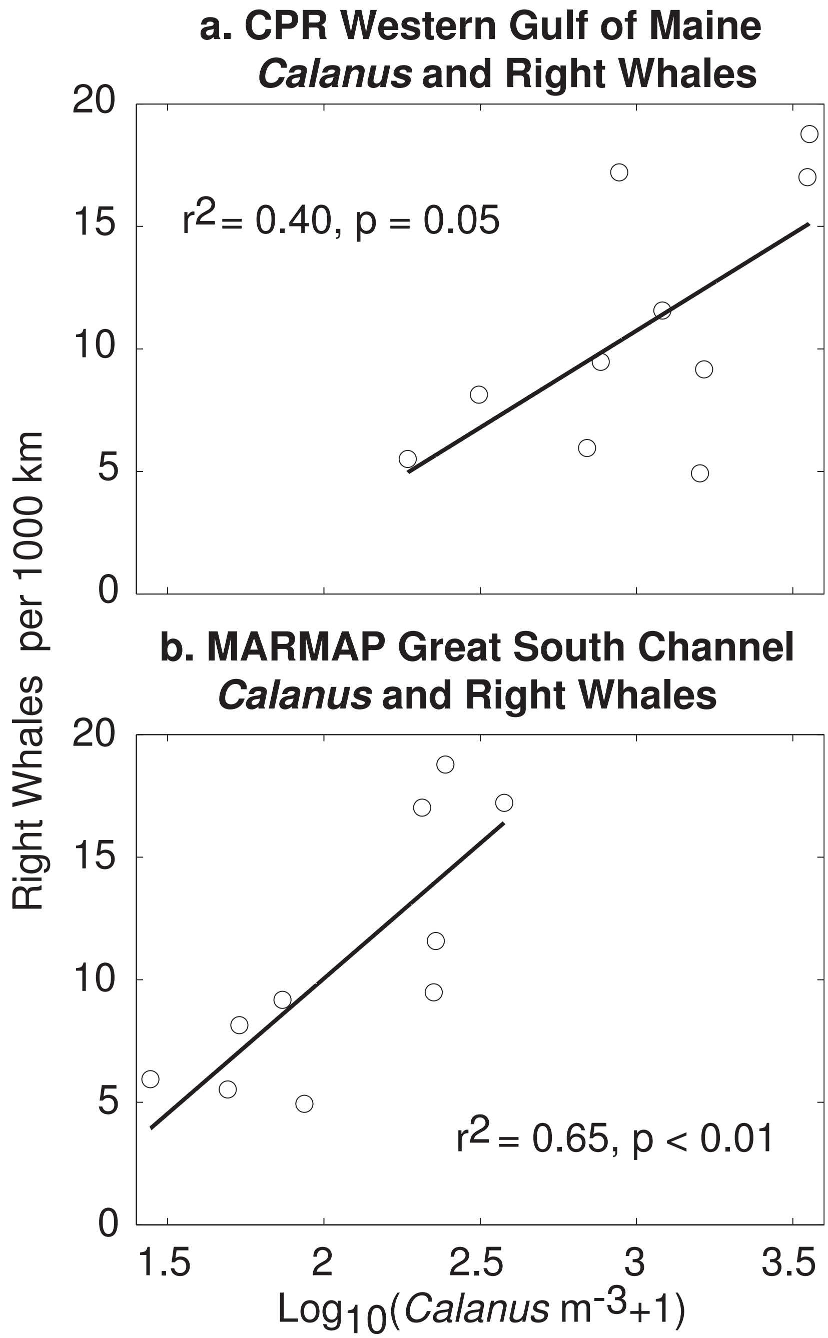

Figure 2.4: *Calanus finmarchicus* and *Eubalaena glacialis*. March through July correlation of climatological right whale SPUE (whales per 1000 km of survey effort) in the Great South Channel (1978 – 2006) versus (a) *C. finmarchicus* from the western Gulf of Maine tract of the CPR (1961 – 2006) and (b) *C. finmarchicus* from MARMAP surveys in the Great South Channel (1977 – 1997). Each point represents the March through July climatological mean

2.4.3 Cape Cod Bay: interannual patterns

During January to February from 1999 to 2006, the range of values spanned by the mean concentration of *Calanus finmarchicus* was less than one order of magnitude. Beginning in March, yearly *C. finmarchicus* time series diverge from one another and years with high concentrations can be visually separated from years with low concentrations (Figure 2.5a). *C. finmarchicus* concentration in 1999, 2001 and 2005 was consistently high through March and April. A comparably high concentration was reached in 2000 and 2003, but during these years the springtime increase in *C. finmarchicus* concentration lagged by 2 to 4 wk. *C. finmarchicus* concentration declined in May during all years except 2002, when the concentration continued to increase throughout May. Because sampling stopped early in some years, there were no *C. finmarchicus* or other copepod data available after the first week of May in 1999, 2000 and 2006.

From 1999 to 2002, the range of values spanned by the mean concentration of other copepods was less than one order of magnitude, with the exception of a lower concentration in April 2002. The concentration of other copepods from 2003 to 2006 declined faster and was more variable than the concentration from 1999 to 2002. Notable examples of this are the years 2003 and 2004. By May 2003, *Calanus finmarchicus* concentration was 1.5 orders of magnitude lower than it was in January 2003. The concentration in early March 2003 was the second lowest for that year, and 6 wk later the concentration was at its peak value for that year. The greatest decline in concentration, over 2 orders of magnitude, occurred from January to May 2004. From mid-February though March 2004, the concentration of other copepods was relatively stable at a value above the 2003 to 2006 average. DeLorenzo Costa *et al.* (2006) reported similar patterns in

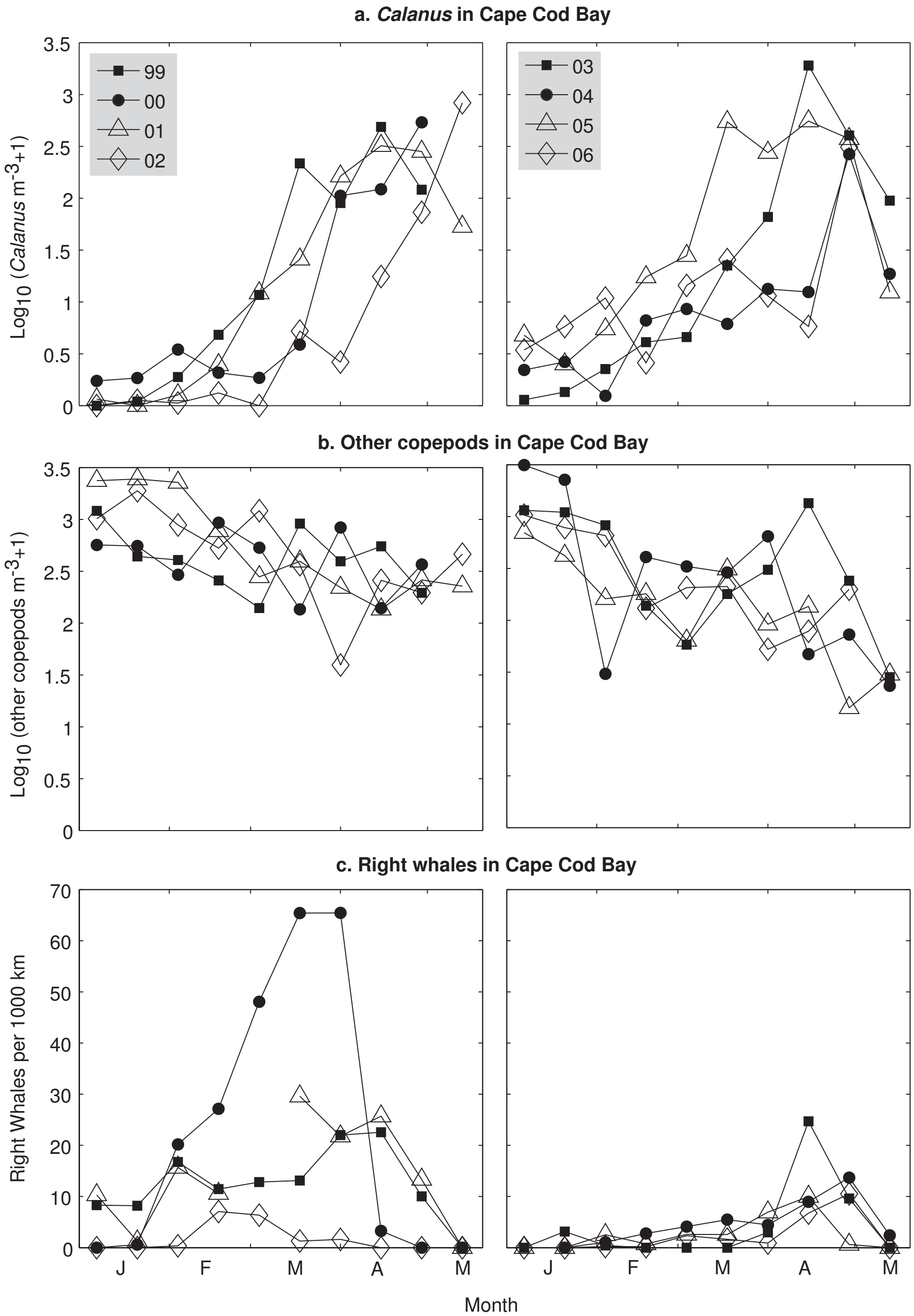

Figure 2.5: *Calanus finmarchicus*, other copepods (*Pseudocalanus* spp. and *Centropages* spp.) and *Eubalaena glacialis*. Yearly time series (1999 – 2006) from Cape Cod Bay of (a) *C. finmarchicus* and (b) other copepods collected by surface tow, and (c) right whale SPUE (whales per 1000 km of survey effort). Each point represents the mean over a 14 d period

their monthly analysis of copepod concentration in Cape Cod Bay from 2000 to 2003.

In general, right whale SPUE was higher from 1999 to 2002 than it was from 2003 to 2006 (Figure 2.5c). In 2000, right whale SPUE was unusually high in Cape Cod Bay; SPUE peaked from mid-March to mid-April, and declined to zero whales per 1000 km by the end of April. During 2002, right whale SPUE peaked in mid- February, 6 to 8 wk before copepod concentration was expected to peak (Figure 2.2b). The years 2003 to 2006 exhibited very similar patterns: a slow increase in right whale SPUE from the beginning of the year until the maximum was reached in April, after which right whale SPUE declined in May. Of the latter 4 yr, the highest right whale SPUE was found in 2003, and it co-occurred with the 2003–2006 maximum concentration of *Calanus finmarchicus* and other copepods.

Broadly speaking, *Calanus finmarchicus* concentration was lower from 1999 to 2002 than from 2003 to 2006. The opposite pattern was exhibited in the concentration of other copepods and right whale SPUE, which were both higher from 1999 to 2002 than from 2003 to 2006.

During January, February and most of March, a generally negative relationship can be seen between regionwide *Calanus finmarchicus* concentration and right whale SPUE in Cape Cod Bay (Figure 2.6a). The apparent negative relationship was strongest in January ($r^2 = 0.37, p = 0.108$; Table 2.2), and was weaker in February and March.

Table 2.2: *Calanus finmarchicus*, other copepods (*Pseudocalanus* spp. and *Centropages* spp.) and *Eubalaena glacialis*. Correlations between relative abundance of right whales (all parameter y = right whale SPUE) and mean copepod concentration (parameter x) in Cape Cod Bay and the Great South Channel

Region	Parameter x		n	r	p
Cape Cod Bay					
	Calanus finmarchicus	1 Jan – 28 Jan	8	0.61	0.11
		29 Jan – 25 Feb	8	0.42	0.31
		26 Feb – 25 Mar	8	0.44	0.27
		26 Mar – 22 Apr	8	0.59	0.12
		23 Apr – 20 May	8	0.06	0.89
	Other copepods	1 Jan – 28 Jan	8	0.07	0.85
		29 Jan – 25 Feb	7	0.60	0.12
		26 Feb – 25 Mar	8	0.40	0.33
		26 Mar – 22 Apr	8	0.73	<**0.05**
		23 Apr – 20 May	8	0.01	0.98
Great South Channel					
	Calanus finmarchicus	1 Jan – 22 Apr	8	0.44	0.28
		23 Apr – 12 Aug	8	0.74	<**0.05**
		13 Aug – 31 Dec	6	0.54	0.27
	Other copepods	1 Jan – 22 Apr	8	–0.50	0.20
		23 Apr – 12 Aug	8	–0.71	<**0.05**
		13 Aug – 31 Dec	6	–0.65	0.22

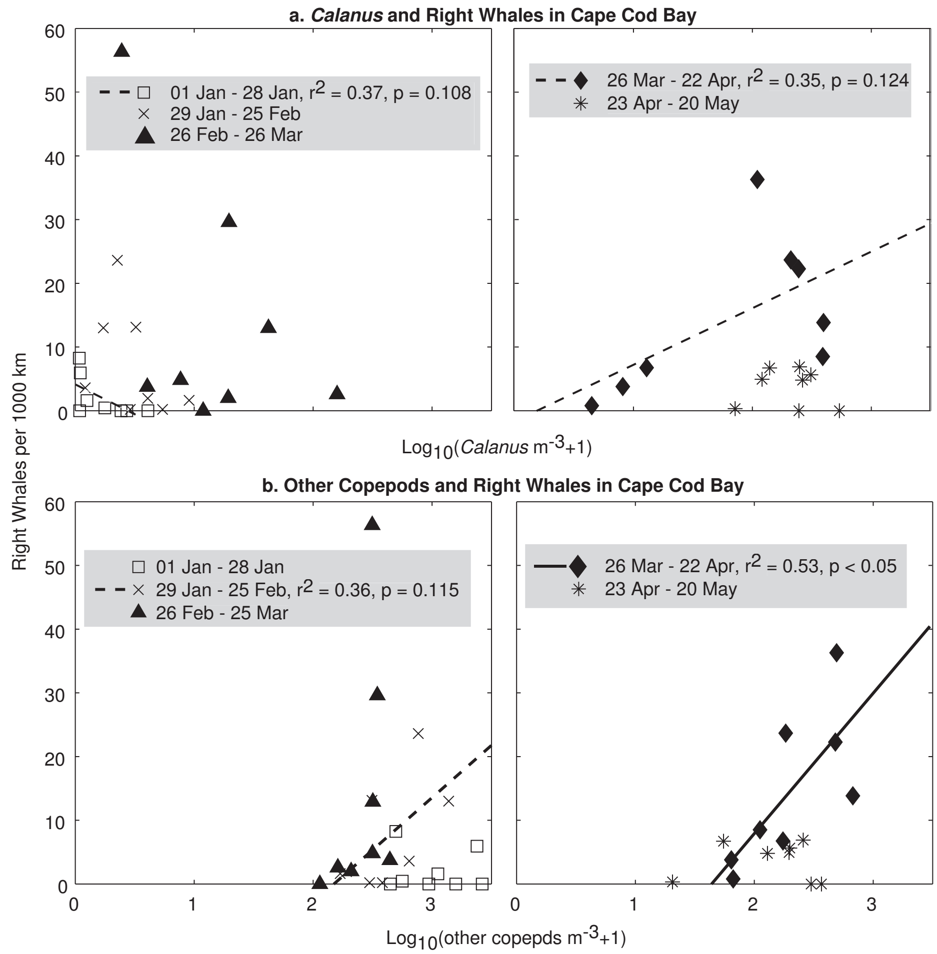

Figure 2.6: *Calanus finmarchicus*, other copepods (*Pseudocalanus* spp. and *Centropages* spp.) and *Eubalaena glacialis*. Cape Cod Bay mean copepod concentration from surface tows versus right whale SPUE (whales per 1000 km of survey effort) within the first five 28 d periods from 1999 to 2006. (a) *C. finmarchicus* and (b) other copepods plotted against right whale SPUE. Lines are linear least squares fits: (—-) $p < 0.05$; (- - -) $p < 0.15$

The relationship between *C. finmarchicus* concentration and right whale SPUE appears to have switched from negative to positive in the period of late March to late April. During this time of year in Cape Cod Bay, *C. finmarchicus* typically becomes a larger proportion of the copepod assemblage (Figure 2.2a), while right whales are sighted with increasing frequency (Figure 2.2c). The relationship between the mean concentration of other copepods and right whale SPUE in Cape Cod Bay was generally positive (Figure 2.6b). During January there was no apparent relationship, but in each of the following 2 time periods (spanning 29 January– 25 March) a positive, but insignificant, relationship can be seen between the concentration of other copepods and right whale SPUE. During the right whale season, when right whales are expected in high numbers (26 March22 April) in Cape Cod Bay, there was a significant association between the concentration of other copepods and right whale SPUE ($r^2 = 0.53$, $p < 0.05$, Table 2.2). There was no discernable relationship between the concentration of other copepods and right whale SPUE in the subsequent 28 d period, from 23 April to 20 May.

2.4.4 Great South Channel: interannual patterns

Western Gulf of Maine *Calanus finmarchicus* concentration from 1999 to 2002 was generally low with high variability, while from 2003 to 2006 the concentration was generally high with low variability (Figure 2.7a). *C. finmarchicus* concentration in 2000 was particularly low in the latter half of the year. The year 2001 was unique in that *C. finmarchicus* increased in the latter half of the year. In 2003 and 2004 the concentration of *C. finmarchicus* rose to near-maximum concentrations about 2 mo before the maximum was reached in mid-May. The years 2005 and 2006 exhibited a different pattern: *C. finmarchicus* concentration rose at about the same rate from January until the yearly maximum concentration was reached in mid-May. Concentration in the latter half of 2005 was the lowest of any year except 2000. There were no data available for mid-May of 1999 or 2001, when the maximum *C. finmarchicus* concentration typically occurred.

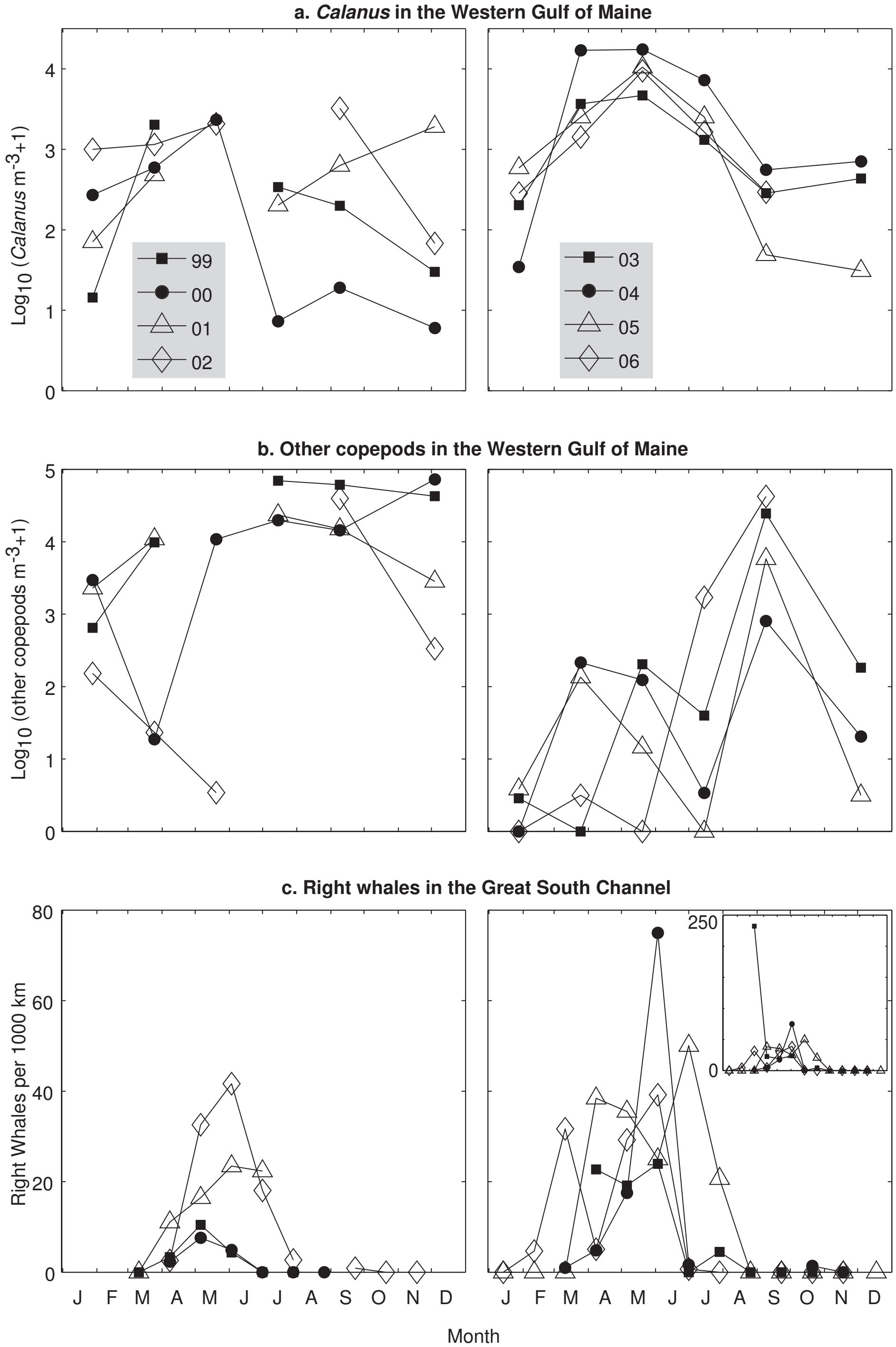

Figure 2.7: *Calanus finmarchicus*, other copepods (*Pseudocalanus* spp. and *Centropages typicus*) and *Eubalaena glacialis*. Yearly time series (1999 – 2006) of (a) *C. finmarchicus* and (b) other copepods from the western Gulf of Maine tract of the CPR. (c) Right whale SPUE (whales per 1000 km of survey effort) in the Great South Channel. Inset shows right whale SPUE outlier from March 2003

The early year concentration of other copepods from the western Gulf of Maine CPR (Figure 2.7b) tract was generally high from 1999 to 2002, and was generally low from 2003 to 2006. With the exception of the second 56 d period, concentrations in 2000 were unusually high. In 1999 and 2000, the end-year decline in concentration, seen in all other years, was not observed. Concentrations from 2003 to 2006 were bimodal, with peaks in concentration early and late in the year. Within all of these years, except 2004, a difference of at least one order of magnitude can be seen between the early and late peaks in concentration.

The yearly right whale SPUE time series (Figure 2.7c) from the Great South Channel shows a great deal of variation from the climatology (Figure 2.3b). Right whales were usually first sighted in the Great South Channel during March (Figure 2.7c). The maximum right whale SPUE was typically reached during May or June, and by August or September right whale SPUE in the Great South Channel was at or near zero. Right whale SPUE was generally lower from 1999 to 2001 than in the following years, and particularly low SPUE values were found in 1999 and 2000. Right whale SPUE from 2003 to 2006 was highly variable within years. In March of 2003, right whale SPUE was very high (Figure 2.7c inset), but subsequently declined to more typical levels. The highest right whale SPUE value, aside from the outlier in March of 2003, was recorded in late May and early June 2004. In 2005 there were 2 right whale SPUE maxima: a local maximum during April, followed by a decline, and then the yearly maximum value in July. This pattern was also observed in 2006, but the time series was shifted back by about one month, so that there was a local maximum in March, followed by a decline, and then the yearly maximum right whale SPUE in June. A small number of survey flights were directed toward the location of suspected aggregations of whales. Records from these flights are not easily identifiable in the NARWC database, and it is possible that the peculiar SPUE peaks seen in March are due to such flights.

Right whale SPUE was usually higher in the Great South Channel when the *Calanus finmarchicus* concentration was high in the western Gulf of Maine (Figure 2.8a). During trimester 1 (January through late April) there was a weak positive association between *C. finmarchicus* concentration and right whale SPUE. During trimester 2 (late April to mid-August) the association was significant and positive ($r^2 = 0.54, p < 0.05$). In trimester 3 (mid-August through December) there was no detectable relationship between *C. finmarchicus* concentration and right whale SPUE. In addition to the correlations, a more general relationship holds: right whale SPUE was relatively low when *C. finmarchicus* concentration was low, and when right whale SPUE was high in the Channel, *C. finmarchicus* concentration was high. No relationship was found between Great South Channel right whale SPUE and *C. finmarchicus* concentration from the Massachusetts Bay tract of the CPR.

Right whale SPUE was usually lower in the Great South Channel when the concentration of other copepods was higher in the western Gulf of Maine (Figure 2.8b). During trimester 1 there was a weak negative association between the concentration of other copepods and right whale SPUE. During trimester 2 (late April to mid-August) the association was significant and negative ($r^2 = 0.51, p < 0.05$), and during trimester 3 right whale SPUE did not vary notably with the concentration of other copepods.

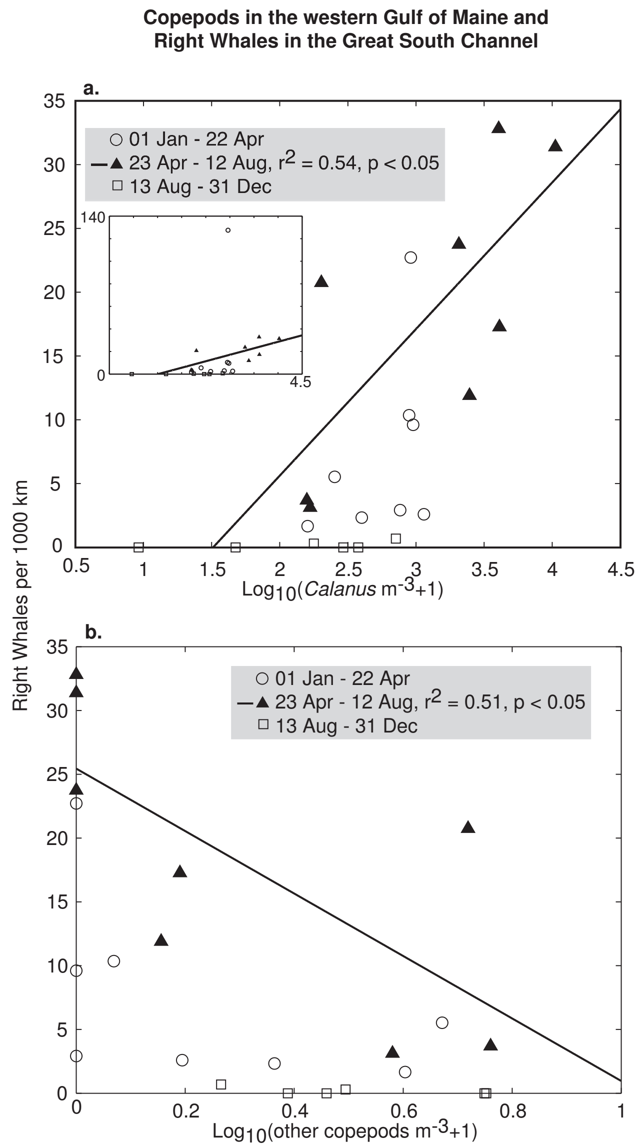

Figure 2.8: *Calanus finmarchicus*, other copepods (*Pseudocalanus* spp. and *Centropages typicus*) and *Eubalaena glacialis*. Mean right whale SPUE (whales per 1000 km of survey effort) from the Great South Channel versus (a) *C. finmarchicus* and (b) other copepods from the western Gulf of Maine tract of the CPR during the following trimesters (1999 – 2006): 1 January – 22 April (○), 23 April – 12 August (▲), 13 August – 31December (□). Inset shows a right whale SPUE outlier from March 2003 that was removed from the dataset

2.5 Discussion

We found that regional-scale mean copepod concentration can be a good indicator of right whale SPUE in 2 right whale critical habitats. The association changes both in time and between habitats, with *Calanus finmarchicus* playing a more important role in the Great South Channel, and other copepods playing a more important role in Cape Cod Bay.

Wishner *et al.* (1995) found significantly higher abundances of stage C5 *Calanus finmarchicus* in areas where whales were present than in areas where they were absent. Baumgartner *et al.* (2003a) found a significant relationship between right whale sighting rate and *C. finmarchicus* abundance at the depth of the stage C5 *C. finmarchicus* diapausing layer (90 to 140 m), but not with whole water-column abundances of *C. finmarchicus*. These studies emphasize the importance of subsurface aggregations of *C. finmarchicus* to feeding right whales and suggest that, due to spatial and temporal heterogeneity in copepod concentration, the regional-scale copepod concentration may not be important. Our results stand in contrast to this suggestion. We found that the regional-scale mean copepod concentration, when measured in near-surface waters and averaged across space (rather than depth), is significantly related to the relative abundance of right whales at certain times of year.

In light of Figures 8a & 6b, and keeping in mind that right whales feed at depth as well as near the surface, we view mean copepod concentration as good proxy for the availability of dense copepods patches to right whales. The results presented here complement those of Wishner *et al.* (1995) and Baumgartner *et al.* (2003a), and others, by expanding the spatiotemporal scale of study and the number of samples (Table 2.1) under consideration.

2.5.1 Cape Cod Bay

From the end of January to late March there is a suggestive, but statistically insignificant, positive relation ship between the concentration of other copepods and right whale SPUE in Cape Cod Bay (Figure 2.6b). Indeed, if right whales are feeding in Cape Cod Bay at this time of year, they could reasonably be expected to feed on the most abundant, available and acceptable copepods, which are the wintertime residents *Pseudocalanus* spp. an *Centropages* spp. (Figure 2.5b). In contrast, there is a suggestive, though statistically insignificant, negative relationship between *Calanus finmarchicus* and right whale SPUE in the Bay during mid-winter (128 January) (Figure 2.6a). This relationship, albeit weak, is surprising. The density of *C. finmarchicus* is low and accounts for a small percentage of the overall copepod assemblage at that time of year, and we would not necessarily expect a strong relationship between *C. finmarchicus* and right whales (Figure 2.2a). One hypothesis to explain this is that when *C. finmarchicus* are abundant in Cape Cod Bay, they are more abundant outside of the bay. This hypothesis is supported by the fact that *C. finmarchicus* arrive in Cape Cod Bay primarily via advection (DeLorenzo Costa *et al.*, 2006; Jiang *et al.*, 2007). Concentration of CPR-derived *C. finmarchicus* is generally higher in Massachusetts Bay (Figure 2.2b) than in the western Gulf of Maine (Figure 2.3a). A high *C. finmarchicus* concentration inside Cape Cod Bay may imply that conditions outside of the bay are more favorable for the production of *C. finmarchicus*. From our analysis, there appears to be no *C. finmarchicus* reason for right whales to be in Cape Cod Bay prior to late March.

The maximum right whale SPUE value in Cape Cod Bay usually occurs in the early spring, during April. The same pattern was noted almost a century ago (Allen, 1916). Typically, the concentration of other copepods has declined by this time of year, and the concentration of *Calanus finmarchicus* has increased to the point where they are on par with that of other copepods. The significant association between the concentration of other copepods and right whale SPUE in Cape Cod Bay at this time of year ($r^2 = 0.53$, $p < 0.05$), and the suggestive (but statistically insignificant) relationship between *C. finmarchicus* and right whale SPUE imply that the mean concentration of copepods in Cape Cod Bay is coupled to the number and quality of copepod patches in the bay, and thus the suitability of the bay for feeding right whales. These results are supported by the findings of Jiang *et al.* (2007) who found a significant relationship (using the criterion $p < 0.10$) between right whale SPUE and *C. finmarchicus* in Cape Cod Bay.

Despite the fact that right whales appear to respond more strongly to other copepods than to *Calanus finmarchicus*, we know that *C. finmarchicus* is an important part of the right whales diet. Given this, why does the number of right whales in Cape Cod Bay decline just as *C. finmarchicus* concentration reaches the seasonal maximum value? Comparing apparent right whale departure and arrival times, inferred from SPUE values, in Cape Cod Bay and the Great South Channel, we see that as right whale SPUE declines in the bay, it increases in the channel (Figures 2.2c & 3b). This shift in the sighting frequency of right whales between the 2 neighboring habitats suggests that whales residing in Cape Cod Bay may move to the Great South Channel at this time. It is plausible that the relative concentration of *C. finmarchicus* and other copepods in neighboring habitats is responsible for shifts in the relative abundance of right whales from Cape

Cod Bay to the Great South Channel, and to other habitats.

If the highest Gulf of Maine *Calanus finmarchicus* abundance occurs over Wilkinson and Jordan Basins, and the lowest *C. finmarchicus* abundances occur in the waters of Massachusetts Bay and Cape Cod during January and February, as Meise and OReilly (1996) reported, why is Cape Cod Bay utilized by right whales during this time of year? One possible explanation for the late winter occurrence of right whales in Cape Cod Bay is that the bay may preferentially attract demographic subsets of the North Atlantic right whale population. A few studies have explored the hypothesis that there is regional segregation of demographic groups in the North Atlantic right whale population, and there are a few examples of sighting heterogeneity related to life history stage. Brown et al. (2001) found lower identification rates for adult female right whales than for male and female juveniles and adult males. Weinrich *et al.* (2000) found longer residence times for mother-calf pairs than for other demographic groups in the Jeffreys Ledge habitat, and Hamilton and Mayo (1990) found that mothers with calves were not sighted in Massachusetts and Cape Cod Bays until after the first week of April. Further analysis of individually identified right whales and their inter- and intra-annual sightings is needed to describe and assess the influence of right whale demography on their pattern of habitat use.

2.5.2 Great South Channel

Our interannual analysis showed that from late April to early August, region-wide mean concentration of *Calanus finmarchicus* was a strong indicator ($r^2 = 0.54$, $p < 0.05$) of right whale SPUE in the Great South Channel. Earlier in the year there was a positive relationship between *C. finmarchicus* and right whale SPUE in the channel, and later in the year there was no detectable relationship between *C. finmarchicus* and right whale SPUE in the channel. Overall, above average *C. finmarchicus* concentration appears to be a necessary condition for high relative abundance of right whales.

We have the most confidence in the result for late April to early August (Figure 2.8a, ▲), since right whale survey effort in the Great South Channel was usually greatest at that time of year. If feeding is one of the primary reasons that right whales visit the Great South Channel, then the significant association between *Calanus finmarchicus* concentration and right whale sighting frequency in this region could be interpreted as an association between region-wide mean *C. finmarchicus* concentration and the number and quality of high-density *C. finmarchicus* patches in the region.

In the Bay of Fundy, Baumgartner *et al.* (2003b) found that the average water-column concentration of stage C5 *Calanus finmarchicus* was lower in 2000 than in 2001, yet discrete layers of *C. finmarchicus* at depth had a higher concentration in 2000 than in 2001. This mismatch suggests that, at the scale of their study (on the order of 50 km^2 and over several days during summer), the density of *C. finmarchicus* patches is not strongly coupled to regional-scale mean *C. finmarchicus* concentration. A critical difference between the study of Baumgartner *et al.* (2003b) and the present study is the temporal range considered (a few days versus months), and the copepod concentration averaging method (water-column averages versus surface spatial averages). Assuming whales require high-density *C. finmarchicus* patches, the present study suggests that at the spatial scale of the Great South Channel and on a temporal scale of 4 mo, the number and frequency of patches increases with the regionalscale mean *C. finmarchicus* concentration.

2.6 Conclusions

Our interannual analysis showed that at certain times of year, the regional-scale mean copepod concentration is an indicator of the relative abundance of right whales in 2 critical habitat areas. During early spring in Cape Cod Bay, there is a significant association between right whale SPUE and the concentration of other copepods (*Pseudocalanus* spp. and *Centropages* spp.). The relationship between *Calanus finmarchicus* and right whale SPUE in the Bay appears to be positive, but it is not statistically significant. The concentration of *C. finmarchicus* in the western Gulf of Maine, an acceptable proxy for the concentration of *C. finmarchicus* in the Great South Channel, is a significant indicator of right whale SPUE in the Great South Channel between late April and mid-August. It appears that use of the Great South Channel by right whales is substantially reduced when the concentration of *C. finmarchicus* is low. In general, *C. finmarchicus* is a conservative indicator of the right whale SPUE in the Great South Channel. Results from our analysis of interannual variability suggest that with seasonal dependence, (1) regional-scale mean copepod concentration is positively correlated to the relative abundance of right whales, and (2) models that forecast copepod concentration on a regional-scale could be useful for predicting where and when right whales are likely to be, and could therefore be useful tools for mitigating anthropogenic risk to North Atlantic right whales.

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CHAPTER 3

WEEKLY ESTIMATES OF NORTH ATLANTIC RIGHT WHALE (*EUBALAENA GLACIALIS*) HABITAT QUALITY IN THE CAPE COD BAY AND GREAT SOUTH CHANNEL

3.1 Introduction

North Atlantic right whales (*Eubalaena glacialis*) are critically endangered. Despite protective measures, collisions with vessels and entanglement in fishing gear continue to pose significant risk to these animals (Kraus *et al.*, 2006). This high level of threat is due, in part, to extensive overlap of right whale habitat with shipping and fishing areas. Thus, there is an economic incentive to resist measures that would protect right whales, especially blanket restrictions. A more dynamic view could ease some of these conflicts.

We know where to find right whales within large spatial and temporal windows (Winn *et al.*, 1986). During winter females can be found giving birth in the coastal waters of the southeast United States (Kraus *et al.*, 2007). From winter to mid-spring, a portion of the population can be found in Cape Cod Bay off the northeast coast of the United States (Mayo *et al.*, 2004). Beginning in mid-spring and extending into the summer a large number of right whales can be found in the Great South Channel (CETAP, 1982). In the late summer and fall right whales can be found in the Bay of Fundy and Roseway Basin (Kraus and Rolland, 2007). With few exceptions (e.g., Kenney (2001)) these patterns are predictable on seasonal timescales and on regional spatial scales. Protective measures such Seasonal Area Management zones (NOAA, 2006), the mandatory ship reporting system (Ward-Geiger *et al.*, 2005), vessel speed restrictions

(DOC, 2008) and the boundaries of the U.S. critical habitats (DOC, 1994) have been based upon these well known distributional patterns.

A leading hypothesis to explain the distribution of right whales is that whales move to areas with high concentrations of prey, relative to nearby regions. Many studies have been undertaken to examine the extent of the relationship between right whales and their primary prey, late-stage *Calanus finmarchicus* (hereafter *Calanus*) (Wishner *et al.*, 1988; Murison and Gaskin, 1989; Wishner *et al.*, 1995; Baumgartner *et al.*, 2003). Pendleton *et al.* (2009) examined abundance of right whales with respect to two groups of prey: 1) *Calanus* and 2) *Pseudocalanus* spp. and *Centropages* spp. The authors found that regional-scale (habitat-wide) mean concentration of prey is a statistically significant predictor of the relative abundance of right whales. Pendleton *et al.* (2009) also found that right whales in Cape Cod Bay appear to respond more strongly to *Pseudocalanus* spp. and *Centropages* spp. than to *Calanus*. However, in the Great South Channel right whale abundance was more strongly correlated with *Calanus* than with other prey taxa. This suggests 1) that the environmental preferences of right whales are dynamic – habitat preferences change on a seasonal basis, and 2) distribution and availability of prey are important factors in determining the distribution of right whales.

Pershing *et al.* (2009a) went on to build and ground-truth a model of *Calanus* abundance throughout the Gulf of Maine, and Pershing *et al.* (2009b) found a statistically significant relationship between modeled concentration of *Calanus* and the arrival date of right whales in the Great South Channel right whale critical habitat. Thus, modeled concentration of *Calanus* has been found to be good predictor of right whale abundance at regional spatial scales.

Finer resolution estimates of where and when right whales are likely to occur, within and between years, are needed so that resource managers can alert mariners when aggregations of right whales are likely to occur. States of heightened alert are already automated with the autobuoy system (http://listenforwhales.org) that detects right whale upcalls in the Cape Cod and Massachusetts bays and issues alerts to vessels in the area. Realtime habitat suitability maps are needed to provide a broader spatial context to acoustic right whale detections.

For this study, we modeled the distribution of right whales on small space ($1km^2$) and short time (weekly) scales. Our objective was to build a model that could identify potential right whale habitat on a weekly timescale, and that was robust to inter-annual variability in the environmental conditions that determine the distribution of right whales. Within that purview, we tested two hypotheses: H_1: that right whale environmental preferences are dynamic on seasonal timescales, and H_2: that prey is an important predictor of the spatial and temporal distribution of right whales.

3.2 Materials and Methods

We built habitat models using maximum entropy density estimation. The models relate a suite of environmental data at the time and place of documented right whale occurrences to inform predictions of habitat suitability over a broader geographic range. Five years of data were available (2002–2006). Cross-validation was used to assess model skill – four years of data were used to train each model, and the fifth year was used to test the model. The cross-validation procedure was repeated five times, each time using a different year to test the model.

To address H_1, that right whale habitat preferences are dynamic, we conducted three experiments. In the first experiment we trained models with data from 1 January – 21 March (*winter*), in the second we we used data from 22 March – 1 June (*spring*), and in the third we used data from 1 January – 1 June (*winterspring*). Differences in the influence of predictors on the model would suggest a difference in the type of habitat selected by right whales in different seasons.

To address H_2, that prey is an important predictor of right whale habitat preference, we compared the predictive accuracy of models trained with and without prey. Prey data were obtained from model-based estimates of *Calanus* abundance. For each time period described above (*winter*, *spring* and *winterspring*), we trained models with *Calanus* (denoted by a subscript C) and without *Calanus*.

Each experiment consists of five cross-validated model runs. Area under the receiver operator curve (AUC), variability in the sensitivity or true positive rate (TPR) and a new metric, the reverse cumulative (RC) curve, were used to assess the predictive capacity of each model.

3.2.1 Data

Region. The geographic domain over which we modeled habitat suitability encompassed the Cape Cod Bay and Great South Channel critical habitats (Figure 3.1). All right whale sightings and environmental data used to train and test the model came from the study area. ***Right whale occurrence records.*** Right

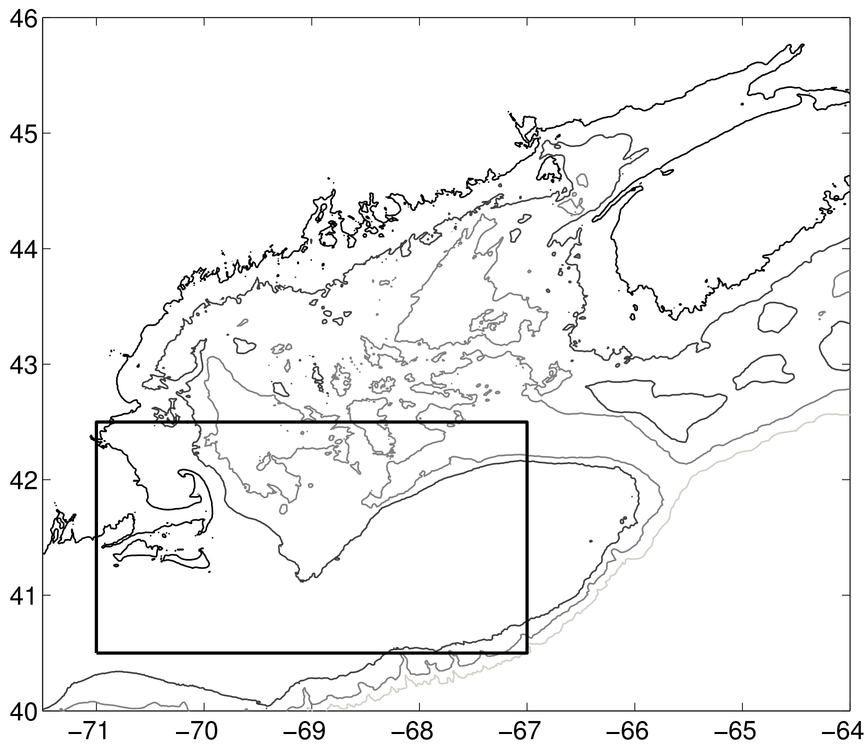

Figure 3.1: Gulf of Maine region. Cape Cod Bay at lower-left and Nova Scotia at upper-right. Bold rectangle is the region for which habitat suitability was estimated. Bathymetry depicted shaded lines: from dark to light, lines represent contours at 0 m, 100 m, 200 m and 1000 m.

whale occurrence records were collected during right whale aerial surveys of the Provincetown Center for Coastal Studies [Mayo et al, 2004] and the National Marine Fisheries Service (NMFS) (Cole *et al.*, 2007). The NMFS conducts ″non-directed″ and ″directed″ surveys. Non-directed surveys are randomized trackline surveys, and directed surveys are focused on areas of known or suspected aggregations of right whales. We used right whale occurrence records from non-directed surveys conducted from the years 2002 to 2006.

Predictor variables. Three dynamic predictor variables and one static predictor variable were used to model right whale habitat suitability. Values of these variables were drawn from georeferenced images, herein referred as environmental data layers. Dynamic predictor variables included surface temperature (SST), chlorophyll, and modeled *Calanus* abundance.

SST measurements were obtained from the Advanced Very High Resolution Radiometer (AVHRR) for the years 2002 and 2003, and from the Moderate Resolution Imaging Spectrometer (MODIS) instrument on the Aqua satellite for the years 2004–2006. Chlorophyll measurements were obtained from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) sensor for the year 2002, and from the MODIS instrument on the Aqua satellite for the years 2003–2006. SST and chlorophyll predictor variables contained the average value at each pixel location within non-overlapping 8-day time periods from 1 January – 1 June. Satellite imagery (SST and chlorophyll) was interpolated to eliminate pixels with missing data, which were a consequence of cloud cover. Abundance values for *Calanus* were generated from a *Calanus* life-history model that was coupled to a physical ocean circulation model. Details of the satellite data processing and the model of *Calanus* abundance are documented in Pershing *et al.* (2009b). The only static predictor variable utilized was a TOPEX-derived bathymetric grid indicating water depth (Smith and Sandwell, 1997). All predictor variables adhered the the same spatial grid, spanning -71° W to -67° W longitude, and -40.5° N to -42.5° N latitude with a resolution of $1km^2$.

3.2.2 Model

The purpose of a species distribution model is to map the potential distribution of a species. This is done by characterizing the species' environmental niche and projecting it onto a set of environmental data layers. The first step in building a species distribution model is to assemble species occurrence records and pertinent environmental data from the time and location of the occurrences. In cases where the time of the occurrence was not recorded precisely, or when the occurrence record has come from a museum collection, matching the time of occurrence with environmental data may not be possible. In this case environmental data is often drawn from climatological datasets such as WorldClim (Hijmans *et al.*, 2005). The WorldClim dataset provides values for many environmental variables over Earth's landmass. Complete coverage is achieved by interpolating between measurements collected over a 50 year time span (1950 to 2000). When climatological environmental data are paired with species occurrence records, predictions of the species distributions will not capture intra- and inter-annual changes in species distributions. In the work presented here, we used environmental data layers with an eight-day temporal resolution – a time frame relevant to resource managers. Not only does this timescale allow us to make predictions on an eight-day timescale, it allows us to examine changes in the predicted species' distribution within and between years.

The second step in building a species distribution model is to choose an algorithm to generate a model of the species' response to its environment, i.e., its environmental niche. The final steps are to project the model onto environmental data layers covering the study area of interest, and to validate the prediction with an independent set of species occurrence records. It is important to note that the model is an equation describing the response of the species to environmental predictor variables. The prediction is then the map that results from applying the model to environmental data layers.

The algorithm used to produce models of species distribution could be as simple as a linear regression. Generalized linear models and generalized additive models have been widely used (Guisan *et al.*, 2005) in species distribution models. However, several novel algorithms have gained popularity in recent years, particularly the Genetic Algorithm for Rule Set Prediction (GARP) (Stockwell and Peters, 1999), boosted regression trees (Elith *et al.*, 2008), artificial neural networks (Hilbert and Ostendorf, 2001; Pearson *et al.*, 2004) and maximum entropy density estimation (Phillips *et al.*, 2006). Elith *et al.* (2006) provides a comprehensive review of traditional and novel species distribution modeling algorithms. Based on this review, we selected maximum entropy density estimation.

The maximum entropy method is machine learning approach to species distribution modeling. Entropy, in the context of information theory, is a measure of uncertainty (Shannon, 1948). Higher entropy corresponds to higher uncertainty. Maximizing entropy is equivalent to assigning equal probability to all possible outcomes about which we have no prior information. In the maximum entropy method we seek to estimate an unknown probability density function π representing the true distribution of the species over a set X of locations. The entropy H of our estimate $\hat{\pi}$ is calculated in the usual way as

$$H(\hat{\pi}) = -\sum_{x \in X} \hat{\pi}(x) \ln(\hat{\pi}(x)). \tag{3.1}$$

Because π is a probability density function, we impose the necessary constraint that $\sum_{x \in X} \hat{\pi}(x) = 1$. The estimated distribution must respect additional constraints derived from the occurrence data. Those constraints are based on the environmental data and are expressed as functions called features and denoted $f(x)$. One such feature might constrain the mean value of each environmental predictor variable in $\hat{\pi}$ to be close to its empirical mean over the species occurrence locations in the training dataset. Features ensure that the estimated distribution has mean, variance and covariance close to what was observed across the occurrence locations in the training dataset. There are many possible features. A discussion of feature selection can be found in Berger *et al.* (1996).

The method of Lagrange multipliers offer an relatively well known way in which to maximize equation 3.1 subject to the constraint that $\hat{\pi}$ sums to one and that the mean of each feature is close to that which was observed over the training data. For this work, the sequential-update algorithm from Dudik *et al.* (2004) was used. The form of the distribution that results is

$$q_\lambda(x) = \frac{exp(\sum_{j=1}^{n} \lambda_j f_j(x))}{Z_\lambda} \tag{3.2}$$

where $f_j(x)$ are the features, λ_j are the lagrange multipliers, and Z_λ is a normalization constant calculated on the training data to satisfy our first constraint, that the distribution sums to one over the study area. In practice, the study area is defined by 10,000 randomly selected locations from the study area. If we were looking for the distribution with strictest adherence to our constraints, we would maximize $1/m \sum_{i=1}^{m} \ln(q_\lambda(x_i))$. However, this would likely overfit the training data. To avoid overfitting a smoothing parameter β is introduced, and in order to find the λ's we maximize

$$\frac{1}{m}\sum_{i=1}^{m} ln(q_{\lambda}(x_i)) - \sum_{j=1}^{n}\beta_j|\lambda_j|. \tag{3.3}$$

The first term is the log likelihood, which grows as the fit of the model to the training data increases. The second term, "regularization", penalizes the use of large λ_j, which are indicative of a more complex model that is more likely to overfit the training data. Values of the λ_j's found in equation 3.3 and empirically derived $f_j(x)$'s are substituted into equation 3.2 to compute habitat suitability for any location.

3.2.3 Model validation

Each model that was trained was validated with right whale occurrence records and environmental data from a year not included in the model training dataset. For example, a model trained using right whale occurrence records and environmental data layers from the years 2003 – 2006 was projected onto environmental data layers from the year 2002. This resulted in estimates of habitat suitability for the year 2002. Locations of right whale occurrences from 2002 were overlayed onto the estimate of habitat suitability corresponding to the 8-day period containing the occurrence record. Measures of model predictive capacity described below were then calculated.

The AUC, or area under the receiver operator characteristic (ROC) curve, is a standard performance metric for presence-only species distribution models, and for many classifiers (Swets, 1988). The ROC curve is a plot of the true positive classification rate (sensitivity) versus the false positive classification rate (1-specificity). The AUC is the total area underneath the ROC curve. In a presence-only model there are no species absences, so computing a false positive rate is not possible. Rather than distinguish presence from absence, we distinguished presence from random or pseudo-absence, and we compute a ”Fractional Predicted Area” (FPA) rather than a false positive classification rate.

We generated ROC curves in the following way: all habitat suitability maps corresponding to 8-day periods during which right whales were observed were layered to create a three dimensional array. From that array, 10,000 coordinates locations, indexed by i, were chosen at random with replacement. The value of habitat suitability, $S(i) \in [0, 1]$, at each of those locations was stored. For a series threshold values, $t \in [0, 1], t = 0, 0.05, 0.01, ..., 1$, FPA was calculated as the percentage of $S(i) \geq t$. The true positive classification rate (TPR) was calculated as fraction of right whale sightings occurring at locations where the habitat suitability value was $\geq t$. TPR was then plotted as a function of FPA to generate an ROC curve.

The AUC is the area underneath the ROC curve. The axes of the plot were scaled so that total area of the plot was equal to 1. A diagonal line from the lower left corner to the upper right corner, having an AUC=0.5, is the theoretical ROC curve for a random, undiscriminating, model. There was one habitat map for each 8-day period in each test year. For a given test year all maps corresponding to times during which there were right whale sightings were concatenated. AUC for each test year was calculated from the concatenated habitat map.

We used the delete-d jackknife resampling procedure (Efron and Tibshirani, 1994) to generate 90% confidence intervals about our estimates of AUC for each test year. The delete-d jackknife procedure is used to generate a confidence interval about a statistic. The procedure is implemented in the following way:

for a dataset containing n observations, a subset of size $n - d$, where $\sqrt{n} \leq d \leq n$, is drawn randomly and without replacement from the original dataset. The statistic of interest is then computed using the $n - d$ observations. The procedure is repeated until the desired number of iterations is reached. In our case, we recalculated the AUC 100 times for each model. The number d was always chosen to be $\sqrt{n}$ rounded up to the nearest integer. Confidence intervals were estimated by ranking the 100 AUC values and plotting the 5th through the 95th greatest values.

AUC scores suffer from at least one potential pitfall: if a large proportion of the study area is predicted to be low quality habitat (rightly or wrongly), the FPA values will be driven down and the ratio of TPR to FPA will be large. This will result in an ROC curve that is closer to the upper-left corner of the plot than it otherwise would have been, which will translate into a higher AUC score. To illustrate this, imagine the case where a model is built to predict the range of a species occurring only at high elevation. Now, project the model onto a study area containing a small area of high elevation and a large area of low elevation. If the area of low elevation is predicted to have low habitat suitability, as it should be, then measurements of FPA will always be high.

Reverse cumulative curves assess a model's ability to predict high habitat suitability without respect to the study area being modeled. This is a subtly different type of information than ROC curves provide. RC curves contain the same information one finds in a histogram, but the information is presented in a format similar to that of an ROC curve. RC curves assess the capacity of the classifier or model to predict high habitat suitability at the time and place of species occurrences, and nowhere else.

RC curves were generated in the following way: the value of predicted habitat suitability at the time and location of each right whale occurrence location was stored. For each threshold value, $t \in [0, 1], t = 0, 0.1, 0.2, ..., 1$, the percentage of all right whale occurrence locations with habitat suitability value $\geq t$ was plotted against t. RC curves were generated in this way for all models.

3.3 Results

We were able to effectively model the potential distribution of North Atlantic right whales on a weekly timescale. The distribution of right whales is best explained by sea surface temperature in the winter and by *Calanus* in the spring, supporting the hypothesis (H_1) that environmental preferences change on a seasonal basis. The inclusion of *Calanus* as a predictor variable significantly improved the predictive capacity of models in *winterspring* and *spring* experiments, while models from the *winter* experiment not effected by *Calanus*. Models trained over a longer time period and over a wider range of environmental conditions (those from the winterspring experiments in particular) had consistently good predictive capacity across years.

3.3.1 AUC

Swets (1988) identified AUC in the range 0.5 to 0.7 as ”poor”, 0.7 to 0.9 as ”reasonable”, and 0.9 to 1.0 as ”very good” discrimination. All AUC scores we obtained were above 0.7. 30% were between 0.7 and 0.799, 53.33% were between 0.8 and 0.899, and 16.67% were between 0.9 and 1.0 (Table 3.1). The mean AUC score over all years within each experiment (Table 3.1) is a measure of predictive capacity of the model. Mean AUC for the winter experiments was higher than for the winterspring experiments, and the score for winterspring experiments was higher than for spring experiments. Mean AUC score for the $winterspring_C$ treatment was higher than that of $winterspring$, and mean AUC score for the $spring_C$ treatment was higher than that of $spring$. In the winter experiments this pattern was reversed - models trained without *Calanus* scored higher than models trained with *Calanus*.

In four out of five models trained with data from the winterspring time span, the inclusion of *Calanus* significantly improved the AUC scores (Figure 3.2). Three out of five models trained with data from the spring season were significantly improved by the inclusion of *Calanus*. Models trained with data from the winter season were not affected by *Calanus*.

Table 3.1: Area under the curve (AUC) scores, calculated from ROC curves (Figure 3.3) from estimates of habitat suitability in each test year for each experiment: $winterspring$ and $winterspring_C$ (1 January – 1 June), $winter_C$ and $winter$ (1 January – 21 March), $spring_C$ and $spring$ (22 March – 1 June). Subscript C indicates models in which *Calanus* was included as a predictor variable.

test year	$winterspring_C$	$winterspring$	$winter_C$	$winter$	$spring_C$	$spring$
2002	0.900	0.876	0.961	0.950	0.867	0.872
2003	0.810	0.770	0.728	0.771	0.823	0.784
2004	0.885	0.838	0.924	0.931	0.808	0.727
2005	0.850	0.821	0.875	0.884	0.854	0.823
2006	0.711	0.758	0.839	0.833	0.707	0.740
mean AUC	0.831	0.813	0.865	0.874	0.812	0.789

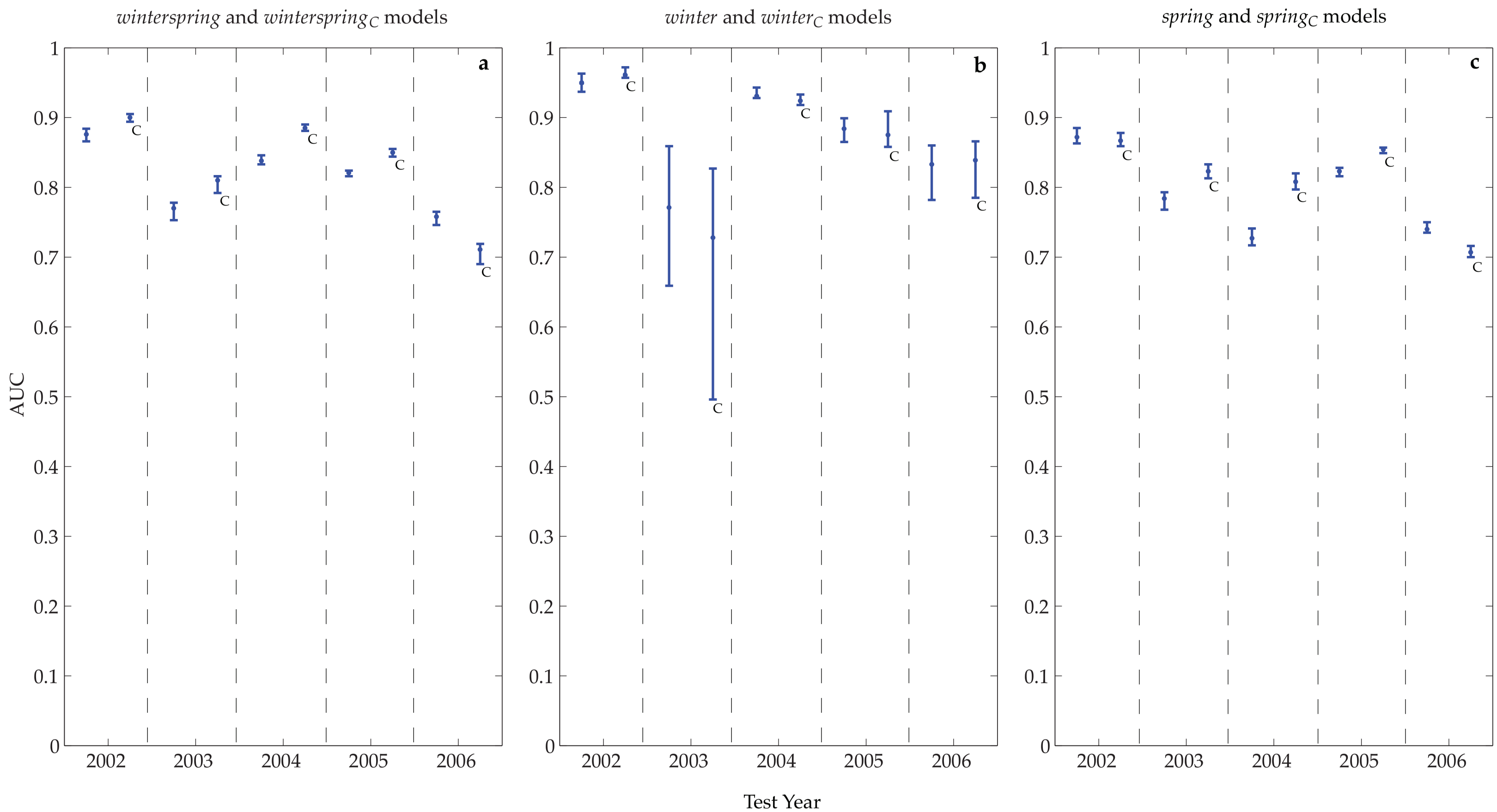

Figure 3.2: 90% confidence intervals, generated with the delete-d jackknife resampling procedure, for each model. Years are separated by dashed lines. Dots are original model AUC scores from Table 3.1. Data on the left side of column is for the model trained without inclusion of *Calanus*, and data on the right side of column, with subscript *c* is for the model trained with inclusion of *Calanus*.

One of the primary objectives of this study was to produce a model that makes good predictions of habitat suitability, not only within each year, but also from year to year. We were therefore interested in models for which AUC scores (Table 3.1), and shape of ROC curves (Figure 3.3), were similar from year to year. As was indicated above, AUC scores for individual years were generally good. The main exception was the score for the year 2006 in $winterspring_C$ and $spring_C$ experiments (Figure 3.3), which was relatively poor. We assessed the sensitivity of models in each experiment to inter-annual variability by plotting TPR variability (Figure 3.4). The plots show variance in the rate of correct classifications (TPR) across test years as a function of fractional predicted area (equivalently, threshold value for good habitat). Low TPR variability is an indication that the predictive capacity of the models was robust to inter-annual variability. Variability in the winter experiments was more than 5 times higher than for winterspring and spring experiments (Figure 3.4a). To more closely examine the low variance results, we removed the higher variance results (Figure 3.4 c and d). Removing the 2006 outlier (Figure 3.4 b and d) had a dramatic effect on the TPR variance of the winterspring and spring experiments. In order from greatest to least degree of robustness to inter-annual variability, when the 2006 outlier is excepted from consideration, we have $winterspring_C$, $spring_C$, *winterspring*, and *spring*. Models trained with *Calanus* estimated habitat suitability with greater consistency across years than models trained without *Calanus*.

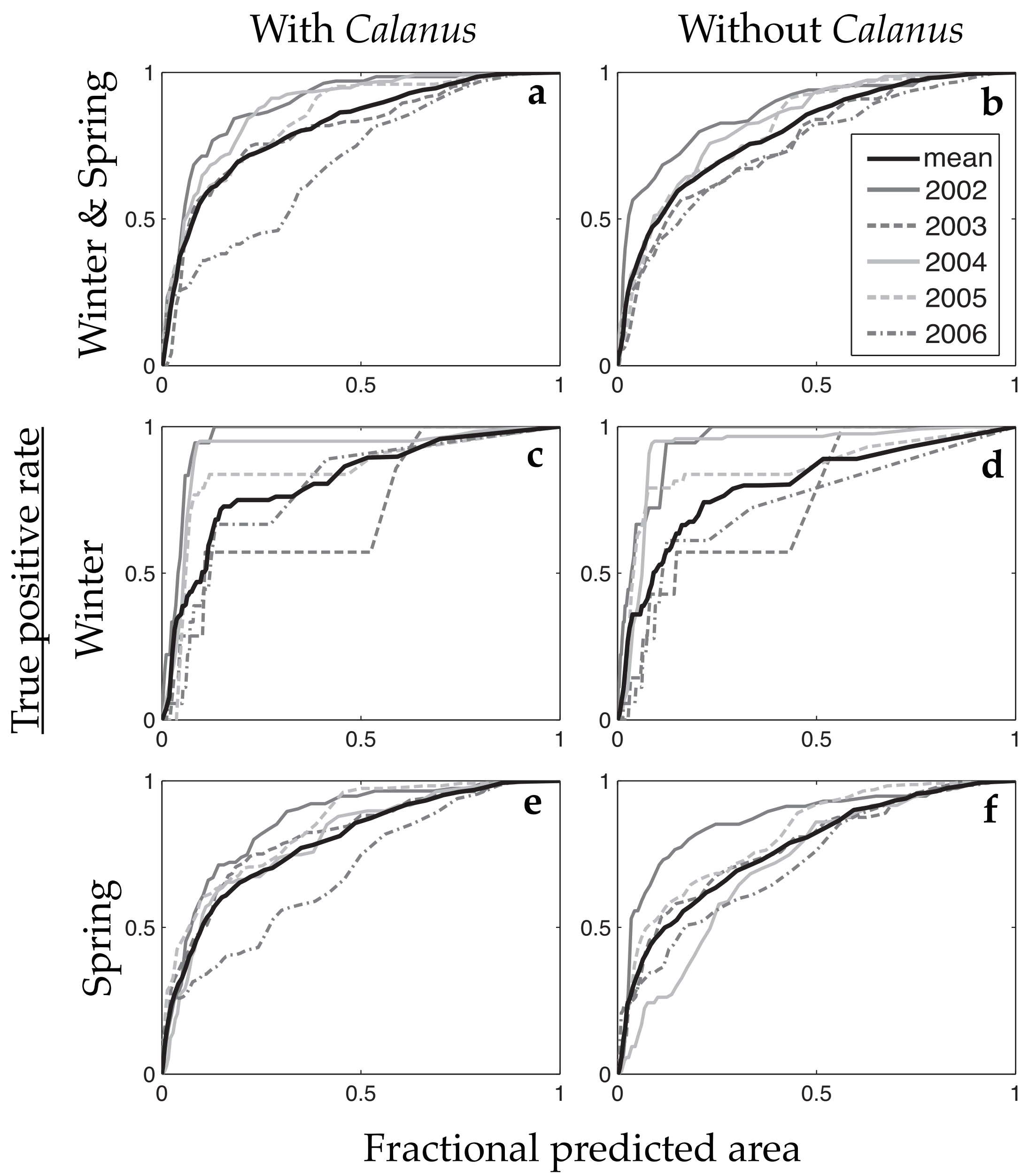

Figure 3.3: Receiver operator characteristic curves for each test year. Thick line is the mean for all years.

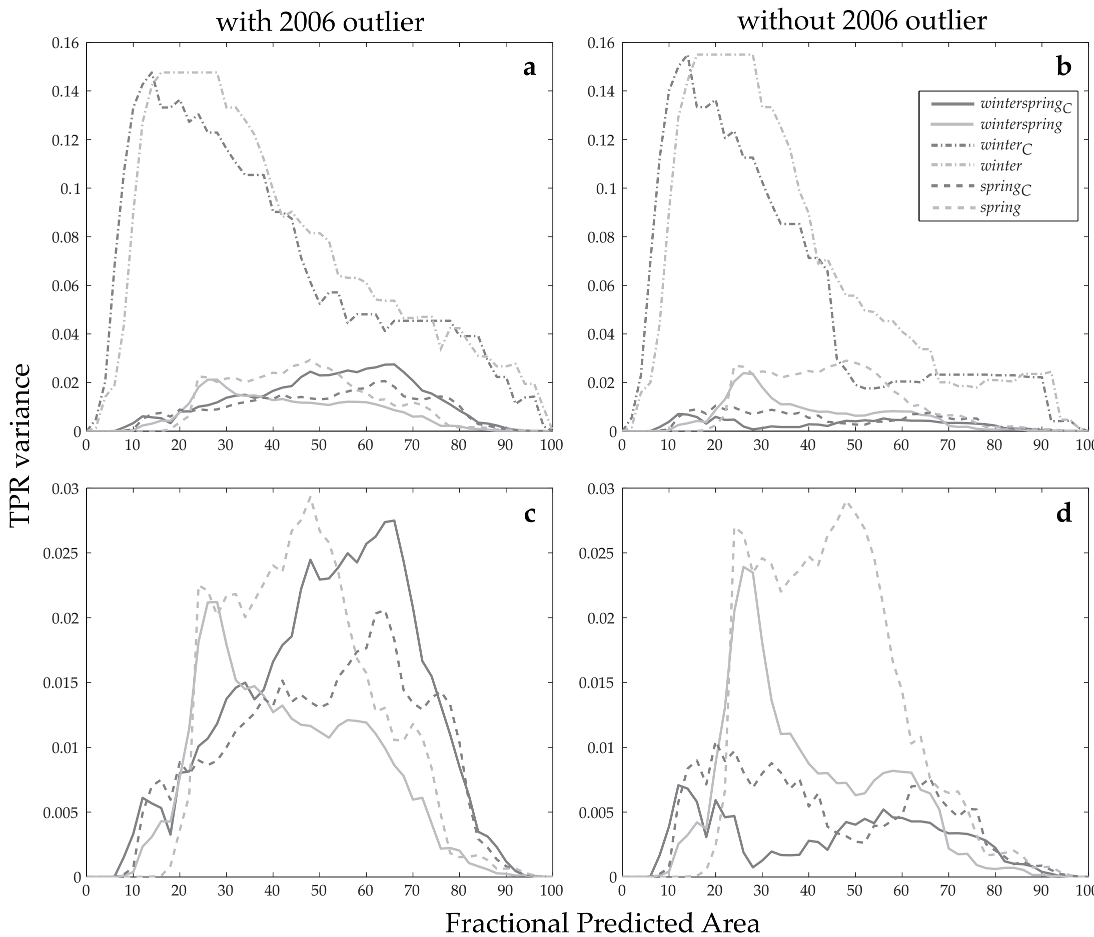

Figure 3.4: Variance in True Positive Rate of right whale classification as a function of Fractional Predicted Area, calculated from ROC curves (Figure 3.3). Subplot columns show variance of each model with (left) and without (right) the 2006 outlier. Subplot rows show TPR variance with (top) and without (bottom) *winter*$_C$ & *winter* experiments in order to better compare models of lower variability. *winterspring* and *winterspring*$_C$ (1 January – 1 June), *winter*$_C$ and *winter* (1 January – 21 March), *spring*$_C$ and *spring* (22 March – 1 June). Subscript C indicates models in which *Calanus* was included as a predictor variable.

3.3.2 Reverse Cumulative curves

In an RC plot a linear line from top-left to bottom-right would indicate that a model does not have a bias towards classifying species occurrences as being in areas of high or low habitat suitability. That is, the percentage of sightings in good habitat decreases linearly with increasing threshold value for good habitat, e.g., 75% of whales are in good habitat when our threshold for good habitat is 25% of the maximum habitat value (usually scaled to equal 1), 50% of whales in good habitat when our threshold for good habitat is 50% of the maximum value, and so on. A concave-down line from upper-left to lower-right corners would indicate that a high percentage of whales were found to be in habitat with a high habitat suitability value, and a low percentage of whales were found to be in habitat with a low habitat suitability value. Conversely, a concave-up line would indicate that the model has a tendency to classify whales in areas of low habitat suitability.

Looking at mean RC curve for each experiment (thick lines in Figure 3.5), the $winterspring_C$ did the best job of predicting high habitat suitability at the time and place of the right whale occurrences, as is indicated by the concave-down shape of the curve (Figure 3.5a). The mean RC curve for $winterspring$ and $spring_C$ has a concave-down shape, but the remaining experiments have more of a linear shape. Looking at the year to year variation in the RC curves, we see relatively little variation in $winterspring_C$ & $winterspring$ experiments, a bit more spread about the mean in $spring_C$ & $spring$, and wide variation about the mean in $winter_C$ & $winter$. According to RC curves for the winterspring and spring experiments, the year 2002 was the year for which habitat suitability was highest at the time and location of right whale occurrences. The year 2004 was

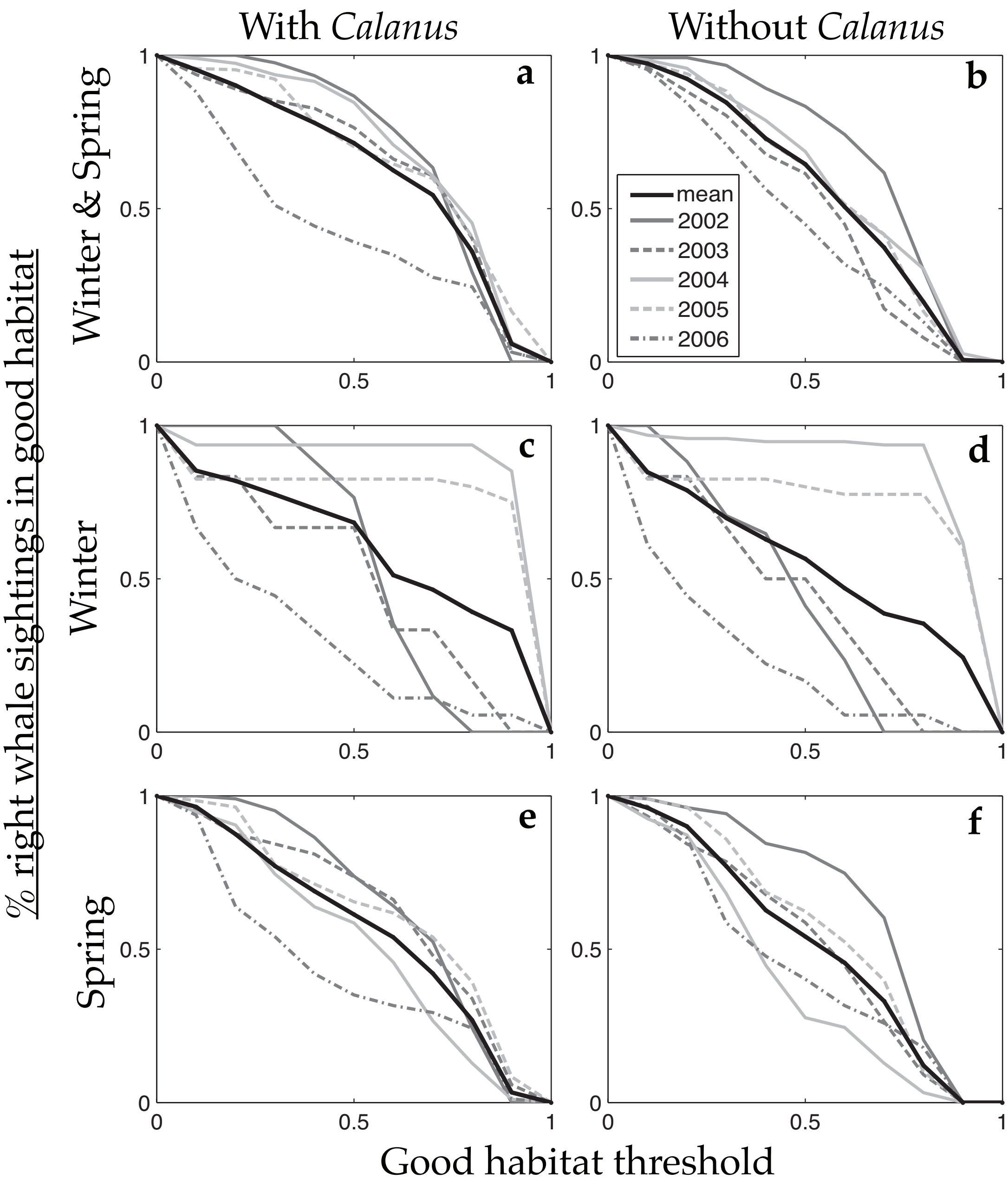

Figure 3.5: Percentage of right whale sightings in suitable habitat as the threshold for suitable habitat was varied from 0 to 1 for each of the six models. Thick line is the mean for all years.

the year in which there was highest habitat suitability at the time and place of right whale occurrence for the winter experiments. The year 2006 was not predicted well by any of the six experiments.

3.3.3 Habitat Suitability Maps

A visual examination of right whale habitat suitability maps (Figure 3.6) confirms what is reflected in the AUC scores. Years with high AUC tend to have more sightings in areas of high habitat suitability, and years with relatively low AUC tend to have fewer sightings in areas of high habitat suitability. The transition of whales from Cape Cod Bay to the Great South Channel is best reflected in maps from the $winterspring_C$ experiment. Maps from winters experiments clearly show that Cape Cod Bay is an area with high habitat suitability from 1 January to 21 March, but they do not capture the transition to the Great South Channel due to their short time span. Maps from the spring experiments (22 March to 1 June) show the shift of good habitat suitability from Cape Cod Bay to the Great South Channel, but that transition is less pronounced than that seen in maps from the winterspring experiments.

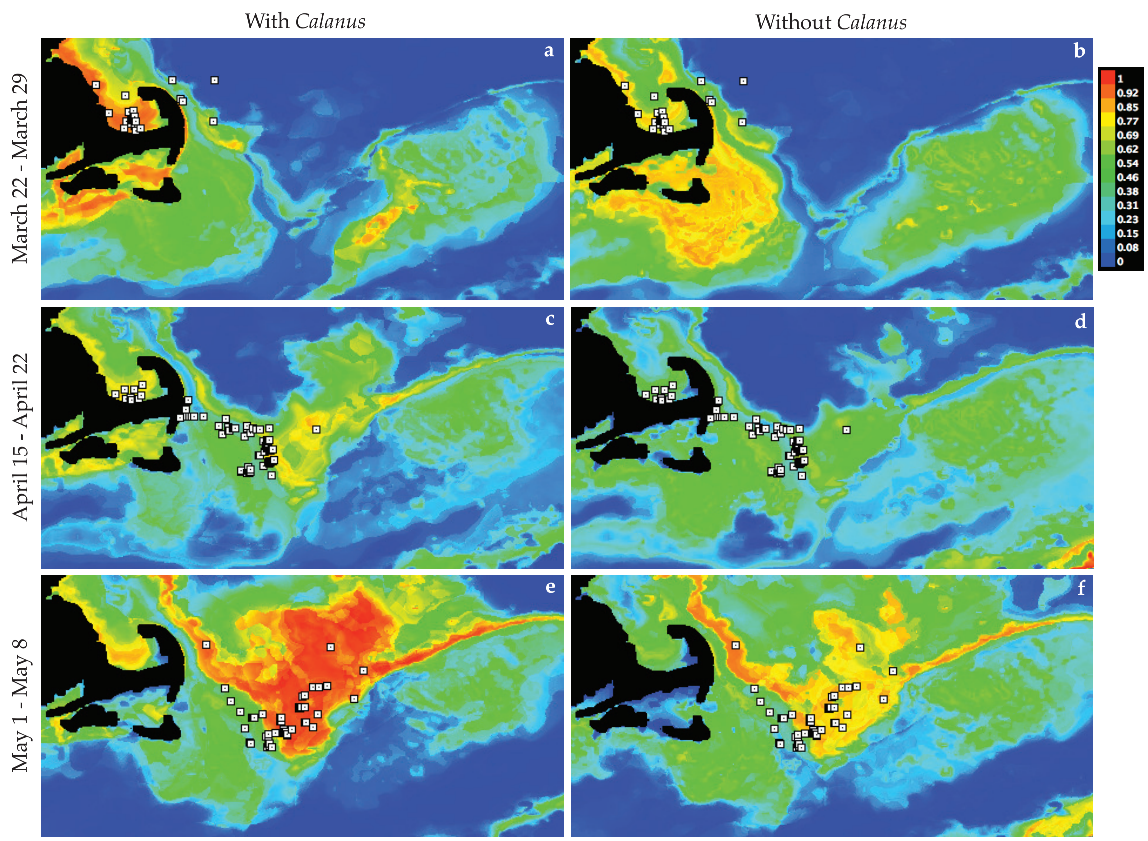

Figure 3.6: Estimates of right whale habitat suitability and right whale occurrences (white squares) for three time periods in the test year 2005. Black is land, with Cape Cod at left. Per the color bar, blue is low and red is high habitat suitability. Maps in the left column are from the *winterspring*$_C$ treatment, and in the right column from the *winterspring* treatment. a) Cape Cod Bay has high habitat suitability in early in the spring season, b) between spring and summer there is a transition of good habitat between Cape Cod Bay and the Great South Channel, c) by the middle of the spring season habitat is more suitable in the Great South Channel than in Cape Cod Bay, and this is reflected in the distribution of right whales.

3.3.4 Habitat Preferences

The magnitude of λ_n in equation 3.2 can be interpreted as the relative influence of each environmental variable on the prediction of habitat preference (Table 3.2). *Calanus* was the most influential predictor in winterspring experiments, and was followed in importance by bathymetry, chlorophyll and finally SST. When *Calanus* was not included as a predictor variable in $winterspring$ and $spring$ experiments, the ranking of variable importance remained the same, with bathymetry being the most influential, followed by chlorophyll and SST. The winter experiments showed the opposite pattern: SST was the most influential predictor, followed by chlorophyll, SST, and *Calanus* when it was included as a predictor variable. There were two exceptions to these trends. In the 2006 $winter_C$ model, bathymetry (22.9%) was slightly more influential than chlorophyll (22.6%). In the 2004 $spring_C$ model, bathymetry (38.6%) was more influential than *Calanus* (35.7%).

Table 3.2: Influence of predictor variables in each experiment: *winterspring* and $winterspring_C$ (1 January – 1 June), $winter_C$ and *winter* (1 January – 21 March), $spring_C$ and *spring* (22 March – 1 June). Subscript *C* indicates models in which *Calanus* was included as a predictor variable. Greatest contribution to each model in bold.

test year	predictor variable	$winterspring_C$	*winterspring*	$winter_C$	*winter*	$spring_C$	*spring*
2002	*Calanus*	**35.3**	na	10.8	na	**45.1**	na
	bathymetry	32.5	**42.6**	20.7	23.2	34.3	**54.3**
	chlorophyll	19.6	33.7	26.9	33.8	12.1	24.0
	sea surface temperature	12.6	23.7	**41.7**	**43.0**	8.4	21.7
2003	*Calanus*	**37.6**	na	17.6	na	**44.4**	na
	bathymetry	28.5	**44.4**	21.1	28.2	35.6	**57.3**
	chlorophyll	18.5	29.0	26.2	30.3	11.2	21.7
	sea surface temperature	15.4	26.6	**35.1**	**41.6**	8.8	21.0
2004	*Calanus*	**36.9**	na	18.7	na	35.7	na
	bathymetry	31.8	**48.4**	22.7	26.3	**38.6**	**56.7**
	chlorophyll	18.0	27.7	24.6	30.0	14.2	22.9
	sea surface temperature	13.4	23.9	**34.0**	**43.7**	11.4	20.4
2005	*Calanus*	**33.2**	na	15.4	na	**42.5**	na
	bathymetry	31.6	**45.0**	20.6	26.7	39.0	**60.6**
	chlorophyll	19.2	35.0	24.3	27.9	11.4	21.4
	sea surface temperature	16.0	25.0	**39.6**	**45.3**	7.1	18.1
2006	*Calanus*	**40.9**	na	16.9	na	**46.3**	na
	bathymetry	31.0	**47.7**	22.9	26.5	34.9	**61.4**
	chlorophyll	15.8	27.8	22.6	31.4	11.6	20.7
	sea surface temperature	12.3	24.4	**37.6**	**42.1**	7.10	17.9

3.4 Discussion

We have found that the weekly distribution of North Atlantic right whales, a highly migratory marine mammal, can be hindcasted, and presumably predicted, with ”reasonable” to ”good” (Swets, 1988) accuracy using a species distribution model. The vast majority of applications of SDMs to date have used multi-year climatological predictor variables, yielding estimates of the absolute range of a species in which year to year variability is averaged out. To the best of our knowledge, this is the first such application of a species distribution model to estimate habitat suitability on a short timescale.

3.4.1 Right whale habitat preferences are dynamic: H_1

Differences between the winter and spring models suggest the habitat preferences of right whales are not static. This result is supported by an empirical study of right whale habitat preference in winter and spring seasons (Pendleton *et al.*, 2009). The winter model suggests that the right whale distribution is determined primarily by SST, the spring model suggests that the distribution is determined primarily by *Calanus*. The winterspring model also suggests that *Calanus* is a primary driver, but to a lesser extent than the spring model. Increasing influence of *Calanus* as the year progresses agrees with what we have observed empirically: in Cape Cod Bay right whales are known to feed on *Pseudocalanus* spp. and possibly *Centropages* spp. in the winter, and they transition to *Calanus* as the availability of that prey taxa increases (Pendleton *et al.*, 2009).

The model result that right whale habitat preferences are dynamic is also supported by general knowledge of the right whale migratory patterns. For example, female right whales on the southeast calving grounds appear to be driven more by the desire to give birth than to feed. As well, juvenile males on the southeast calving ground appear to be there for social reasons rather than to feed (M. Zani, 2009 *pers. comm.*). If right whale habitat choice was always driven by the need to find food, we would not have such observations. It is not known what energetic benefit exists, if any, for the presence of non-breeding and reproductively immature right whales in the calving grounds.

A more in depth view of right whale habitat preferences would take into account the possibility that subsets of the population may have different environmental needs. For example, habitat preferences could depend on age, sex, reproductive stage, or membership of a right whale in a genetic subpopulation, e.g., the Fundy/non-Fundy whales documented by Malik *et al.* (1999). A fruitful extension of the research presented here would be to train models right whale habitat suitability with a demographically partitioned right whale occurrence dataset.

3.4.2 Prey data improves predictive capacity: H_2

Torres *et al.* (2008) found that predictive capacity was not improved with the inclusion of prey data in a generalized additive model of bottlenose dolphin habitat. In four ($winterspring_C$, $winterspring$, $spring_C$ and $spring$) of our six experiments, the use of modeled prey abundance (*Calanus*) improved predictive capacity, robustness to inter-annual variability, and the users ability to discriminate good from bad habitat (i.e. greater dynamic range of habitat maps equals greater ability to discriminate good from bad habitat). Because we are modeling right whale habitat suitability in areas where whales are known to feed much of the time (Goodyear, 1996; Mayo and Marx, 1990; Wishner *et al.*, 1995), it makes sense that the availability of prey would be in important predictor of the distribution of whales.

It is well known that right whales feed on ultra-dense patches of copepods (Watkins and Schevill, 1976; Wishner *et al.*, 1988; Mayo and Marx, 1990; Beardsley *et al.*, 1996), often occurring at the scale of 1 to 10s of meters. Given this, it is interesting that our estimates of copepod abundance at $1km^2$ resolution served as an important predictor of the distribution of potential right whale habitat. This, along with Pendleton *et al.* (2009) and Pershing *et al.* (2009a), reinforce the view that high regional-scale mean abundance of copepods increases the likelihood of formation of ultra-dense patches of copepods, upon which right whales feed.

3.4.3 Inter-annual variability

Inter-annual variability was well captured in the $winterspring_C$ experiment. At the other end of the spectrum were the winter models, which performed well in some years and poorly in other years. Decision makers often want to threshold habitat suitability maps to simplify the identification of good and bad habitat. The point at which all curves, with the exception of 2006, come together in Figure 3.5a shows that there was consistent predictive capacity across years. For that reason, the good habitat threshold at this point (0.72) would be an temping place to threshold predictions from the models of the $winterspring_C$ experiment.

We could not find a reason for the poor predictions in 2006. We reasoned that it was from an unusual distribution of right whales in the year 2006, or, after looking at the below average ROC curves for 2006 in models trained with *Calanus* (Figure 3.3 a, e), because of an unusual distribution of *Calanus* in 2006. We found no evidence for either hypothesis. However, results from 2006 were instructive in a diagnostic sense: $winter_C$ and *winter* AUC scores for 2006 do not appear out of the ordinary, but RC curves for these models show 2006 as being poorly predicted. This is likely due to the relatively small area from which winter sightings were drawn (mostly in and around Cape Cod Bay) with respect to the larger 4° by 2° study area. Such disparities have been known to inflate AUC scores. Better results would likely be obtained if the study area were restricted to the spatial extent of the occurrence locations. Without an analysis of RC curves, it would be tempting to conclude from the AUC scores that *winter* and $winter_C$ models are reasonable.

3.5 Conclusions

We have found that right whale habitat suitability can be estimated on a weekly timescale with only four predictor variables. Models that incorporated data from both winter and spring were more accurate and more robust to interannual variability than winter-only or spring-only models. Our results confirmed empirical observations that right whale habitat preferences change on a seasonal timescale. The inclusion of prey as a predictor variable improved predictive capacity of models. The methodology presented in this work could be a powerful tool to resource managers who want to find areas likely to host aggregations of right whales on an operational timescale in order to reduce human-caused risk to whales. The approach could also be extended to populations of mobile animals, both on land and in the ocean.

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CHAPTER 4

AN OPERATIONAL ECOSYSTEM FORECASTING MODEL OF NORTH ATLANTIC RIGHT WHALE HABITAT

4.1 Abstract

The overlap of right whale feeding and calving grounds with economically important coastal waters has resulted in increased mortality of the critically endangered North Atlantic right whale (*Eubalaena glacialis*) population . They are an internationally protected species, yet present-day human-caused injury and mortality is thought to be the primary reason for their slow recovery from industrial whaling. We demonstrate the feasibility a system to make predictions of right whale habitat suitability on an operational time scale. Our modeling system was trained with aerial sightings of right whales and satellite and modeled environmental data from the years 2003 – 2006 in Cape Cod Bay. Weekly predictions of right whale habitat suitability were generated for the year 2009. The accuracy of the predictions was good. The model was then projected beyond the model-training region, into neighboring Massachusetts Bay. A significant relationship was found between predicted habitat suitability and acoustic detections of right whales in that region. To address a current management issue – moving shipping routes to reduce risk of whale-vessel collisions – we calculated the quality of predicted right whale habitat within three shipping routes in Cape Cod Bay. Time of vessel transit was more important than the route of vessel transit.

4.2 Introduction

North Atlantic right whales (*Eubalaena glacialis*) are critically endangered. Despite 75 years of protection from commercial whaling, the population has not recovered. Reasons for the lack of recovery range from changes in the availability of prey (Greene and Pershing, 2004) to ship strikes and fishing gear entanglements (Knowlton and Kraus, 2001).

The North Atlantic right whale Recovery Plan (NMFS, 2005) identified reduction or elimination of ship-strike and gear entanglement as the primary need for the recovery of the species. Extraordinary monitoring efforts are being taken to prevent human-induced injury to right whales. Exhaustive aerial and vessel-based surveys report right whale presence to the National Oceanic and Atmospheric Administration's Sighting Advisory System, which posts the locations of right whale occurrence on the internet. The high level of effort put into locating right whales by government agencies and conservation organizations is a testament to the importance of real-time detection of right whales, both for the preservation of the species and in order to maintain compliance with federal statutes.

All right whale management plans depend on knowing when and where right whales are located. Current management plans, such as ship speed restrictions in Seasonal Management Areas (predefined regions in which speed limits are enforced for a predetermined period of time), are based on well known distributional patterns that are assumed to be static from year to year. Intra- and inter-annual changes in the distribution of right whales must be detected by aerial, shipboard or acoustic monitoring programs. Forecasts of the spatial distribution of right whales would allow decision makers to anticipate changes in the distribution of right whales and to allocate resources accordingly.

A common approach for estimating the geographic range of a species is with an environmental niche model (ENM). ENMs relate environmental variables to species occurrences to predict species distributions. In most settings, ENMs provide estimates of the absolute distribution of the species. In the some cases, estimates of the distribution within seasons have been provided (Surez-Seoane *et al.*, 2008). In the case of North Atlantic right whales, extensive survey effort has already provided us with climatological annual and seasonal geographic distributions. These form the basis of current management.

The objective of this study was to build a prototype system to forecast the suitability of habitat for right whales in the Cape Cod Bay right whale critical habitat; CCB is an important feeding and nursing ground and an area determined to be critical to the species, in accordance with the Endangered Species Act. Cape Cod Bay is used intensely by humans for commercial and recreational purposes, and it is home to a robust observational program. Our goal was to create a system that would provide habitat maps to decision makers on a weekly time scale, and that could be combined with other data sources (e.g., data on shipping or fishing activities) to estimate the risk of ship-strike or gear entanglement.

4.3 Methods

We combined North Atlantic right whale occurrence records with multiple remotely sensed and modeled data sources to make forecasts of right whale habitat quality in Cape Cod Bay. We used data from 2003 to 2006 to build a model of right whale habitat suitability. That model was projected onto environmental conditions from 2009 to make predictions for that year. The 2009 predictions were evaluated using right whale occurrence records from that year. The model was then extended into Massachusetts Bay. Predictions in this region were validated with acoustic detections of right whales. Predicted habitat suitability was measured within three Cape Cod Bay shipping routes in order to assess the impact moving shipping routes to reduce the risk of whale-vessel collisions.

4.3.1 Right whale data

Right whale occurrence records used in this study were collected as part of aerial surveys by the National Marine Fisheries Service (Cole *et al.*, 2007) and the Provincetown Center for Coastal Studies (Jaquet *et al.*, 2006) from 2003 to 2006, and from 2009. Occurrence records for 2007 and 2008 were not available.

4.3.2 Satellite data

Sea surface temperatures were obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument on the Aqua satellite. Chlorophyll data was also obtained from the MODIS instrument on the Aqua satellite. SST and chlorophyll data were processed into 8-day composite images with a 1 km^2 spatial resolution. Details of the data processing were described by Pershing *et al.* (2009).

4.3.3 Copepod modeling

Abundance of late-stage *Calanus finmarchicus* and *Pseudocalanus* spp. were estimated using an enhanced version of the SEASCAPE (Satellite-based Estimates and Analysis of Stage-resolved Copepod Abundance in Pelagic Ecosystems) model described in Pershing *et al.* (2009). Several improvements to this model were made to provide higher-resolution information on right whale feeding conditions in Cape Cod and Massachusetts Bays. Notably, we used hourly high resolution circulation fields from the Finite Volume Coastal Ocean Model (Chen *et al.*, 2003). The parameterization of the copepod population dynamics was optimized using a genetic algorithm (Record *et al.*, 2010) by tuning to observations from 2003. Finally, we assimilated zooplankton observations from Cape Cod Bay using an ensemble Kalman filter (Evensen, 1997). The copepod model was run for 2003 to 2006, and 2009, with an ensemble size of 200, and output was saved every 8 days. On the 8-day interval following a zooplankton cruise and corresponding assimilation, a new ensemble was created. The new ensemble had the same mean as the post-assimilation ensemble, but the variance was increased. This ensured that the ensemble captured the full range of variability in copepod abundance.

4.3.4 Environmental niche modeling

We employed an environmental niche model (ENM) to combine right whale occurrence records with environmental data to characterize the environmental niche occupied by right whales. There are many approaches to estimating the potential distribution of a species based the environment at occurrence locations

(Elith *et al.*, 2006). We used maximum entropy density estimation – a machine learning technique for estimating an unknown probability density function. The principle of maximum entropy has been applied to many problems (Buck and Macauley, 1991). In our case we used it to estimate the p.d.f. describing the true distribution of the species *Eubalaena glacialis*. We briefly describe the method.

Given the environmental data from the time and place of each species occurrence, we can summarize what is known about the distribution. This knowledge can be formalized as a set of real valued functions, called *features* of the environmental data. Features can be used to develop constraints on the estimated distribution. There will typically be many distributions that satisfy the constraints, and the problem becomes one of choosing among the distributions.

The principle of maximum entropy says that, subject to what is known (i.e. subject to a set of constraints), we should choose the distribution with maximum entropy. Higher entropy corresponds to higher uncertainty, which translates into greater uniformity. This may seem counterintuitive, but consider that given a uniform distribution all outcomes are equally likely. In the absence of any information, we have no reason to prefer one outcome over another, and we therefore have 1) the highest possible uncertainty and 2) maximum entropy. In the maximum entropy method, we choose the distribution with highest entropy that satisfies known constraints. Implicit in this method is the assumption that the least assuming distribution is the "best" distribution. Further details of the method have been provided in a number of publications (Berger *et al.*, 1996; Phillips *et al.*, 2006), Chapter 2 of this volume.

4.3.5 Predictions of habitat suitability

After pairing right whale occurrence records with environmental data (SST, chlorophyll, modeled *C. finmarchicus* and *Pseudocalanus* spp., and bathymetry from Smith and Sandwell (1997)) from the time and place of the right whale occurrences in Cape Cod Bay between 2003 and 2006, we used maximum entropy density estimation to build a model of right whale habitat suitability. We projected the model of habitat suitability onto environmental conditions to generate a prediction of habitat suitability in Cape Cod Bay for each 8-day period from 1 January to 1 June in the year 2009. The accuracy of our predictions was measured by overlaying right whale occurrence records from each 8-day period to corresponding predictions of habitat suitability, and by calculating the area under the receiver operator characteristic curve.

An additional set of predictions was made for Massachusetts Bay. This region represents a special challenge and opportunity for our model. Aerial surveys were not available for this region, however, acoustic detections of right whale up-calls were available from a array of 10 hydrophones located in the Boston traffic separation scheme (Figure 4.1). Up-calls are also known as contact calls, and they are the most common and most easily identified sound produced by right whales. Up-call detections from the acoustic array from the year 2009 were compared with predictions of habitat suitability for the area immediately surrounding each acoustic buoy. Due to the high density of shipping in Massachusetts Bay, the ability to predict the occurrence of whales in this region would be especially valuable. To assess the accuracy of model predictions in this region, we compared the total number of right whale up-calls with the mean habitat suitability within a 12 n mi buffer centered about the acoustic buoys

(Figure 4.1). Predictions of habitat suitability have a pixelated spatial resolution of 1 km^2. To insure that we calculated habitat suitability over the entire listening distance of 5 n mi around each buoy (C. Clark, *pers. comm.*), we used a buffer of 12 n mi rounded to the nearest pixel.

4.3.6 Assessing potential risk of whale-vessel collisions

Reducing risk of whale-vessel collisions is a top priority for management of the North Atlantic right whale population(NMFS, 2005; Kraus *et al.*, 2006). To address this issue we evaluated the effect of moving a shipping lane based upon predicted habitat suitability. Evaluation was done by calculating the mean habitat suitability in three shipping routes connecting the Cape Cod Bay canal with the Boston traffic separation scheme (Figure 4.2). The first (WG05) was determined from the band of high ship traffic density seen in Figure 2 of Ward-Geiger *et al.* (2005), which was calculated from data collected between 1999 and 2002 according to the Mandatory Ship Reporting System (DOT, 2001). The second route (NMFS06) was comprised of the 2006 National Marine Fisheries Service recommended route for vessels in Cape Cod Bay. A segment was added to that route so that the endpoint would match that of WG05. A third, alternative, route (ALT) was evaluated. ALT lies midway between WG05 and NMFS06. It represents the only other practical straight-line route connecting the Cape Cod Bay canal to the Boston traffic separation scheme.

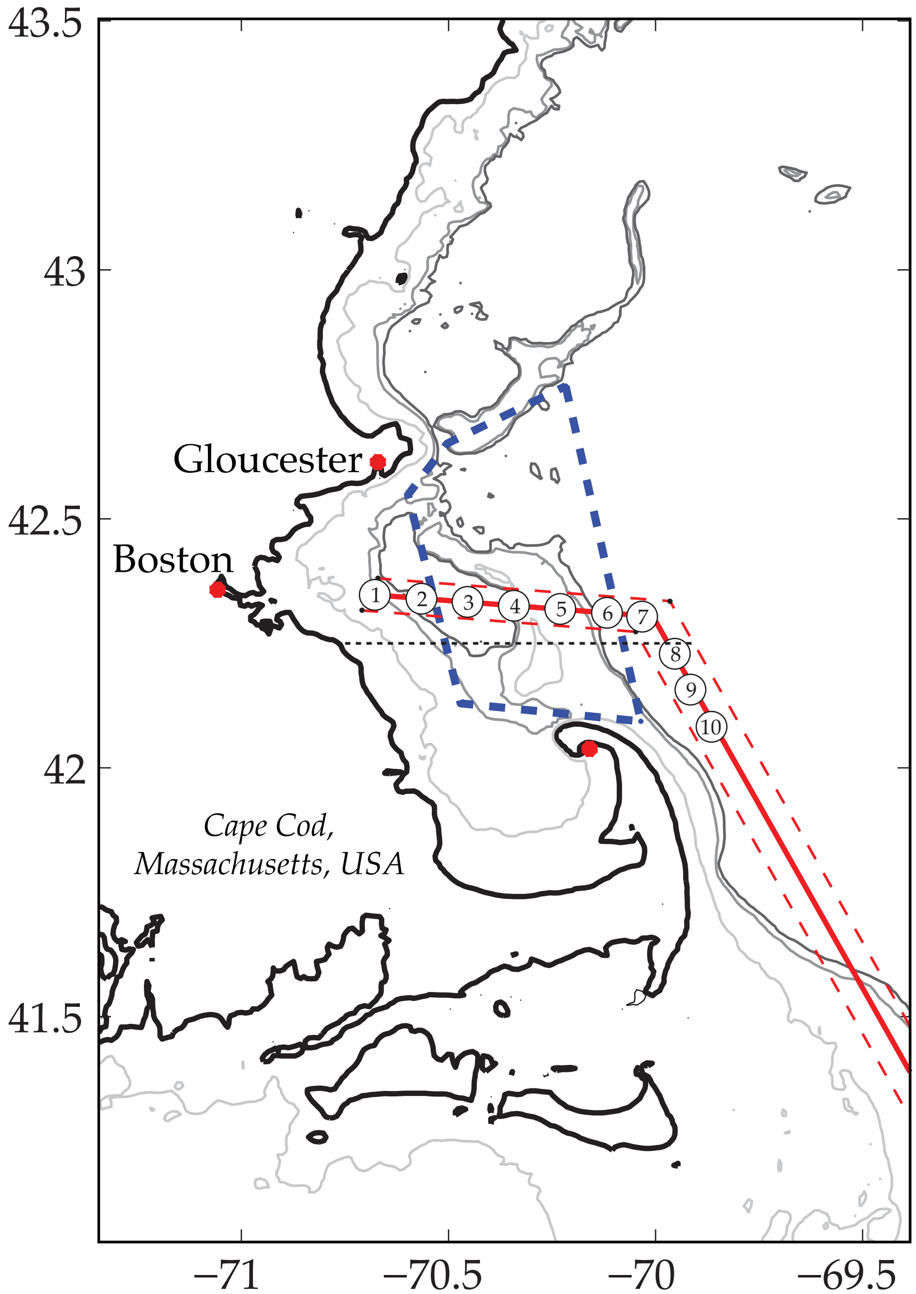

Figure 4.1: Cape Cod and Massachusetts Bays. Solid black line is the coast of Massachusetts, USA. Shaded contour lines from lightest to darkest are at 30 m, 60 m, and 70 m. Dashed blue outline is the boundary of the Gerry E. Studds Stellwagen Bank National Marine Sanctuary. Dashed and solid red lines show the Boston Traffic Separation Scheme. Acoustic buoys are identified by numbered circles in the traffic separation scheme. Dashed black line represents the northern boundary of the Cape Cod Bay model-training region.

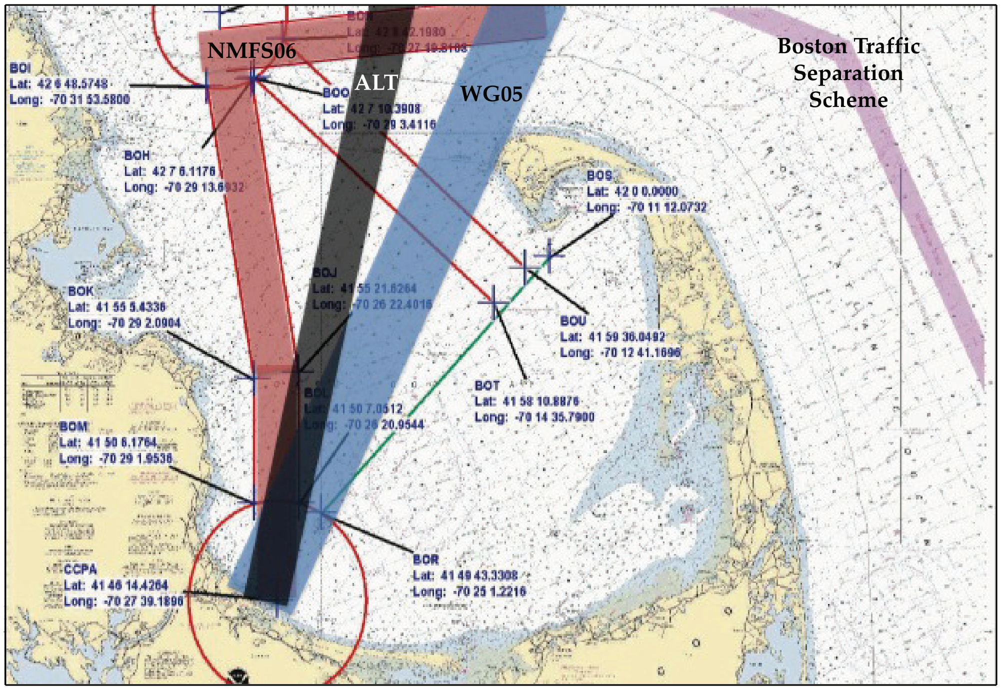

Figure 4.2: Cape Cod Bay nautical chart showing three shipping routes. NMFS06, in red, is the National Marine Fisheries Service recommended route. Top section was added to by DEP to bring vessels to the Boston traffic separation scheme. WG05, in blue, was the lane determined from 1999–2002 ship traffic density data reported in Ward-Geiger *et al.* (2005). ALT represents an alternative shipping route located midway between NMFS06 and WG05. Chart obtained at http://www.nmfs.noaa.gov/pr/shipstrike/routes.htm

4.4 Results

4.4.1 Influence of individual predictor variables

The prediction of habitat suitability was a function of five environmental variables. Modeled *Pseudocalanus* spp. (40.1%) had the greatest influence on the predictions, followed by bathymetry (25.6%), sea surface temperature (16.3%), chlorophyll (11.3%), and modeled *C. finmarchicus* (6.7%).

4.4.2 Accuracy of predictions

The predictive accuracy of our system was measured by the area under the receiver operator characteristic curve (AUC) (Figure 4.3). The AUC of 0.726 obtained for the 2009 predictions is considered to be "reasonable" (Swets, 1988) and is considerably higher than 0.50 for a random model. No precedent has been set for using the AUC to assess the accuracy of predictions that vary on short (e.g., weekly) timescales, where the job of accurately predicting habitat suitability is more difficult than in the standard, time invariant, case.

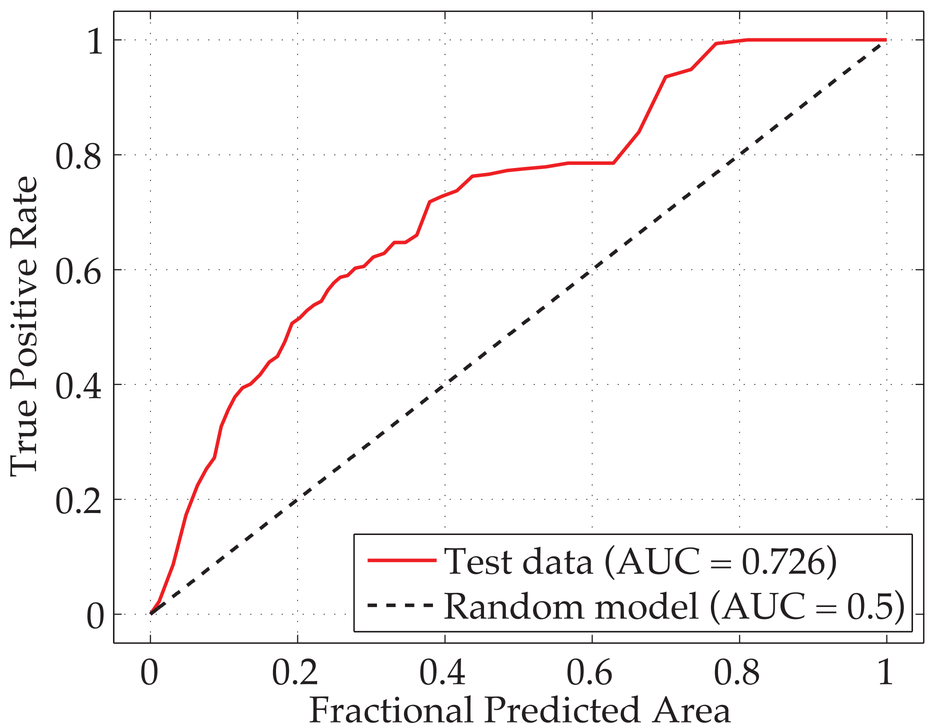

Figure 4.3: Receiver operator characteristic curve and area under the curve (AUC) score for 2009 predictions of habitat suitability (Figure 4.4). White squares are right whale occurrence records from 2009 which were used to generate the AUC statistic.

As a reference for how accurately our system could forecast future conditions versus present or past conditions, we measured the AUC score in each training year and found that for 2003, AUC=0.714 (n = 45), for 2004 AUC=0.891 (n = 178), for 2005 AUC=0.783 (n = 100), and for 2006 AUC=0.827 (n = 102), where n is the number of right whale occurrence records in the year. The mean AUC score for years 2003 to 2006 of 0.804 was moderately better than the score for 2009 reported above and in Figure 4.3.

4.4.3 Predicted habitat suitability in Cape Cod Bay

Predictions of habitat suitability have a high degree of spatially heterogeneity, with large changes in the pattern of habitat suitability from week to week. In the last week of January (Figure 4.4 a) all highly suitable habitat (≥ 0.75 on an increasing scale of suitability from 0 to 1) was concentrated near Provincetown Harbor at the tip of Cape Cod and near the entrance to the Cape Cod Bay canal. During February (Figure 4.4 b, c, d) large portions of Cape Cod Bay had high suitability, however there were only a few confirmed right whale occurrences. During March (Figure 4.4 e, f, g) the suitability of habitat was far more spatially heterogeneous than in the previous month, and the number of right whale occurrences increased substantially. In several of the predictive maps, an arc of high habitat suitability can be seen extending in a southwesterly direction from Provincetown Harbor. Habitat suitability maps for the second week of April (Figure 4.4 h) appear similar to the maps for March. In the third week of April (Figure 4.4 i) there was less contrast in suitability across Cape Cod Bay and the southwest quadrant of the bay – an area identified as highly suitable in most previous maps – had especially low habitat suitability.

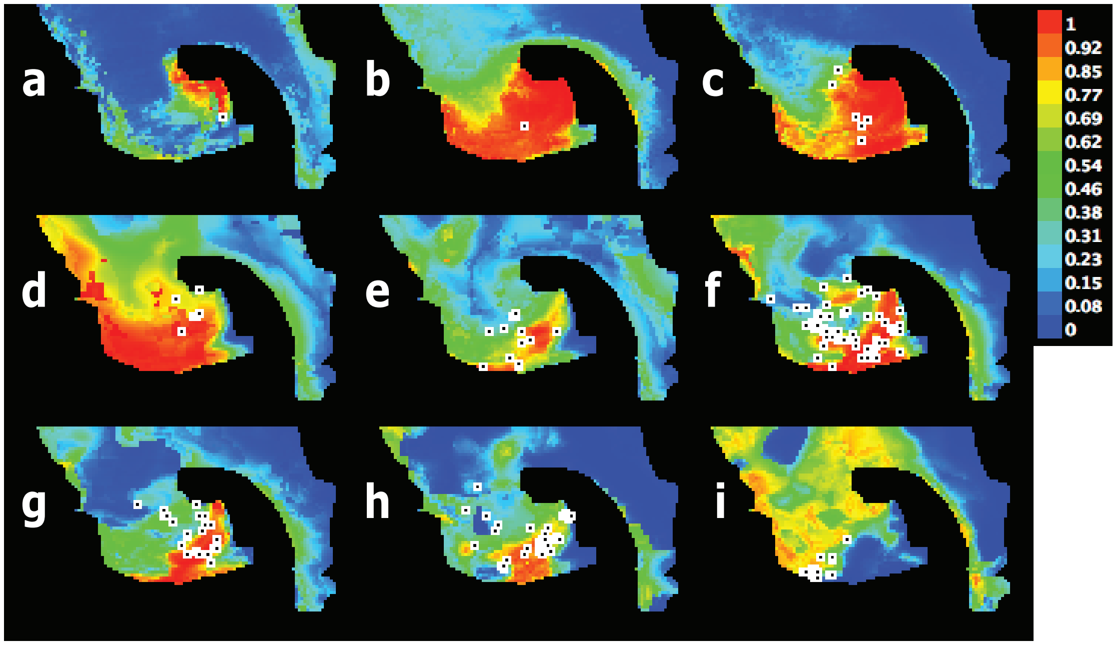

Figure 4.4: Predictions of right whale habitat suitability and right whale sightings for the year 2009 in Cape Cod Bay. Per the color bar, red indicates high habitat suitability and blue indicates low suitability. White squares are documented right whale occurrence records. a) 25 January – 1 February, b) 2 February – 9 February, c) 10 February – 17 February, d) 18 February – 25 February, e) 6 March – 13 March, f) 14 March – 21 March, g) 22 March – 29 March, h) 7 April – 14 April, i) 15 April – 22 April.

4.4.4 Predicted habitat suitability in Massachusetts Bay

We projected the same model that produced the habitat suitability maps of Figure 4.4 onto Massachusetts Bay (Figure 4.5). The model was trained using only data from the Cape Cod Bay, the region below the white line in Figure 4.5 and below the black dashed line in Figure 4.1. The upper portion of each map represents a speculative prediction. Habitat suitability in this region was considerably lower than suitability in Cape Cod Bay. The highest suitability values can be seen in at the entrance to Boston Harbor (Figure 4.1). This area appears to "turn on", as in Figure 4.5 (a) and (c), and "turn off", as in Figure 4.5 (d) and (i). In several of the maps (Figure 4.5 b, d, e , f, i) low habitat suitability was predicted in the southwestern portion of Stellwagen Bank Marine Sanctuary, in the Stellwagen Basin, with higher suitability in shallower water surrounding this basin (Figure 4.1). Habitat suitability was low at the northern boundary of the maps.

There was significant relationship between total number of right whale up-calls and mean habitat suitability within a 12 n mi buffer centered on the network of acoustic buoys in the Boston traffic separation scheme (Figure 4.6, Spearman rank: $p < 0.05$, $r^2 = 0.51$, $n = 19$). We made predictions for 19 8-day periods in 2009 (Figure 4.5). In 72% of cases, from one period to the next, the sign of change (+ or –) was the same for the number of up-calls and mean habitat suitability within the 12 n mi buffer surrounding the autobuoy network (Table 4.1). Buoys 1 – 7 are outside of the model-training region, while buoys 8 – 10 are not. To address this issue, we conducted an additional comparison of mean habitat suitability in the 12 n mi buffer centered on buoys 1 – 7 with the number of up-calls from those buoys. Results of this comparison showed a significant relationship (Spearman rank: $p < 0.05$, $r^2 = 0.50$, $n = 19$).

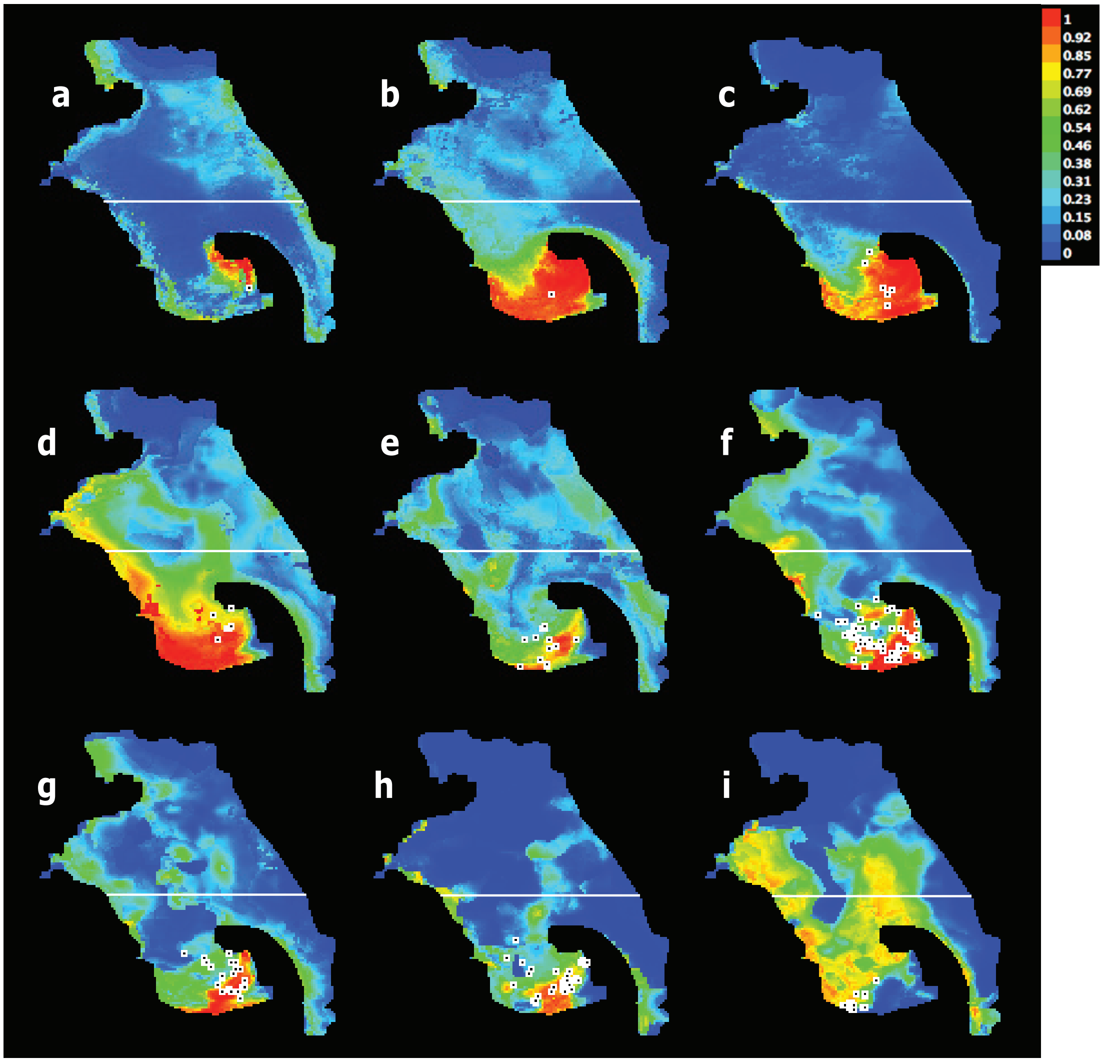

Figure 4.5: Predictions of right whale habitat suitability and right whale sightings for the year 2009 in Cape Cod Bay, and projections of the model into Massachusetts bay (above the white line). Per the color bar, red indicates high habitat suitability and blue indicates low suitability. White squares are documented right whale occurrence records. a) 25 January – 1 February, b) 2 February – 9 February, c) 10 February – 17 February, d) 18 February – 25 February, e) 6 March – 13 March, f) 14 March – 21 March, g) 22 March – 29 March, h) 7 April – 14 April, i) 15 April – 22 April.

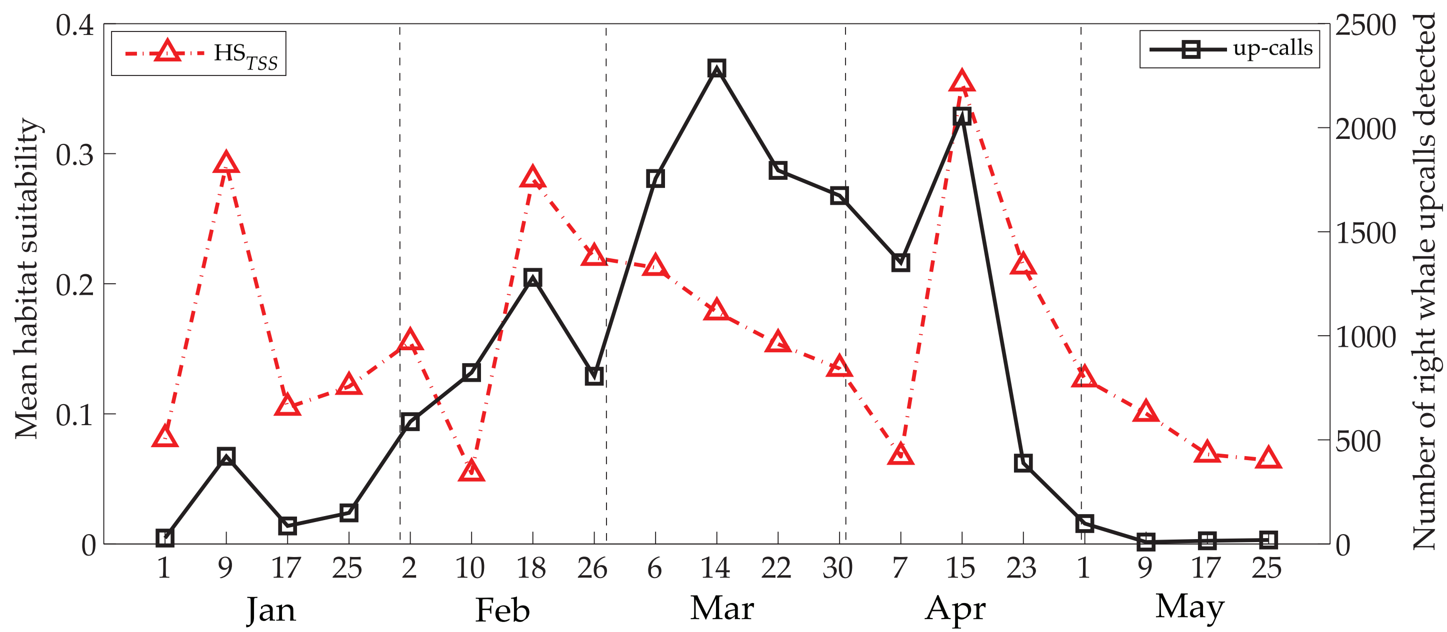

Figure 4.6: Acoustic detections of right whale up-calls from 10 buoys in the Boston Traffic Separation Scheme (TSS) and habitat suitability in a 12 n mi buffer centered on the TSS (HS$_{TSS}$).

Table 4.1: Positive (+) or negative (–) change in total number of up-calls, and in mean habitat suitability in the Boston traffic separation scheme (HS_{TSS}) for each time step in Figure 4.6

Time Step	No. up-calls	HS_{TSS}
1	+	+
2	–	–
3	+	+
4	+	+
5	+	–
6	+	+
7	–	–
8	+	–
9	+	–
10	–	–
11	–	–
12	–	–
13	+	+
14	–	–
15	–	–
16	–	–
17	+	–
18	+	–

4.4.5 Habitat suitability in shipping routes

The patterns of right whale habitat suitability within the three shipping lane choices were remarkably similar (Figure 4.7). All three routes displayed an oscillating pattern that was low in January, and increased dramatically during February. March values were on par with those in January, and in late April values were on par with values from February. Across shipping routes, the maximum habitat suitability value in February was 2.75 times the maximum in January, and the maximum in April was more than 2 times the maximum in March. Habitat suitability in May declined slowly from relatively high values in April.

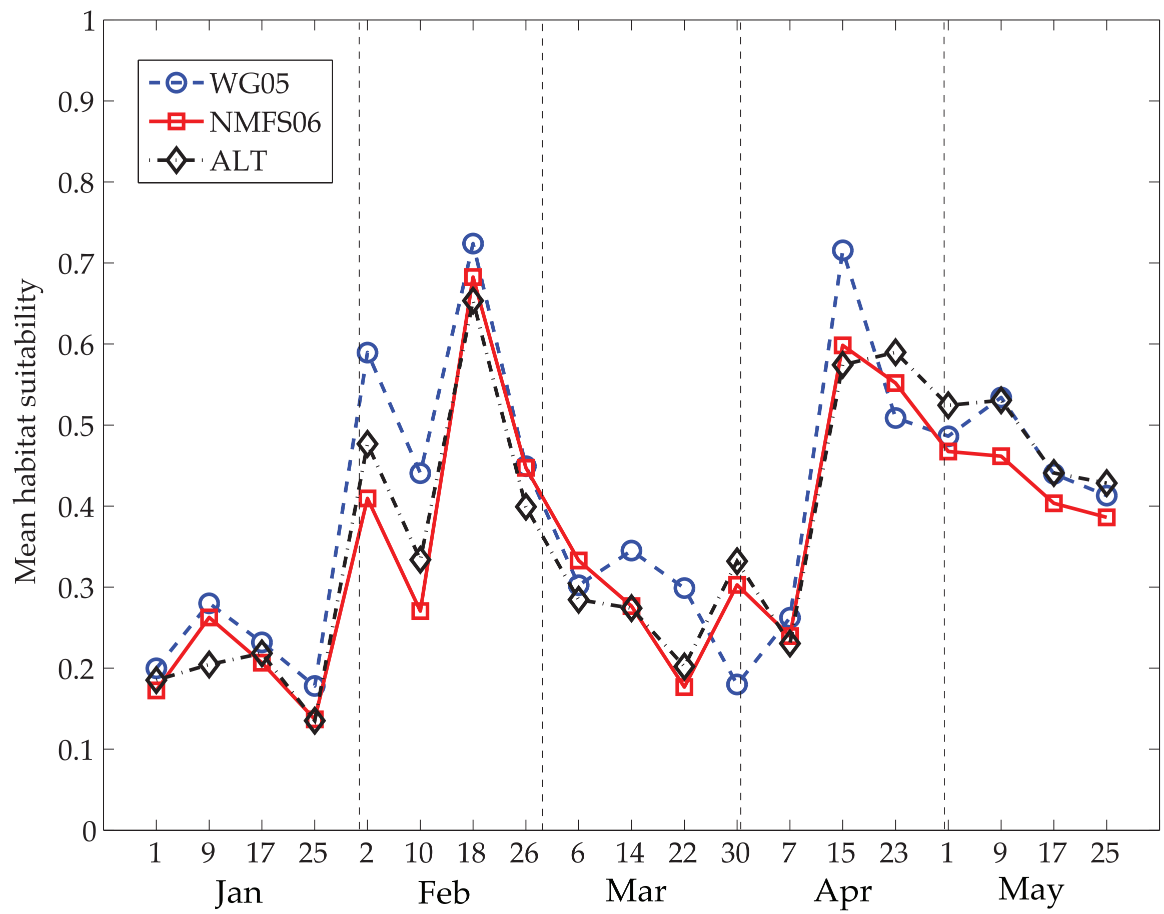

Figure 4.7: Mean habitat suitability in three shipping routes from 1 January to 1 June, 2009. WG05 is a shipping route identified in Ward-Geiger *et al.* (2005), NMFS06 is the recommended route published by the National Marine Fisheries Service in 2006, and ALT is an alternate shipping route midway between WG05 and NMFS06 (Figure 4.1).

Despite similarity in the general patterns of habitat suitability within shipping routes, there were variations in suitability between the routes from week to week. The NMFS06 route had the lowest mean habitat suitability (0.36), indicating that a vessel transiting through NMFS06 would travel through an area less suitable for right whales than the ALT route (mean habitat suitability = 0.37) or the WG05 route (mean habitat suitability = 0.40). There were relatively large differences in mean habitat suitability within the shipping routes during 1) the first and second week of February when mean habitat suitability in NMFS06 was 31% and 39% lower than in WG05, 2) the third week of March, when mean habitat suitability in NMFS06 was 40% lower than in WG05, and 3) the fourth week of March when mean habitat suitability in WG05 was 45% less than in ALT.

4.5 Discussion

Habitat suitability maps represent potential habitat, which is important for a recovering population that may be expanding its range into habitats from which it was extirpated. The work presented here is proof-of-concept that, given forecasts of environmental data and copepod concentration, *Pseudocalanus* spp. in particular, it is possible to issue weekly predictions of right whale habitat suitability. The accuracy of habitat suitability maps is reasonable, however, there is room for improvement. We predicted habitat suitability beyond the training region, into Massachusetts Bay, and found a statistically significant relationship between habitat suitability and the number of acoustic detections of right whale up-calls. This result is particularly meaningful because it suggests that systems such as ours can be used to forecast habitat quality beyond the area in which the model was trained. We directly addressed the issue of moving shipping routes in order to reduce the risk of whale-vessel collisions by measuring predicted habitat suitability in three shipping routes. Our results suggest that, in Cape Cod Bay, the timing of vessel transit is more important than the route of vessel transit.

4.5.1 Drivers of predictions

Our predictions of right whale habitat suitability in Cape Cod Bay are strongly dependent on the modeled concentration of *Pseudocalanus* spp., and weakly dependent on the modeled concentration of *C. finmarchicus*. This result is not surprising in light of Pendleton *et al.* (2009), which found a strong relationship between right whales and in situ *Pseudocalanus* spp., and a weak but positive correlation between right whale abundance and in situ *C. finmarchicus* in Cape Cod Bay. Many studies have established a link between right whales and late-stage, lipid-rich *C. finmarchicus* (Wishner *et al.*, 1988; Murison and Gaskin, 1989; Wishner *et al.*, 1995; Baumgartner *et al.*, 2003). This study supports the view that, even though *Pseudocalanus* spp. has lower caloric value than *C. finmarchicus*, it may be the best available food source in Cape Cod Bay during winter and spring. Our work underscores the need for further work in determining the biotic and abiotic environmental drivers of the distribution of right whales, both to better our understanding of the ecology of the species and because that knowledge will inform conservation actions. Equally important to the discovery of environmental drivers are the spatial and temporal scales at which they are relevant (Kenney *et al.*, 2001).

4.5.2 Cape Cod Bay

The 2009 habitat maps presented in Figure 4.4 are independent of the training dataset. By this we mean that no data from the year 2009 was used to build the model that generated the 2009 predictions. The geographic area is the same in training and test datasets, but the combination of environmental variables at each pixel location is not. Bathymetry is the only static variable. In this sense the maps in Figure 4.4 represent true future predictions of habitat suitability. The AUC score of 0.726 is reasonable, but is lower than the average score for 2003 to 2006. The decline in skill for 2009, compared to the years used to build the model, is expected. Just as the quality of the copepod distributions is improved by assimilating copepod data, the skill of the environmental niche model could be improved by assimilating right whale occurrence records.

4.5.3 Massachusetts Bay

The significant relationship between habitat suitability and right whale acoustic detections demonstrates that our model can provide valuable predictions of where and when right whales are likely to occur outside of the spatial and temporal domain of model-training. This result is strengthened by fact that the model was trained with aerial sightings of right whales, yet we were able to validate it with acoustic detections of right whales. Clark *et al.* (2010) did not find a positive correlation between aerial sightings and acoustic detections of right whales. A reasonable conclusion from our results and those of Clark *et al.* (2010) is that the model of habitat suitability is sensitive to some of the important environmental conditions that are prerequisites for the presence of right whales, and that survey methodologies are not sensitive to these conditions.

Little is known about the rate at which right whales produce up-calls, so it is not possible to translate the number of up-calls into an estimate of right whale abundance. An additional caveat is that, due to the distance between and listening range of the acoustic buoys, an up-call elicited in between two buoys may be detected by both buoys. The relationship between predicted habitat suitability and number of up-calls provides strong evidence that the projection of our model, trained in Cape Cod Bay, provides accurate information on the level of right whale activity in Massachusetts Bay.

4.5.4 Model transferability

The ultimate goal of this type of modeling presented here is two-fold: 1) to create ecological forecasts of currently managed areas in order to inform or assess conservation actions, and 2) to generate objective estimates of habitat use in regions or time periods beyond those included in the initial model fitting. Model transferability is the projection of a model onto a temporally and/or spatially distinct region. We transferred a model fit with environmental data from 2003 – 2006 to the environment in 2009. Our confidence in the 2009 Cape Cod Bay predictions is improved because the geographic domain of model projection is the same as for model training, the level of survey effort in 2009 was equivalent to effort levels from 2003 to 2006, and the AUC score was reasonable. By projecting the model into Massachusetts Bay (Figure 4.5) we made predictions into a region and a time for which the model was not trained. Our validation of predictions in Massachusetts Bay (Figure 4.5) strongly suggests that our modeling system could be transferred with some degree of confidence to other regions. Developing measures of confidence, and determining when and where models can be projected will be an important next step for this work.

4.5.5 Habitat suitability within shipping routes

Habitat that is less suitable for whales is more suitable for vessels. According to our results, a vessel traveling through the National Marine Fisheries Service recommended route (NMFS06) will travel through less suitable right whale habitat than vessels in either alternative route examined in this study. However, the difference in suitability between routes is small. The main message from the application of our habitat suitability predictions to shipping routes (Figure 4.7) is that the timing of vessel transit in Cape Cod Bay is more important than the route of vessel transit.

Predictive maps of potential habitat only tell us about the suitability of right whale habitat. They do not tell us how likely it is that right whales will be in a given area. However, identifying potential habitat of recovering populations is important because as the size of the population continues to grow, it is conceivable that areas long ago utilized will be reclaimed.

Despite this, if there are no whales in an area identified as highly suitable, then there is no risk of whale-vessel collisions. It is important that when predictions of habitat suitability are used to inform actions such as issuing alerts about when it is or is not safe to travel through a region, that information on the historical distribution and recent observations of whales be presented alongside predictions and recommendations.

4.6 Conclusions

Small populations are less resilient to human-induced or environmental change. Balancing our desire to preserve endangered populations with a growing human population and climate change will require careful planning. There is a need for ecological forecasting models that can help us find endangered populations, and to inform proposed conservation strategies before they are implemented. We view our approach as a major forward towards the goal of managing endangered species in a changing world.

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