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Model-based estimates of right whale habitat use in the Gulf of Maine

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ABSTRACT: Balancing human uses of the marine environment with the recovery of protected species requires accurate information on when and where species of interest are likely to be present. Here, we describe a system that can produce useful estimates of right whale *Eubalaena glacialis* presence and abundance on their feeding grounds in the Gulf of Maine. The foundation of our system is a coupled physical–biological model of the copepod *Calanus finmarchicus*, the preferred prey of right whales. From the modeled prey densities, we can estimate when whales will appear in the Great South Channel feeding ground. Based on our experience with the system, we consider how the relationship between right whales and copepods changes across spatial scales. The scale-dependent relationship between whales and copepods provides insight into how to improve future estimates of the distribution of right whales and other pelagic predators.

KEY WORDS: *Eubalaena glacialis* · *Calanus finmarchicus* · Gulf of Maine · Population dynamics · Model

INTRODUCTION

In order to balance human use of the marine environment with the protection of living marine resources, we need to know where species of concern are likely to occur. Due to their status as protected species, considerable attention has been given to understanding cetacean distributions, to avoid interactions with human activities such as shipping (e.g. Laist et al. 2001), mineral exploration (e.g. CETAP 1982), fishing (e.g. Kaschner 2004) or acoustic activities (e.g. Nowacek et al. 2007). The desire to know where whales and dolphins are likely to be found has spawned a growing field of cetacean habitat modeling (Redfern et al. 2006). Most habitat modeling efforts begin with a database of sightings of a particular species. Then, a statistical model is built relating the sightings to environmental data from *in situ* observations or satellites. This approach has been used to define relationships between oceanographic features and a variety of cetaceans (Forney 2000, Hamazaki 2002, Biggs et al. 2005, Hastie et al. 2005, Tynan et al. 2005, Kaschner et al. 2006, Ferguson et al. 2006, Keller et al. 2006, Firestone et al. 2008, Skov et al. 2008).

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The main drawback to the empirical habitat modeling approach is that it is often difficult to know exactly what the relationships mean. Typically, the environmental data act as a proxy for another variable such as prey abundance. An alternative approach is to use what is known about the species in question to build a dynamical model from the bottom up. Here, we describe a system for estimating the presence of North Atlantic right whales *Eubalaena glacialis* based on a dynamical model of their main prey species. We chose to focus on feeding areas as the whales spend the majority of the year on the feeding grounds in the Gulf of Maine (Winn et al. 1986). Furthermore, there is growing evidence that prey abundance drives the distribution of right whales on many spatial scales (Mayo & Marx 1990, Kenney et al. 2001, Baumgartner et al. 2003a, Baumgartner & Mate 2003, Pendleton et al. 2009, this volume). Thus, we propose that model-based estimates of the abundance of the right whale's prey should provide a good indicator of where right whales can be found.

The North Atlantic right whale is one of the most endangered cetacean populations (Kraus et al. 2005), and the remaining population is concentrated along the east coasts of the US and Canada (Winn et al. 1986, Kraus & Rolland 2007). During late autumn, pregnant females migrate to the southern calving grounds off Florida and Georgia. In late winter, the entire population begins to move onto the northern feeding grounds, roughly north of 41° N, where they remain through autumn. Right whales feed on mesozooplankton, especially copepods (Nemoto 1970), and their movements through the feeding grounds coincide with the seasonal cycle of copepods, especially *Calanus finmarchicus* (Kenney et al. 1995, Wishner et al. 1995, Baumgartner et al. 2003a).

Calanus finmarchicus dominates the biomass of zooplankton over much of the North Atlantic, including the right whale feeding areas in the Gulf of Maine (Davis 1987). *C. finmarchicus* has a unique life history that strongly influences its distribution and annual abundance pattern in the Gulf of Maine. During late autumn and early winter, the majority of the population is comprised of pre-adults (fifth-stage copepodids known as C5s). These individuals are in a state of reduced activity known as diapause and are typically found below 150 m (Durbin et al. 1997). This restricts their distribution to the deep basins of the Gulf of Maine and the slope waters south of the continental shelf break (Fig. 1). Early in the year, C5s ascend to the surface, mature into adults and begin actively feeding and reproducing. The population begins to increase rapidly, with a new generation of C5s and adults appearing in mid-April. This pulse, known as G1, represents the maximum *C. finmarchicus* abundance in the Gulf of Maine. Through the summer, the active population of *C. finmarchicus* declines while the population of diapausing C5s builds.

Right whale movements between feeding areas follow the seasonal cycle of copepods in the Gulf of Maine, especially *Calanus finmarchicus*. Right whales begin arriving on the feeding grounds in late winter when *C. finmarchicus* abundance is low. The most important feeding habitat during this period is Cape Cod Bay (Schevill et al. 1986), and smaller copepods such as *Pseudocalanus* spp. and *Centropages typicus* are important prey during this period (Mayo & Marx 1990, DeLorenzo Costa et al. 2006, Pendleton et al. 2009). As *C. finmarchicus* abundance increases in early spring, increasing numbers of this species are transported into coastal regions like Cape Cod Bay (DeLorenzo Costa et al. 2006, Jiang et al. 2007), and *C. finmarchicus* becomes a larger component of the right whales' diet. Even though *C. finmarchicus* abundance increases in the spring in Cape Cod Bay, the abundance is even higher in deeper habitats (Meise & O'Reilly 1996) and right whale sightings in Cape Cod Bay begin to decline.

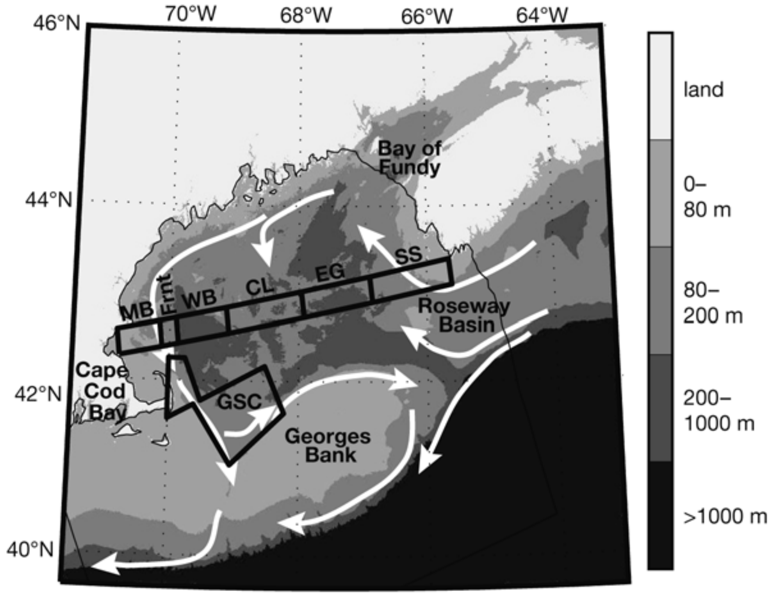

Fig. 1. Bathymetry (shading) and circulation (white arrows) of the Gulf of Maine. Regions referenced in this study are indicated by black polygons. The Great South Channel (GSC) is the major late-spring–early summer right whale feeding ground. The Gulf of Maine continuous plankton recorder survey route was divided into 6 regions based on bathymetry: MB (Massachussetts Bay), Frnt (Front Region), WB (Wilkinson Basin), CL (Central Ledges), EG (eastern Gulf of Maine) and SS (Scotian Shelf). Boundary of the finite element mesh used by the model indicated by thin black line (see Pershing et al. 2009, this volume)

The Great South Channel is the most important right whale feeding area in the late spring and early summer (Kann & Wishner 1995, Kenney et al. 1995). The high concentrations of *Calanus finmarchicus* that draw whales to this region are created by a combination of physics and biology. Surface waters enter the Gulf of Maine from the western Scotian Shelf, travel around the deep basins of the Gulf, and exit through the Great South Channel (Fig. 1) (Brooks 1985). This flow pattern leads to a convergence in the surface waters over the Great South Channel (Chen et al. 1995). Combined with the early-summer peak in *C. finmarchicus* abundance, this means that the highest *C. finmarchicus* abundances in the Gulf of Maine can be found in the Great South Channel during this period.

Later in summer, as the proportion of the *Calanus finmarchicus* population in diapause increases, whales move to deeper habitats such as Roseway Basin on the Scotian Shelf and the Bay of Fundy (Kraus et al. 1982, Murison & Gaskin 1989, Baumgartner et al. 2003b). Some portion of the whales that do not migrate to the southern calving grounds in the winter appear to remain in the central Gulf of Maine (T. V. N. Cole pers. obs.), but other than Cape Cod Bay, there are no known aggregation areas in the winter months.

Based on these characteristic movements, we hypothesize that the mean abundance of copepods, especially *Calanus finmarchicus*, determines when and how many whales will appear in a particular region. The number of right whales observed in Cape Cod Bay varies from year to year, and this variability has been linked to the abundance of *C. finmarchicus* (DeLorenzo Costa et al. 2006, Jiang et al. 2007) and the abundance of non-*C. finmarchicus* copepods, likely *Centropages typicus* and *Pseudocalanus* spp. (Pendleton et al. 2009). In the Great South Channel, interannual variability in the number of right whale sightings is strongly correlated with the abundance of *C. finmarchicus* in the western Gulf of Maine (Pendleton et al. 2009). A corollary to this hypothesis is that if we could predict where copepods will be abundant, we could predict where right whales will be found. Thus, rather than attempting to derive a relationship between right whales and environmental data, our project proceeds by using environmental data, namely *C. finmarchicus* abundance, that has a well-known relationship with whales, and then using the known relationship to infer whale distributions.

Unlike physical properties like temperature and salinity, the abundance of plankton is difficult to measure automatically or synoptically. The main exception to this are estimates of chlorophyll concentration based on fluorescence and ocean color. In a companion paper (Pershing et al. 2009, this volume), we present a model-based system for estimating *Calanus finmarchicus* abundance in the Gulf of Maine. This system is based on 2 facts: the development rate of *C. finmarchicus* is largely a function of temperature (Campbell et al. 2001), and egg production in this species is largely a function of food availability, expressed as chlorophyll concentration (Runge & Plourde 1996, Durbin et al. 2003). Both temperature and chlorophyll can be measured from satellites.

The model is initialized on 1 January with a population of C5s and adults, concentrated over the deep basins in the Gulf of Maine. The initial abundance varies from year to year based on the concentration measured by the Gulf of Maine continuous plankton recorder (CPR) survey (Jossi & Goulet 1993) during the first 50 d of the year. Adults produce eggs at a rate determined by the abundance of chlorophyll according to the relationship from Durbin et al. (2003). From eggs, the copepods transition through 6 naupliar stages and 5 copepodid stages before becoming adults. The rate at which the population transitions through these stages is determined primarily by temperature and secondarily by chlorophyll according to the relationships from Campbell et al. (2001). Temperature and chlorophyll, both measured by satellite, are also used to determine mortality rates for each stage using the function described by Speirs et al. (2006).

In addition to the satellite data, the model requires the user to specify 3 external forcings: the initial conditions, the circulation field and the boundary conditions. *Calanus finmarchicus*'s diapause behavior restricts its winter distribution to the deep basins over the Gulf of Maine and also means that the stage structure is dominated by C5s. We initialize our model on 1 January and use an initial condition with very low abundance in areas shallower than 100 m, higher abundances over the deep basins and split evenly between C5s and adults. This initial condition is then scaled using the Gulf of Maine CPR data to capture some of the year-to-year variability in the size of the diapausing stock. The model copepods are transported through the Gulf of Maine by the bimonthly climatological circulation fields from Naimie (1996). These fields capture seasonal changes in circulation, but do not change from year to year. Even so, they are a good representation of the Gulf of Maine, especially for time scales longer than a week (Lynch & Naimie 2002). The Naimie (1996) climatologies have an open boundary with realistic inflow of water from the Scotian Shelf into the domain. We specify the concentration of *Calanus finmarchicus* along the open boundary to mimic the seasonal changes in abundance in this region.

As configured, the model is able to capture the development of the *Calanus finmarchicus* population in the Gulf of Maine, both in time and space. The interannual variability in the model exhibits a weak but statistically significant correlation with the interannual variability in the CPR data. This is somewhat surprising given the limited amount of *C. finmarchicus* data available during the winter and the correspondingly simplistic initial conditions. More importantly, the model can reproduce many of the observed within-year changes, such as the recovery of the *C. finmarchicus* population in 1999 (MERCINA 2004). Given the limitations of the model, notably the simplified initial and boundary conditions and the climatological circulation fields, it is most representative of conditions in the western Gulf of Maine, including the Great South Channel, on scales of weeks and 10s to 100s of kilometers. For the present study, we explore whether model-derived *C. finmarchicus* abundances can provide an index of right whale presence and abundance in the Great South Channel.

METHODS

The main goal of the present study was to examine the potential for using a physical–biological model of *Calanus finmarchicus* population dynamics to synthesize satellite observations into information that can be used to infer right whale distributions. In the present study, we seek simple correlations between whale observations and output from the *C. finmarchicus* model. We view this as a first step toward a more dynamical characterization of the interaction between these 2 species.

Right whale data. Right whale sightings for the years 1998 through 2006 from the North Atlantic Right Whale Consortium database (Right Whale Consortium 2007) were used to examine right whale distributions relative to our *Calanus finmarchicus* fields. We focused on the Great South Channel region, since it is the major spring habitat and the whales are likely feeding on *C. finmarchicus* (Kann & Wishner 1995, Kenney et al. 1995). The right whale sighting dataset for the Great South Channel region includes sightings from aerial and shipboard platforms; however, the dataset during this period is dominated by aerial surveys conducted by the National Marine Fisheries Service (NMFS) (Cole et al. 2007). From 1998 to 2001, NMFS conducted multiple surveys of the Great South Channel habitat per week during the spring. After 2001, the sampling effort in the Great South Channel was reduced to allow sampling over a broader area; however, the area was still surveyed multiple times per month during the spring (Cole et al. 2007). Sightings and effort included in our analysis met standardized minimum conditions: sea state of Beaufort 3 or below, visibility of at least 2 nautical miles (3.7 km), an altitude of less than 1200 feet (366 m) for aerial surveys and at least one observer on watch. Most of the aerial surveys were conducted at an altitude of 750 to 1000 feet (229 to 305 m) and at a groundspeed of 100 to 120 knots (185 to 222 km h^{-1}). Further details on the processing of the sightings data are available in Pendleton et al. (2009). We restricted the present study to the boundaries of the designated Great South Channel Critical Habitat plus an adjacent region extending north to 42.25° N and west to 70° W (Fig. 1). The additional area to the northwest is oceanographically similar to the Great South Channel, and this area contains consistent survey effort and right whale sightings during the early spring.

We normalized the total number of individual right whales sighted by the total length of survey trackline to produce an index of sightings per unit effort (SPUE). Sightings and survey effort were binned spatially into cells measuring 5 min of longitude by 5 min of latitude, and temporally into non-overlapping 14 d periods, with the last period in each year containing 15 d in non-leap years and 16 d in leap years. SPUE reported for the Great South Channel is the mean SPUE over a maximum of 148 discrete cells.

Analysis. To compare with the *Calanus finmarchicus* model output, we computed 2 indicators of right whale distributions in the Great South Channel. The mean SPUE between Days 84 and 210 (26 March to 29 July) provides an indication of the number of whales using the Great South Channel habitat in a particular year. We also created an index of when whales became common in the Great South Channel. This ‘arrival date’ was computed by linearly interpolating the 14 d mean SPUE to find the date when SPUE crossed a threshold of 0.01 whales km^{-1}. Thus, for each year, we have 2 numbers that summarize aspects of the use of the Great South Channel by right whales.

The modeled *Calanus finmarchicus* abundances were compared to both the arrival date and mean right whale SPUE using linear correlations. As right whales preferentially feed on late-stage *C. finmarchicus* (Kann & Wishner 1995, Baumgartner et al. 2003a), we combined the C5 and C6 abundances from the model. The model output was divided into 7 regions, the Great South Channel plus 6 regions along the Gulf of Maine CPR survey track. Although the Great South Channel was our target region, we compared the right whale time series to *C. finmarchicus* abundance in regions across the Gulf of Maine. Based on our analysis of *C. finmarchicus* abundance in both the model and the CPR dataset (Pershing et al. 2009), changes in *C. finmarchicus* abundance in one part of the Gulf of Maine are strongly tied to changes in other regions. The limitations of the model, for example the lack of variability in the circulation field and uncertainties in the initial conditions, mean that some areas may be better indicators of variability in the Great South Channel. Thus, comparing the right whale observations in the Great South Channel to model output from a broader region should increase our chance of developing a useful index of right whale patterns in the Great South Channel as well as providing insight into the model's behavior.

For each model year, the data from each region were binned into 10 d intervals and averaged. Thus, for each region and period, we have an annual time series that we compared with the 2 right whale time series. Using output from model Days 60 through 150 gives 10 time intervals, and combining these with the 7 regions yields a total of 70 comparisons with each whale time series. To account for spurious significant correlations due to the large number of comparisons, we employed a Monte Carlo-based test of 'field significance' (Wilks 1997, Barton et al. 2003). To estimate the probability of finding N correlations with one of the whale time series at a particular significance level, we generated a random whale time series and computed the correlations with the model output. The random whale series was created by selecting (with replacement) from the 9 yr of that time series (either arrival date or mean SPUE). We then totaled the number of correlations that were significant at the desired level. We repeated this process 10 000 times to produce a probability distribution for N. We also computed the probability of finding N correlations of a particular sign.

RESULTS

Right whale SPUE in the Great South Channel varies considerably in both magnitude and timing (Fig. 2). Although whales may be observed in this region at any time during the year, the majority of sightings occur between 1 March and 19 July (Days 60 to 200), with the main peak in sightings occurring after 1 May (Day 120). In several years, e.g. 2003 and 2006, there is an early peak in SPUE in mid-March (Day 70) followed by a brief period of low sightings before the main peak. The early peak was composed largely of sightings from the northwest area, while the second peak corresponded to the designated critical habitat. Sightings were relatively rare during the first 3 yr of the study; however, there were several sightings before mid-February (Day 50). From 2001 onward, the number of sightings increased and was concentrated after the end of April (Day 120). The arrival date, defined as the day at which sightings reach a value of 0.01 whales km^{-1}, varied between Day 63 (4 March) in 2003 and Day 117 (27 April) in 2000.

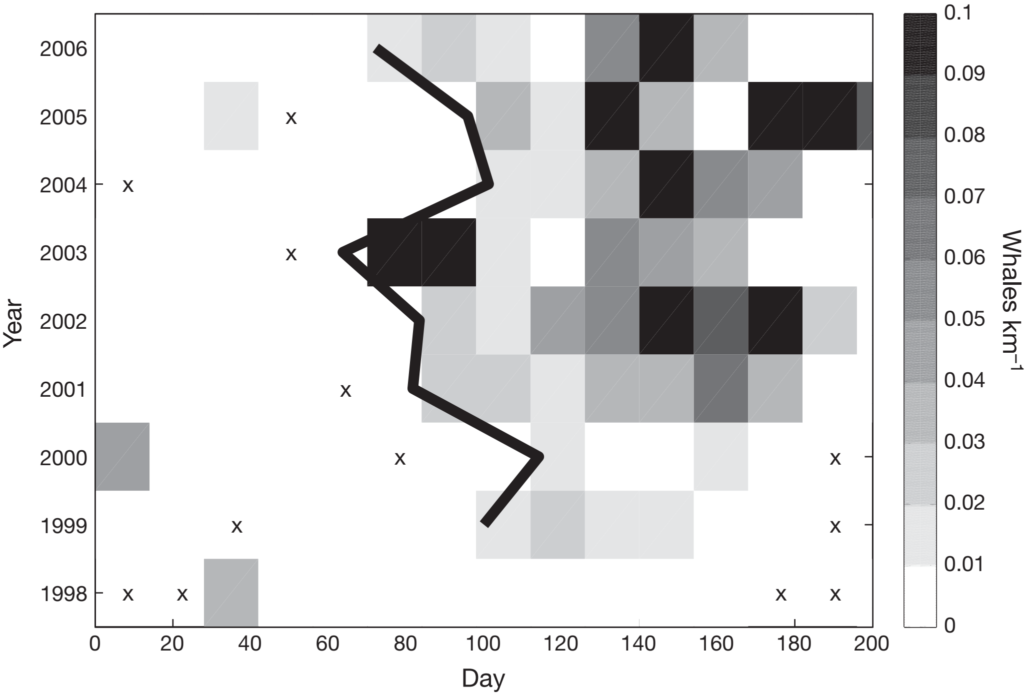

Fig. 2. *Eubalaena glacialis.* Right whales per unit effort in the GSC area. Each column of blocks represents the mean right whale sighting rate for all surveyed 10 × 10′ grid cells for a 14 d period in the years indicated on the left. Shading is proportional to the sightings per unit effort (SPUE) expressed as mean sightings per kilometer surveyed. x: Blocks with missing data; (▬) 0.01 whales km^{-1} contour used to define the arrival date

Calanus finmarchicus and right whales

A detailed evaluation of our model as a representation of interannual variability in *Calanus finmarchicus* is provided in Pershing et al. (2009). To evaluate the potential of this model to provide information on right whales in the Gulf of Maine, a brief discussion of *C. finmarchicus* patterns in the Gulf and our model's ability to simulate those patterns is necessary. *C. finmarchicus* has a well defined seasonal cycle in the Gulf of Maine (Fig. 3a). At the beginning of the year, there is a modest, but declining, population of pre-adults (C5) and adults (C6) over the deep basins. The abundance of these 2 stages increases dramatically around mid-April (Day 100), as individuals spawned in the previous months recruit into the C5 and C6 stages. The main peak in right whale sightings corresponds with the spring increase in *C. finmarchicus*, in both the model and observations (Fig. 3a).

The *Calanus finmarchicus* model displays substantial interannual variability in abundance. Some years, e.g. 2000 and 2006, display consistently positive or negative abundance anomalies. Other years, e.g. 1999, change signs within the year. Some of the variability in the model is due to the initial conditions, which are based on the abundance observed by the CPR, but the majority of the variability after Day 50 comes from the SST data, with the chlorophyll data playing a smaller role.

The ultimate goal of our project is to develop a system that can provide near real-time estimates or even forecasts of right whale distributions in the Gulf of Maine. A first step towards this capability is to demonstrate a correspondence between the *Calanus finmarchicus* abundance from the model and whale patterns in the Great South Channel. Given that our time series only encompasses 9 yr, our correlation analysis focused more on documenting how the relationship between the *C. finmarchicus* model and the right whale data change in space and time than in establishing strict statistical significance. The interannual variability in *C. finmarchicus* abundance from the model shows some correspondence with the patterns in the right whale SPUE data (Fig. 2). In particular, the abrupt increase in right whale usage in the Great South Channel after 2000 coincided with an increase in *C. finmarchicus* visible in both the model (Fig. 3b) and the CPR data (Fig. 4c in Pershing et al. 2009). The right whale arrival date showed a consistent negative relationship with the *C. finmarchicus* model over much of the Gulf of Maine (Fig. 4a). A negative correlation between *C. finmarchicus* abundance and arrival date implies that whales arrive early in the Great South Channel habitat when modeled *C. finmarchicus* abundance is high in the region in question. The correlation between whale arrival and *C. finmarchicus* abundance in the western Gulf of Maine began on 31 March (Day 90) and strengthened as the simulation pro-

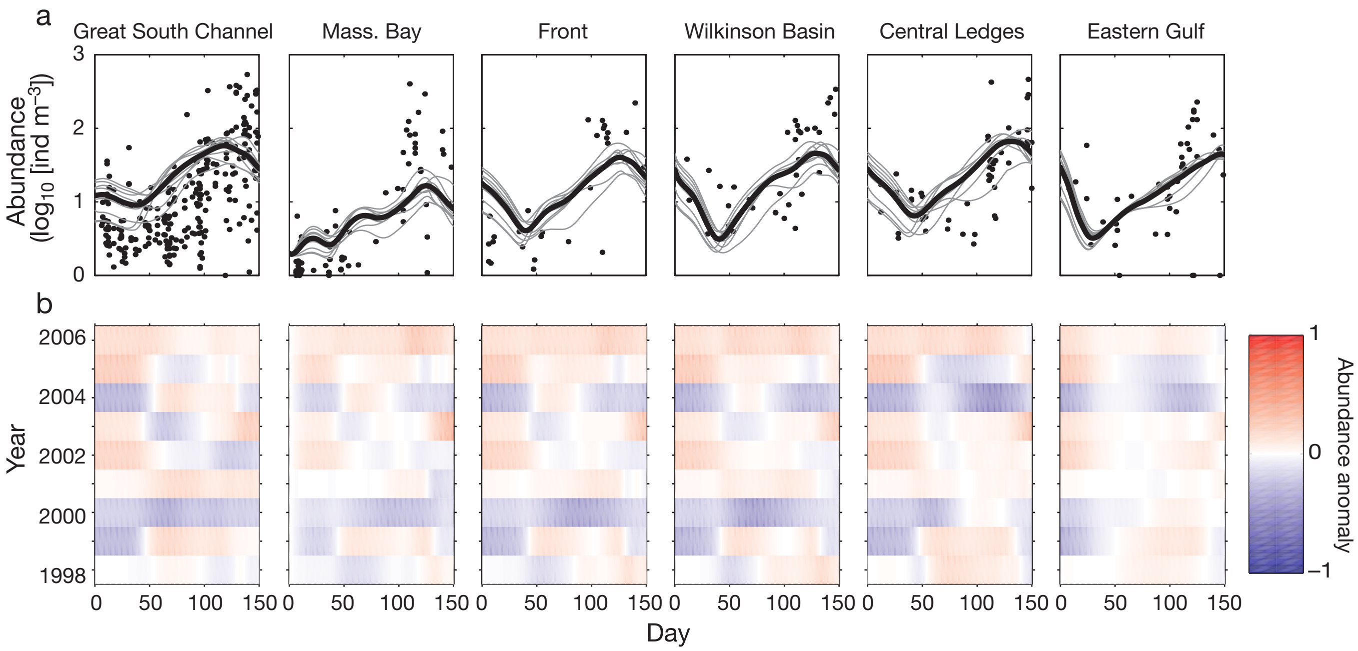

Fig. 3. *Calanus finmarchicus*. (a) *C. finmarchicus* abundance from the model (lines) and from NMFS Marine Resources Monitoring, Assessment and Prediction program (MARMAP) surveys (circles). The thick lines represent the average *C. finmarchicus* abundance from the 1998–2006 model runs (thin lines). (b) Interannual variability of *C. finmarchicus* abundance estimated by the model. Data are displayed as anomalies relative to the 1998–2006 climatology (thick lines in [a]), with blue indicating lower than average abundance, and red indicating higher than average abundance

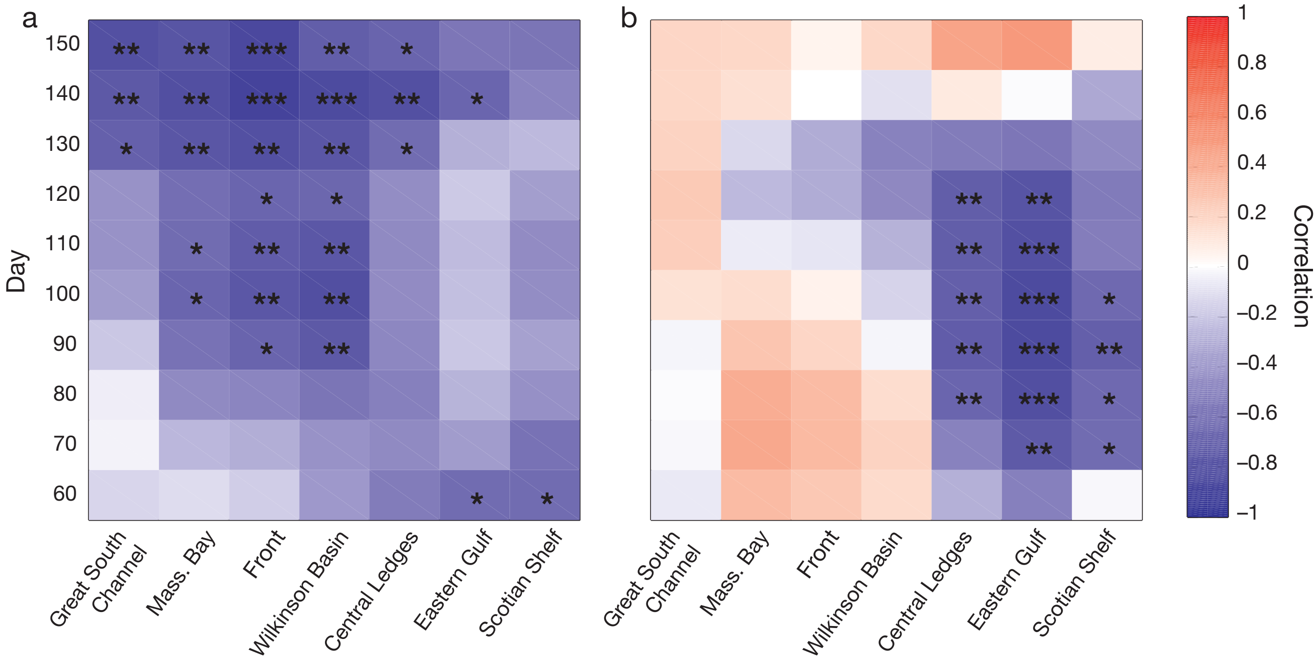

Fig. 4. *Calanus finmarchicus* and *Eubalaena glacialis*. Correlation between the *C. finmarchicus* model and (a) right whale arrival date and (b) mean sightings per unit effort (SPUE). Each square indicates the strength of the correlation between either arrival date or mean SPUE and a yearly time series of *C. finmarchicus* from a single region and 10 d interval. For example, the box in the upper left-hand corner of (a) represents the correlation between arrival date and *C. finmarchicus* abundance at the end of the simulation in the Great South Channel (i.e. the last column in Fig. 3b). *, **, ***: Correlations significant at the 90, 95 and 99 % levels, respectively

gressed. The correlations in the Great South Channel became significant towards the end of the simulation. Three of the correlations were significant at the 99 % level, 17 were significant at 95 % and 28 were significant at the 90 % level. Our field significance tests indicate that the chance of finding this number of correlations by chance is highly unlikely (Table 1). Furthermore, all 70 correlations had r-values less than 0. The chance of finding this many negative correlations by chance is less than 1 in 1000.

The pattern of correlation between mean SPUE and modeled *Calanus finmarchicus* abundance is more complex than for arrival date (Fig. 4b). Between Days 60 and 100 (1 March to 10 April), there was an area of strong negative correlation centered on the eastern Gulf of Maine. A negative correlation with abundance suggests that high abundance in the region indicates few whales in the Great South Channel. We found 4, 12 and 15 correlations significant at the 99, 95 and 90 % level, respectively (Table 1). The field significance tests suggest that the overall pattern of correlations is weakly significant ($p = 0.06$, 0.08 and 0.16 for the 99, 95 and 90 % level correlations, respectively). Nearly half (34) of the correlations were negative, and the probability of finding this number by chance is, not surprisingly, near 0.5 (0.53).

For most management decisions, defining when whales are likely to be in a given area is at least as important as estimating the number of whales. The arrival date correlations are a concrete way of providing this kind of information. Examining these correlations more closely, modeled *Calanus finmarchicus* abundance in the Front Region on Day 140 explained more than 75 % of the variability in the whale arrival

Table 1. Results of the field significance tests of the correlations in Figs. 4a,b & 6b. Using the Monte Carlo procedure described in 'Methods', we computed the probability of finding N or more correlations that are significant at the 99, 95 and 90 % level, where N is the number found in our study. We also computed the probability of finding N or more negative correlations. SPUE: Sightings per unit effort; SST: sea-surface temperature

Whale time series	Correlations	N	Probability
Arrival date	$p < 0.01$	3	0.0930
	$p < 0.05$	17	0.0312
	$p < 0.10$	28	0.0217
	$r < 0$	70	0.0096
Mean SPUE	$p < 0.01$	4	0.0611
	$p < 0.05$	12	0.0781
	$p < 0.10$	15	0.1569
	$r < 0$	34	0.5261
SPUE corrected for SST	$p < 0.01$	0	1.00
	$p < 0.05$	3	0.39
	$p < 0.10$	7	0.41
	$r < 0$	44	0.36

date ($r^2 = 0.76$, $p < 0.01$) (Fig. 5a). However, the earliest whale arrival date was nearly 2 mo before the first significant correlation with the Front Region *C. finmarchicus* abundance. To investigate the potential for forecasting right whale presence in the Great South Channel, we re-ran the simulations, but replaced the satellite data after Day 70 with the 1998–2006 climatological average (Fig. 5b). Although the correlation is weaker ($r^2 = 0.59$), it is still significant ($p < 0.05$).

DISCUSSION

Our relatively simple *Calanus finmarchicus* model was able to provide an index for right whales in the Great South Channel habitat. Specifically, we found strong correlations between the western Gulf of Maine *C. finmarchicus* abundance and the date at which right whales arrive in the Great South Channel habitat, as well as a correlation between *C. finmarchicus* abundance in the eastern and central Gulf of Maine and the mean number of whales in the Great South Channel habitat. The first relationship is consistent with the hypothesis that *C. finmarchicus* abundance drives the movement of whales in the Great South Channel habitat: when *C. finmarchicus* is abundant early in the year, whales arrive early in the habitat. However, there are 2 surprising outcomes of the correlation analyses. First, although the abundance of *C. finmarchicus* in the Great South Channel is related to arrival date, *C. finmarchicus* abundance from other regions, especially the Front Region, are better indicators of when whales will arrive in the Great South Channel (Fig. 4a). The low correlations in the Great South Channel are likely due to the complexity of the physical oceanography in this region. On the western side of the Great South Channel, there is a strong southward-flowing current that links the Great South Channel to the regions to the north, especially the Front Region (Fig. 1). Particle tracking experiments using the Naimie (1996) flow fields indicate that waters in the western Great South Channel arrive from the Front Region. This oceanographic connection explains why the *C. finmarchicus* abundance in the Front Region has a strong correlation with arrival date in the Great South Channel. However, the particle tracking experiments indicate that some of the waters in the northeast portion of the Great South Channel arrive from the southeast and have spent time over the shallow cap of Georges Bank, and before that, in the eastern Gulf of Maine. *C. finmarchicus* taking this pathway experience different temperature and chlorophyll conditions than animals arriving via the western Gulf of Maine. The net effect is to reduce the overall correlation in the Great South Channel.

The second surprise is that right whales arrive well before the model begins to exhibit a statistically significant relationship. We believe an explanation lies in the dynamics of *Calanus finmarchicus* during this period. Beginning in mid-March (Day 70), the *C. finmarchicus* population enters a period of rapid growth (Fig. 3a). A change in the population growth rates would appear as a small anomaly at the beginning of this period that would then grow. The tendency of the model, and likely the *C. finmarchicus* population, to magnify anomalies during the last half of the simulation is apparent in the model output (Fig. 3b). Up to Day 70, anomalies in the model output are directly attributable to the initial conditions. Around Day 70, there is a white band in Fig. 3b indicating small anomalies followed by generally strengthening anomalies. Thus, the signal of interannual variability tends to strengthen towards the end of the simulation as individuals recruit into the C5 and C6 stages, providing greater dynamical range for the correlations. Our ability to forecast arrival dates using climatological satellite data after Day 70 (e.g. Fig. 5b) is a good example of how anomalies propagate through the model. Because interannual signals are not present in the climatological satellite data, any interannual variability in the abundance on Day 150 in these simulations must be due to processes before Day 70. For example, elevated winter chlorophyll levels will lead to a larger than average cohort of eggs and nauplii on Day 70. The model then advances this cohort through the stages. Because mortality decreases with increasing size, the later stages tend to accumulate individuals, amplifying the Day 70 signal. Adding interannual changes in SST or chlorophyll during this time refines this signal.

Although output from the *Calanus finmarchicus* model exhibits a strong correlation with right whale arrival date, its correspondence with the number of whales in the GSC is less clear. In the western regions, we found positive, but non-significant, correlations between *C. finmarchicus* abundance and mean SPUE. This relationship is consistent with the correlation between *C. finmarchicus* abundance in the western Gulf of Maine from the CPR and SPUE data reported by Pendleton et al. (2009). Assuming the correlation in Pendleton et al. (2009) is correct, we expect that continued refinement of our *C. finmarchicus* model will result in improved skill at estimating right whale abundance in the Great South Channel.

The significant negative correlations between model abundance in the eastern Gulf and mean SPUE are unexpected, and we believe they may indicate a stronger role for circulation variability in explaining right whale use of the Great South Channel. The regions with the strongest correlation with SPUE are located near the open boundary on the Scotian Shelf.

In the model, the flux of copepods through this boundary varies seasonally, but doesn't change from one year to the next. This means that variability in abundance in these regions is due almost exclusively to the influence of temperature and chlorophyll on the population dynamics. One possible explanation is that the negative correlations in the east reflect a more direct correlation between whale abundance in the Great South Channel and temperature or chlorophyll. SST anomalies are strongly correlated between regions (Pershing et al. 2009), and mean SPUE is negatively correlated with the SST data used to drive the model ($r^2 = 0.44$, $p = 0.05$) (Fig. 6a). If we correlate the model output with the residuals from the SST–SPUE relationship, a new pattern emerges (Fig. 6b). Although the negative correlations in the east remain, they are weaker, while the positive correlations in the west become stronger. Several of the correlations in the western regions are significant; however, the field significance tests suggest that these could be due to chance (Table 1). Given that we have only a few years of data, we interpret the consistent positive correlations in the west as indicative of a relationship that merits future study, even if the exact strength of the relationship cannot be assessed at this time.

We hypothesize that the SST–SPUE correlation is due to changes in circulation. Positive temperature anomalies indicate an earlier spring warming and increased stratification. As the Gulf of Maine becomes more stratified, the recirculation over the shallow banks that border the Great South Channel increases (Naimie 1996), the flow out through the Great South Channel increases and fewer copepods will be retained in the Great South Channel habitat. Thus, the negative SST–SPUE correlation likely reflects interannual changes in the Gulf of Maine circulation that are not represented in the climatological circulation fields. Adding more realistic circulation should improve the ability of the model to represent *Calanus finmarchicus* in the Great South Channel and provide information on right whale abundance.

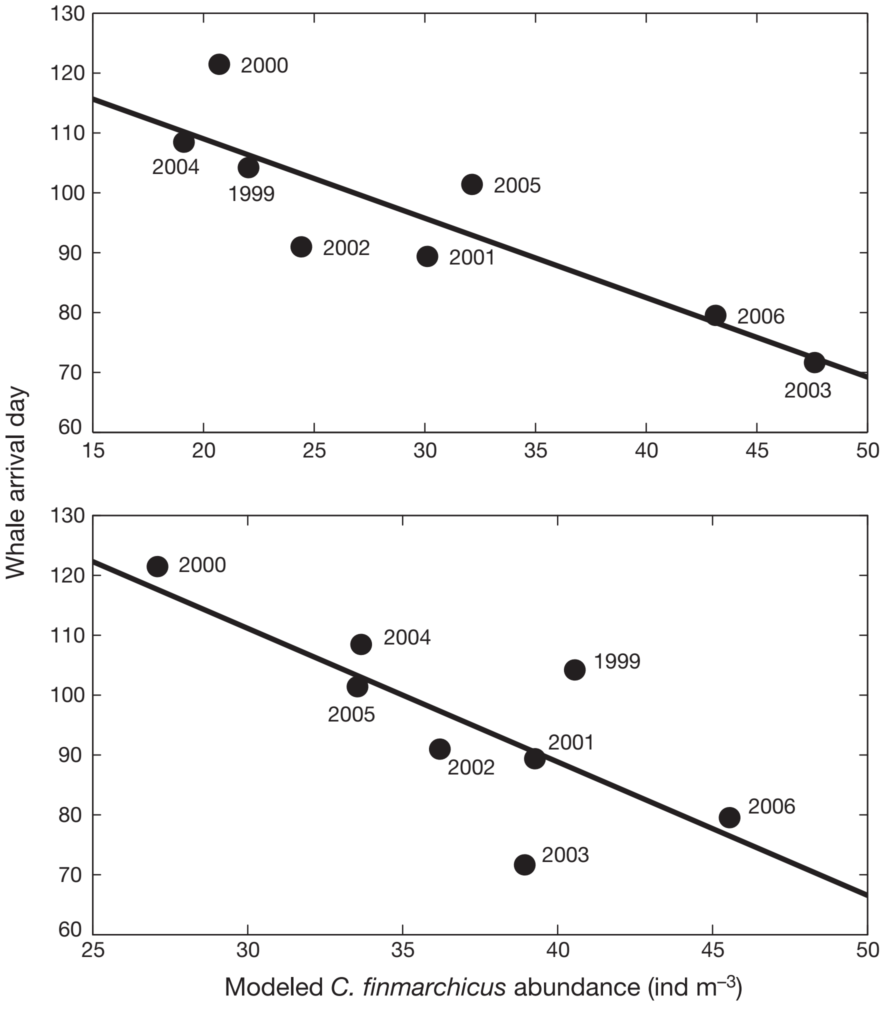

Fig. 5. *Calanus finmarchicus* and *Eubalaena glacialis*. (a) Correlation between modeled *C. finmarchicus* abundance in the Front Region on Day 140 and right whale arrival date in the Great South Channel ($r^2 = 0.76$, $p < 0.01$). (b) Same correlation, but the satellite data used to drive the model were replaced by the climatology after Day 70 ($r^2 = 0.59$, $p < 0.05$)

Our study complements other work on the importance of zooplankton abundance, specifically the role of *Calanus finmarchicus* in structuring the distribution and abundance of right whales. Work on right whale foraging can be organized by spatial scale. At scales of several meters, the formation of high densities of zooplankton requires fine-scale convergent features (Beardsley et al. 1996). For example, Mayo & Marx (1990) identified a critical feeding threshold of 4000 m^{-3}, an order of magnitude greater than the concentrations produced by our model. Baumgartner et al. (2003b) found whales in Roseway Basin feeding on dense layers of *C. finmarchicus.* In both studies, the authors identified fine-scale physical processes that produced the dense aggregations, surface convergences such as Langmuir cells in Cape Cod Bay or the bottom boundary layer in Roseway Basin. The present study examined zooplankton distributions on scales of 100 km or more. At this scale, average zooplankton abundance seems to influence the choice of feeding areas. Pendleton et al. (2009) found positive correlations between CPR-measured *C. fin-*

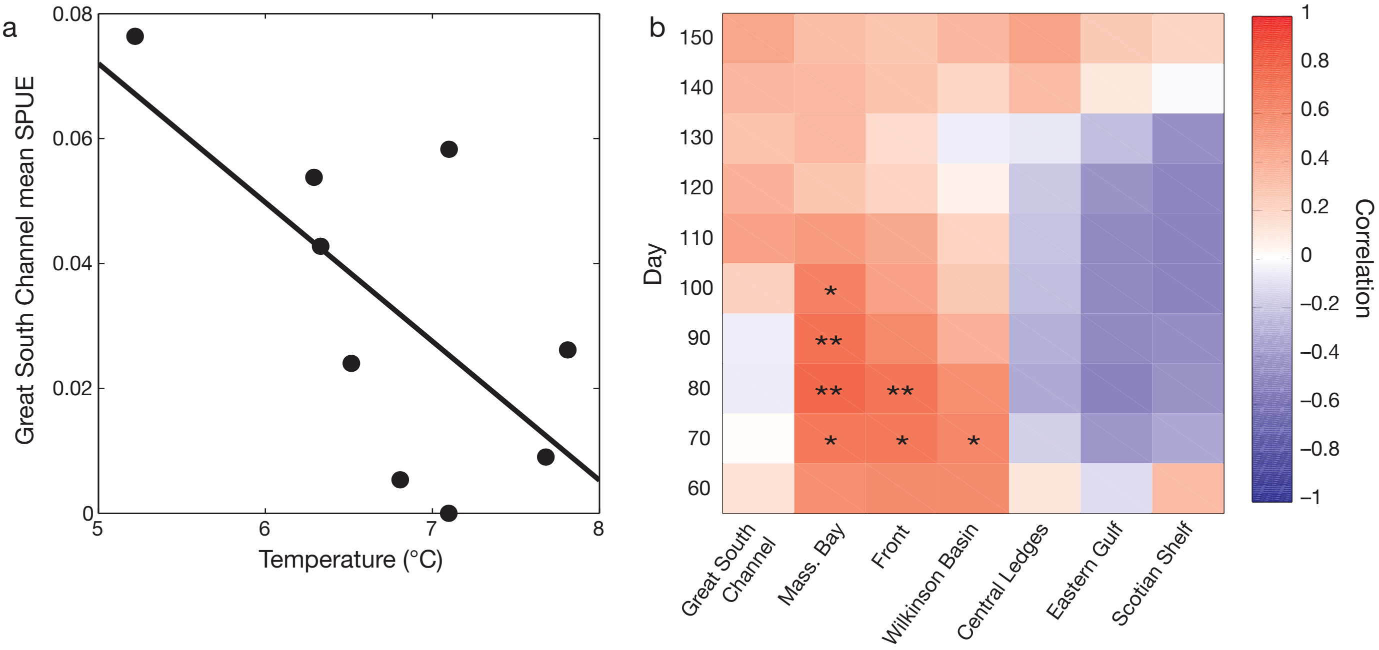

Fig. 6. *Calanus finmarchicus* and *Eubalaena glacialis*. (a) Relationship between the sea-surface temperature (SST) in the Great South Channel on Day 120 and the mean right whale sightings per unit effort (SPUE). (b) Correlation between the *C. finmarchicus* model and the residuals from the SST–SPUE relationship in (a)

marchicus abundance in the Wilkinson Basin and right whale SPUE in the Great South Channel and between right whales and non-*C. finmarchicus* copepods in Cape Cod Bay. On intermediate scales, DeLorenzo Costa et al. (2006) found an association between right whales and zooplankton abundance, with variability in wind-driven currents playing a dominant role in determining plankton abundance. Particle tracking simulations support the assertion that circulation variability strongly influences copepod abundance and right whale feeding conditions, especially in coastal habitats (Jiang et al. 2007).

Kenney et al. (2001) considered how the sensory mechanisms and foraging strategies used by right whales could change across spatial scales. Extending their ideas, we propose a conceptual model of how variability in physical and biological conditions influences right whales on several scales (Fig. 7). A distance of 400 km characterizes both the length of the Gulf of Maine (Boston, Massachusetts to Yarmouth, Nova Scotia) and its width (coast of Maine to the shelf break). This scale captures the seasonal movements of right whales between feeding areas. At this scale, our model results suggest that *Calanus finmarchicus* abundance is a function of the mean circulation, represented by the Naimie (1996) climatological flow fields, and *C. finmarchicus* population dynamics (Fig. 7a). Variability in *C. finmarchicus* abundance at this scale is strongly influenced by temperature and the supply of animals from the Scotian Shelf (MERCINA 2004, Pershing et al. 2009). This scale captures differences in the relative quality of critical habitat areas such as Cape Cod Bay, Great South Channel or Roseway Basin. As we found, variations in copepod production can provide useful information on when and possibly how many whales will appear in a feeding area.

The 4 primary right whale feeding areas — Cape Cod Bay, Great South Channel, Roseway Basin and the Bay of Fundy — can be characterized by an average length scale, which ranges from 20 km for the coastal habitats of Cape Cod Bay and the Bay of Fundy to 75 km for the Great South Channel. Most habitats are small enough that *Calanus finmarchicus* population dynamics play a secondary role to circulation in determining feeding conditions. Using 50 km as the representative scale of a critical habitat and the average velocity in the Naimie (1996) climatology of 0.08 m s^{-1} as a representative velocity, the time for water to pass through a habitat is 7.23 d. At this time scale, variations in *C. finmarchicus*' egg production or development time will be insignificant relative to changes in circulation. Thus, circulation variability should be the dominant process determining right whale foraging conditions on a scale of 10s of kilometers (Fig. 7b). This variability would include changes in the position of density fronts as well as the strength and direction of horizontal currents. Information on these processes could be used to route ships away from potential whale aggregations and to identify aggregations outside of the critical habitats.

On a scale of 10s of meters, boundary layer phenomena such as Langmuir cells, turbulence and internal waves are the dominant physical processes. Zooplankton have considerable control of their position at these scales, and thus, the distribution of plankton results from the interaction between behavior and physics (e.g. Pershing et al. 2001, Genin et al. 2005). This is the scale that determines the position of individual whales. Information at this scale on the mechanisms behind patch formation and right whale foraging behavior are especially relevant to management actions to reduce entanglement, including the design of whale-safe fishing gear.

Although the processes we emphasize in our conceptual model are particular to right whales and *Calanus finmarchicus*, the idea of organizing predator–prey relationships at the patch, habitat and regional scales should apply generally to large predators. For example, humpback whales *Megaptera novaengliae* feed mainly on planktivorous fish such as herring and sand lance. Assuming *C. finmarchicus* is a major component of the diet of these fish, the scales and processes in Fig. 7 should govern the distribution of these fish. From the humpbacks' point of view, the most obvious change will occur at the habitat and patch scales. At these scales, fish behaviors such as schooling and spawning will play a larger role.

CONCLUSIONS

There is growing evidence that right whale movements in the Gulf of Maine are tied to the distribution and abundance of copepods. The correlation between right whale arrival date in the Great South Channel and our first generation modeled *Calanus finmarchicus* abundance estimates suggests that real-time information on copepod distribution could be useful for right whale management. Before applying these or any

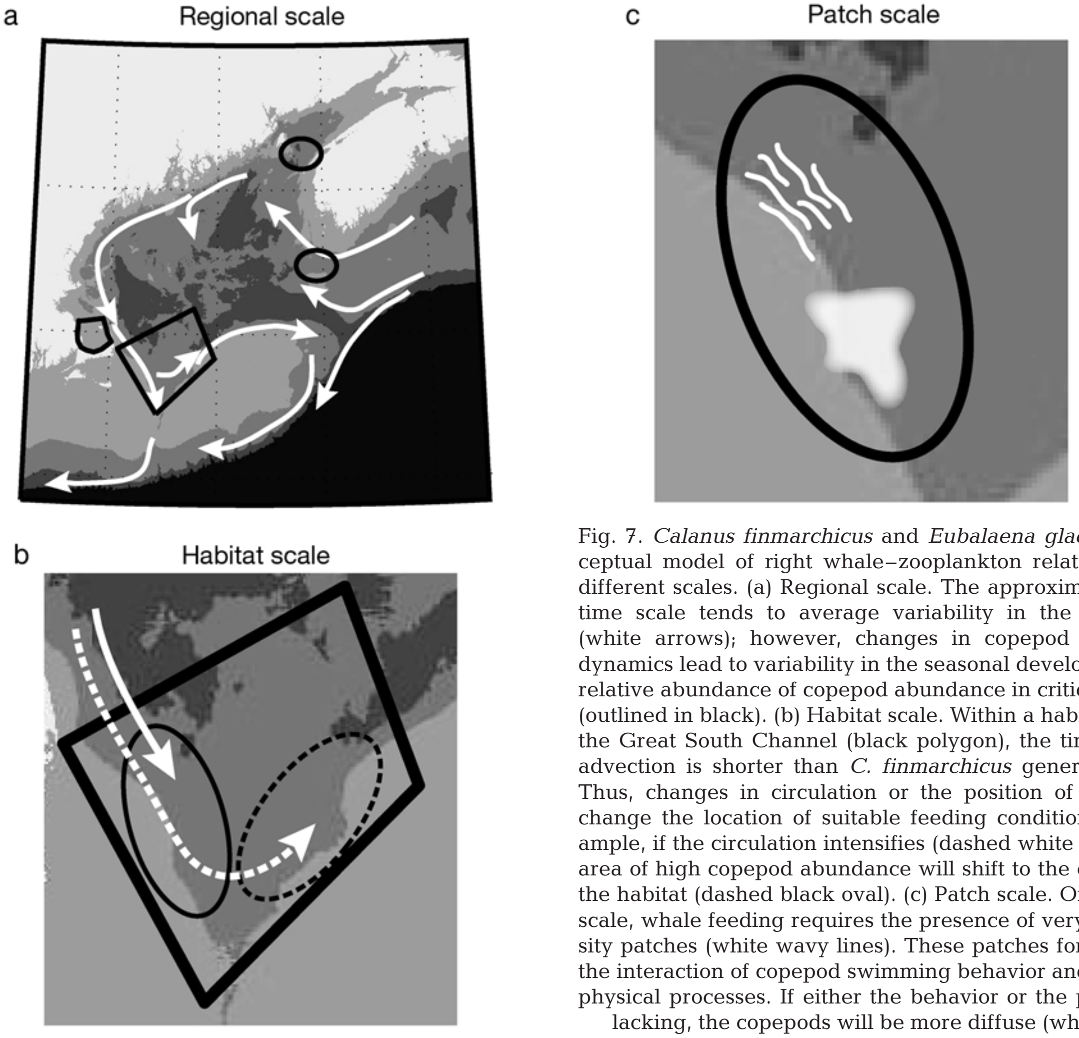

Fig. 7. *Calanus finmarchicus* and *Eubalaena glacialis*. Conceptual model of right whale–zooplankton relationships at different scales. (a) Regional scale. The approximately 1 mo time scale tends to average variability in the circulation (white arrows); however, changes in copepod population dynamics lead to variability in the seasonal development and relative abundance of copepod abundance in critical habitats (outlined in black). (b) Habitat scale. Within a habitat such as the Great South Channel (black polygon), the time scale of advection is shorter than *C. finmarchicus* generation time. Thus, changes in circulation or the position of fronts will change the location of suitable feeding conditions. For example, if the circulation intensifies (dashed white arrow), the area of high copepod abundance will shift to the east side of the habitat (dashed black oval). (c) Patch scale. On the finest scale, whale feeding requires the presence of very high density patches (white wavy lines). These patches form through the interaction of copepod swimming behavior and fine scale physical processes. If either the behavior or the physics are lacking, the copepods will be more diffuse (white blob)

model values, it is critical to understand the processes captured by the model and the scales at which the model applies. This first generation forecast represents the seasonal development of *C. finmarchicus* on scales of 100s of kilometers. Our approach could be extended to finer spatial and temporal scales by incorporating improved circulation forecasts and assimilating zooplankton observations. Our 'bottom-up' approach to predicting right whale distributions could be enhanced by a more dynamical model of whale behavior and could be extended to other species and regions.

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