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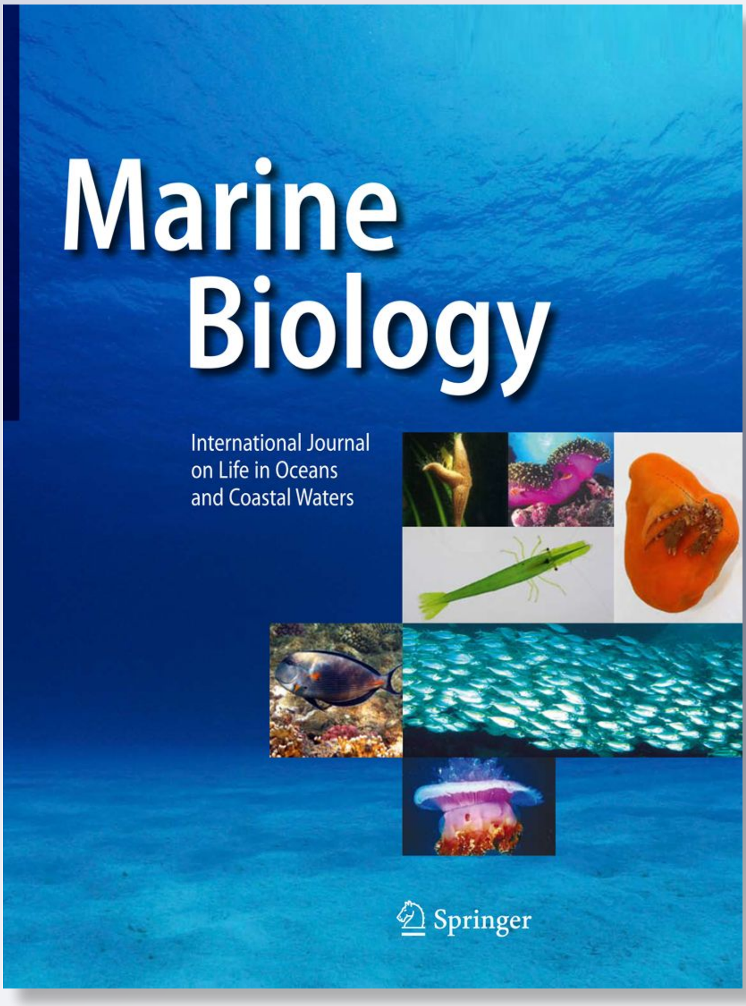

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ORIGINAL PAPER

Predicting regional spread of non-native species using oceanographic models: validation and identification of gaps

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Abstract Predicting spread is a central goal of invasion ecology. Within marine systems, researchers have increasingly made use of oceanographic circulation models to estimate currents and track species dispersal. However, the accuracy of these models for predicting biological patterns, particularly for non-native species, has generally not been validated. Particularly, we wished to examine the ability of models to predict physical and biological processes, which jointly determine the spread of marine larval organisms. We conducted two empirical studies—a recruitment study and a drift card study—along the coast of New England, USA, focusing on two invaders of concern—the European green crab (*Carcinus maenas*) and the Asian shore crab (*Hemigrapsus sanguineus*), to explicitly evaluate the ability of oceanographic models to predict patterns of spread. We used data from the large-scale drift card study to validate our ability to capture dispersal patterns driven purely by physical processes. Next, we conducted a recruitment study to evaluate our ability to reproduce patterns of biological dispersal. We were generally capable of reproducing drift cards patterns—suggesting that the physical mechanics in the model were predictive. However, predicted biological patterns were inconsistent—we were able to predict dispersal patterns for *H. sanguineus* but not for *C. maenas*. Our results highlight the importance of validating models and suggest that more work is necessary before we can reliably use oceanographic models to predict biological spread of intertidal organisms.

Introduction

Non-native species are a growing environmental problem; thousands of introduced species are being transported around the world every day (Carlton 1999; Ricciardi 2007). Once a non-native species becomes established, the population can reproduce and release propagules. Secondary spread occurs when these propagules are transported to new locations by physical and biological processes (Queiroga and Blanton 2004; Byers and Pringle 2006). Researchers and managers need to manage and predict secondary spread because it determines the extent of the ecological and economic impacts of biological invasions (Lodge et al. 1998). Forecasting the spread of a species has both pure and applied ramifications and has been studied for decades (Fisher 1937; Skellam 1951; Shigesada and Kawasaki 1997; Yoshimura et al. 1999; Leung and Mandrak 2007). Despite this long history of study, the ability to accurately forecast the spread of non-native species has been limited, particularly in marine systems (Grosholz 1996; Wonham and Lewis 2008).

Most marine species have one or more planktonic life stages that are transported by ocean currents. Given the importance of currents in steering these propagules, oceanographic models designed to estimate and forecast currents could be valuable for forecasting the spread (Queiroga and Blanton 2004; Wonham and Lewis 2008). Oceanographers are interested in the processes and mechanics and thus tend to

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focus on the large spatial scale and not often on small-scale biological problems. Most models are used to predict large-scale particle movements far from shore, and their ability to forecast the spread of coastal organisms is rarely examined (e.g., Werner et al. 1993; Hannah et al. 2000, 2001). For the aforementioned models to be applicable to most planktonic species, we would need to model the input of propagules into the water column, the passive advection of propagules by currents, the active behavior of these propagules within the water column, and stochastic effects (i.e., diffusion), all at high enough resolution to predict where on the coast the larvae will settle.

Passive advection of particles vertically in open water is uncommon and is often assumed to be zero in oceanographic models. However, when the modeled particle is a larva, vertical movement is common and is controlled largely by diel vertical migration (DVM) and ontogenetic migration (i.e., the vertical migration pattern of the larva as it develops) (Cronin 1982; Epifanio 1988; Forward 1988; Palmer 1995; Queiroga and Blanton 2004 and references therein; Paris and Cowen 2004; Park et al. 2004; Park and Shirley 2005; Voss et al. 2007). Given vertical variation in currents (i.e., shear), the position of the larva in the vertical axis can have an important outcome on its horizontal path (Queiroga and Blanton 2004). Although DVM is believed to be important in the prediction of secondary spread, the timing, amplitude, and functional form of these behaviors are poorly understood, especially for invaders in an introduced range along the coast. To date, few studies have explicitly considered the value of larval behaviors such as DVM in oceanographic models (but see Paris and Cowen 2004; Fox et al. 2006; Voss et al. 2007; North et al. 2008; Gallego 2011).

While complex and promising models have been developed to predict the spread of marine non-native species, unfortunately most of these models are not validated (Dunstan and Bax 2007). Exceptions to this statement include models that have successfully predicted the recruitment of native species with larval behavior such as cod and haddock (Werner et al. 1993), but these simulations were run in essentially the center of the model's domain rather than along the coastline for organisms living in the intertidal zone. Standardized datasets at large spatial scales are required to assess whether these regional models are predictive and whether or not they are able to reproduce dispersal patterns at relevant regional scales. Unfortunately, such datasets are uncommon; more commonly, researchers use oceanographic models without adequate data for proper validation of biological invasions (e.g., Dunstan and Bax 2007).

In this study, we collected and used standardized, regional datasets to examine the ability of existing oceanographic models to describe patterns of biological invasions. Particularly, we assessed whether simple oceanographic models and our current understanding of the biology of organisms are sufficient to predict the spread of biological organisms, and if not, which factor(s) is most likely to be currently limiting. We used a simple accessible oceanographic model (Hannah et al. 2001), with the expectation that more complex (but less accessible) models would perform even better, and used two well-known invaders (*Carcinus maenas* and *Hemigrapsus sanguineus)* as our case study. We used values from the literature coupled with field data, to predict spread, comparing the output of the model to the observed large-scale patterns of drift cards (driven only by physical factors) and larval settlement (affected by both physical and biological factors) in the Gulf of Maine. We endeavored to separate the influence of physical and biological drivers of spread. Our expectation was that if the physical model used in our study was the limiting factor, the model should fail to predict either drift cards or larval settlement. If the oceanographic model adequately described the physical processes but our understanding of the biology was inadequate, then the model should fit the drift card patterns but not the larval recruitment patterns. If both physical model and our current biological understanding were sufficient, we would expect to describe both drift cards and larval recruitment patterns. Regardless of the mechanism, we tested whether our current biological understanding and physical models are adequate for predicting spread in this system.

Study organisms

In this study, we focus on the European green crab (*C. maenas*) and Asian shore crab (*H. sanguineus*) in New England. *Carcinus maenas* has been present in this region since the 1800s (Carlton and Cohen 2003). *Hemigrapsus sanguineus* was first detected in 1988 in New Jersey, then later in the 1990s in New England (McDermott 1998). They are both invaders that can cause ecological and economic impacts (Grosholz and Ruiz 1995, 1996; Walton et al. 2002; Brousseau and Baglivo 2005; Griffen and Delaney 2007; Kraemer et al. 2007; Griffen and Byers 2009), and they are still spreading (Klassen and Locke 2007; Behrens Yamada and Gillespie 2008; Delaney et al. 2008). *Carcinus maenas* is a highly fecund generalist that can be transported by multiple vectors and has obtained a global distribution (Broekhuysen 1936; Ropes 1968; Grosholz and Ruiz 1996; Carlton and Cohen 2003). *Carcinus maenas* can be found on sections of all non-polar continents (Carlton and Cohen 2003). As an adult and to a certain extent as a larva, the species can tolerate a wide range of salinities and temperatures (Broekhuysen 1936; Eriksson and Edlund 1977; Dawirs 1985; Dawirs and Dietrich 1986; Anger et al. 1998). The timing and duration of the breeding season of *C. maenas* varies by geographic region (Behrens Yamada 2001 and references therein), but we commonly observed ovigerous females along the coast of New England from June to September. The free swimming, planktonically dispersed larvae are transported by surface currents as they undergo four zoeal stages before metamorphosing into megalopae that become benthic adults (Crothers 1967; Behrens Yamada 2001). The amount of time spent as plankton is temperature dependent, at 18°C, *C. maenas* spends between 29 and 37 days (Dawirs 1985). Others state that it can take up to 90 days for *C. maenas* to metamorphose into benthic-dwelling, post-larval crabs (GCC 2002). *Carcinus maenas* undergoes vertical migration as a zoea and megalopa (Zeng and Naylor 1996; Queiroga et al. 1997; Behrens Yamada 2001).

The life cycles and larval behaviors of *H. sanguineus* and *C. maenas* are similar though some subtle differences exist in their ecology (McDermott 1998; Park et al. 2004). As with *C. maenas,* the adults and larvae of *H. sanguineus* are tolerant to a range of temperatures and salinities (Epifanio et al. 1998; McDermott 1998). The breeding season along the east coast of North America is late April through September (McDermott 1998). *Hemigrapsus sanguineus* can produce multiple broods in a single breeding season and is highly fecund (McDermott 1991, 1998). Like *C. maenas* and most other marine larvae, the rate of *H. sanguineus* development and the duration of its planktonic zoeal stages is temperature dependent and has been shown to vary from 16 to 55 days before metamorphosing into a megalopa (Epifanio et al. 1998). *Hemigrapsus sanguineus* has an additional fifth zoeal stage that is not present in the development of *C. maenas*, before becoming a megalopa (Epifanio et al. 1998). Yet the general timing and length of its breeding season for the population found along the east coast of North America is similar to *C. maenas* (McDermott 1998). *Hemigrapsus sanguineus* is adaptable but prefers to hide under rocks, where *C. maenas* lives under rocks and macrophytes and seems be to better adapted for living in estuaries.

Methods

Drift card study

From June to September 2007, we conducted a drift card study with multiple deployments of drift cards released from the intertidal zone throughout the breeding season from 11 locations from Oak Bluffs, Massachusetts (41.433°N, −70.556°W) to Schoodic Peninsula, Maine (44.336°N, −68.056°W) (Fig. 1). The locations provided coverage across the coast, but the specific locations were subject to the availability of groups to deploy the cards. Each of the 83 deployments comprised 30 cards labeled with contact information and a unique identification number that identified the location, time, and date of its release. We used non-lead-based paint on the biodegradable cards that were 15 cm × 10 cm × 0.3 cm. Cards were released

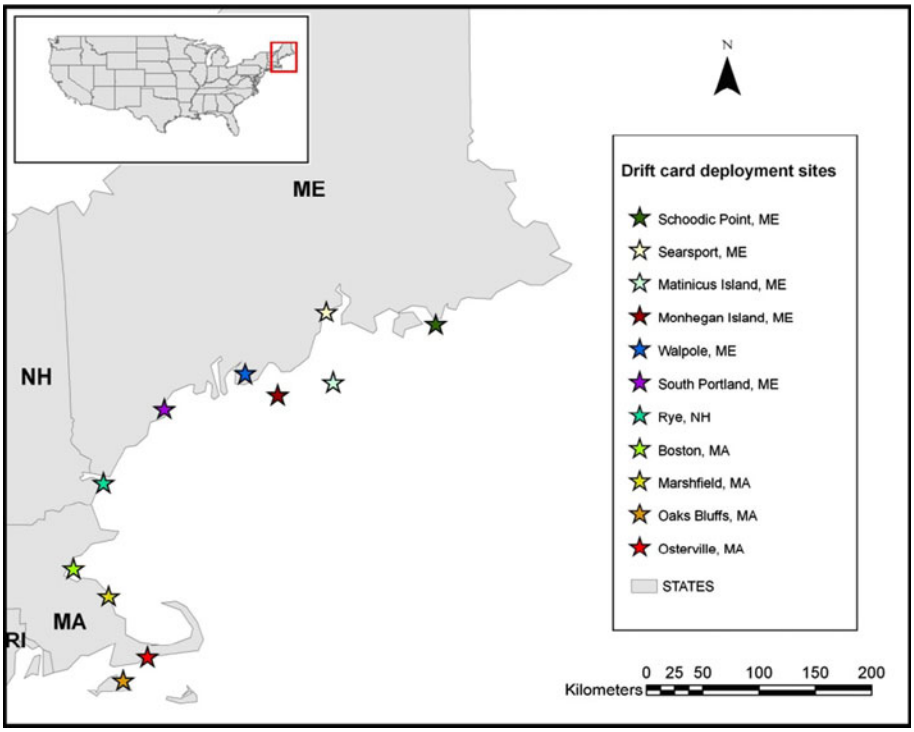

Fig. 1 The 11 locations, from Oak Bluffs, Massachusetts (MA) to Schoodic Peninsula, Maine (ME), where drift cards were deployed from June to September, 2007

throughout the breeding season and at various tidal conditions at each of the sites. Each site had deployments during the ebb of an outgoing spring tide, the flood of a neap tide, and a deployment at a randomly chosen tidal state.

Recruitment study

We conducted a recruitment study during the summer of 2007, at 20 sites from New Bedford, Massachusetts (41.595°N, −70.911°W) to Machias, Maine (44.628°N, −67.385°W) (Fig. 2). At each site, we deployed 5 collectors in the intertidal zone approximately 0.5 m below the mean lower low water line. For each collector, we used a 20 cm × 20 cm piece of green indoor/outdoor plastic carpeting that was approximately 2–3 cm thick. The carpeting is widely available, imitates macroalgae, and acts as a standardized settlement collector for larvae of decapod species (Amaral and Paula 2007). We used cable ties to attach the piece of carpeting to a 40.64 cm × 20.32 cm × 5.08 cm red brick, which acted as an anchor. The collectors were deployed in an interspersed order, rather than north to south across the study range to avoid confounding latitudinal changes with order effects. After approximately 30 days, we retrieved the collectors in the same random order in which they were deployed. The samples were soaked and rinsed with freshwater, which was then filtered to collect the larvae from the carpeting (van Montfrans et al. 1990). Then, the material was put into a Petri dish for examination under a dissecting microscope to identify the larvae of all decapod species. The specimens were classified into two groups, non-native and native species. Non-native species were identified to the species level using descriptions and figures in the literature (Muraoka 1971; Hebling 1982; Williams 1984; Hwang et al. 1993; Behrens Yamada 2001; Johnson and Allen 2005; Kornienko et al. 2008; Lee and Ko 2008). This process was repeated for a second set of 5 collectors deployed at 18 of the 20 original study sites from mid-July to mid-August.

Oceanographic model

We used a 3-D vector field of currents through time generated by a hydrodynamic model developed by Hannah et al. (2001). The domain of the model is from the outer tip of Cape Cod, Massachusetts, USA to the eastern tip of Cape Breton Island, Nova Scotia, Canada (Fig. 3). This model uses circulation derived from the tides, the seasonal mean circulation, wind-driven circulation, and a surface-wind drift as a vector field for offline particle tracking (Hannah et al. 2000, 2001). The existing advection model was modified to incorporate stochasticity by including a parameterized spread term that incorporates diffusion and other factors (e.g., eddies, nearshore dynamics) not explained in the original model (Eq. 1). Diffusion is used as a surrogate for the combined effect of all unmodeled processes:

$$p = \alpha e^{-\alpha d} \tag{1}$$

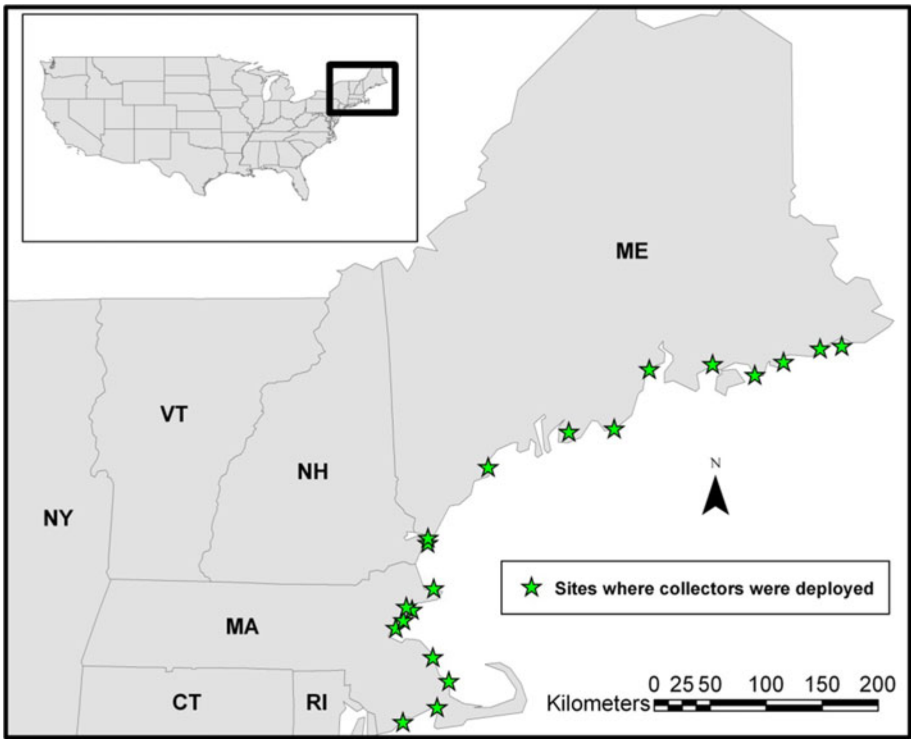

Fig. 2 The locations from New Bedford, MA to Machias, ME where settlement collectors were deployed from June to August, 2007

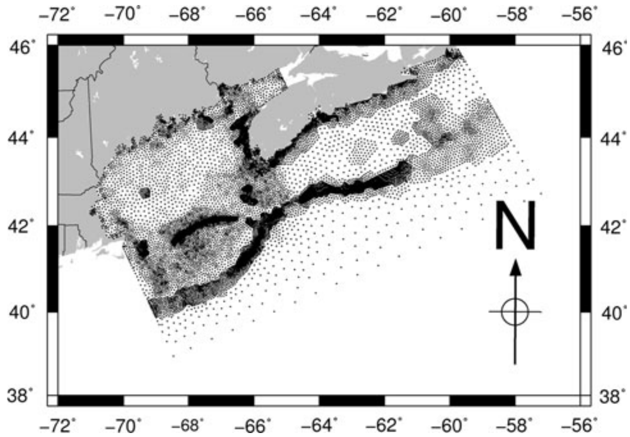

Fig. 3 The domain of the model from the outer tip of Cape Cod, Massachusetts, USA to the eastern tip of Cape Breton Island, Nova Scotia, Canada

where p is the probability of a given spread distance, d, and α is a diffusion coefficient that controls the magnitude of spread. This spread routine was executed at each time step of the model run (i.e., 15 min). The α parameter (i.e., diffusion) was fit to the observed drift card data using an algorithm that minimized the Minimum Energy Test score between the predicted (modeled) and observed (drift card recoveries) datasets (Baringhaus and Franz 2004; Aslan and Zech 2008). The stock model does not allow particles to reach the coast due to its limited resolution. To conduct our study, we built a wrapper around the model that would catch particles leaving the edge of the model and move them to the coast.

Before larval behavior was added, the stochastic model was validated using experimental drift card data to examine whether it could predict the spread of passive particles. Only 6 of the 11 drift card deployment sites were located within the domain of the model, so we used three of these sites (Deer Island, MA; Monhegan Island, ME; and Searsport, ME) to fit the diffusion coefficient (Eq. 1). We validated the oceanographic model by predicting recovery locations of drift cards deployed from the other 3 sites (Marshfield, MA; Matinicus Island, ME; and Schoodic Peninsula, ME). We binned predicted and observed data and determined the fit across a range of spatial scales, because there was no a priori rationale to select one scale over another. Specifically, we bounded the domain of analysis at each site to the minimum and maximum coastal extent of recovery points for the site and divided that distance into 3 (largest scale) to 99 bins (smallest scale) of equal size. We calculated the rank Spearman correlation coefficient for each bin size (Costanza 1989). The model predictions were evaluated against complete spatial randomness (CSR)—a classical null model for spatial analysis (Gillis et al. 2006). We plotted the cumulative distribution of the observed drift cards and predicted locations along the coast compared with CSR.

We then applied the model using recruitment data to predict biological spread. We included parameters for the average depth and amplitude of diel vertical migration for young (i.e., first 10 days), intermediate (i.e., from 10 to 20 day period), and old larvae (i.e., last 10 days), which were quantified by taking minimum and maximum values for brachyuran species as in Queiroga and Blanton (2004) (Table 1). The simulations were run for 30 days from mid-June to mid-July—approximately corresponding to the period of time the settlement collectors were left out. Then, the model was run for the mid-July to mid-August period during which the second set of collectors was deployed.

To estimate inputs of propagules into the model system, we used regional datasets of abundance. Data quantifying propagule pressure in open systems and over large spatial scales are needed to predict spread, but such datasets are rare or non-existent. Lacking more direct information, using proxies of propagule pressure may be the only way to proceed on the large spatial scales. The density of intertidal adult populations, which directly influences propagules released, is used as a surrogate of propagule pressure. For both *C. maenas* and *H. sanguineus,* the propagule pressure from a site was estimated from the abundance of adult crabs in regional surveys of the coastline from New Jersey to Maine conducted in 2005 and 2006 (Griffen and Delaney 2007; Delaney et al. 2008). For sites we monitored both in 2005 and 2006, we averaged the densities for both years. Using our adult density data, we estimated the density along the entire coast using a linear interpolation of our data. We used 52 discrete points evenly spaced along the coast, simulating propagule release based on the interpolated adult densities. We assumed no density dependence, so the number of propagules released from a site would scale linearly with the number of adults at the site. Due to computational limitations, the number of propagules was scaled:

$$f(\rho_i) = \frac{1{,}000\rho_i}{\rho_{\max}} \tag{2}$$

$$n_i = \begin{cases} \lfloor f(\rho_i) \rfloor; \; f(\rho_i) > 1 \vee f(\rho_i) = 0 \\ \quad 1; \; 0 \le f(\rho_i) \le 1 \end{cases} \tag{3}$$

where ρ_i is the density of adults at site i, $\rho_{\max}$ is the maximum density of adults across all sites, $\lfloor \rho \rfloor$ is the floor function which rounds the value of ρ to the lowest integer that is less than or equal to ρ, and n_i is the number of propagules deployed from site i. The result of Eqs. 2 and 3 is that the number of propagules deployed is an integer between 0 and 1,000 that is proportional to the

Table 1 The parameters for both *C. maenas* and *H. sanguineus*

α of *C. maenas*	α of *H. sanguineus*	AMP1 (m)	ZBAR1 (m)	AMP2 (m)	ZBAR2 (m)	AMP3 (m)	ZBAR3 (m)
0.0074	0.1641	17.5	17.5	25.0	25.0	50.0	50.0

Diffusion ("α") was fitted using the mid-June to mid-July data. The amplitude ("AMP1") and mean depth ("ZBAR1") of young larvae, the amplitude ("AMP2") and mean depth ("ZBAR2") of more developed larvae, the amplitude ("AMP3") and mean depth ("ZBAR3") of the most developed larvae were quantified using the minimum and maximum values for brachyuran crabs in Queiroga and Blanton (2004)

number of adults at the site, generating a relative measure of propagule pressure. Since the species recruit continuously during the breeding season, the modeled number of propagules was released at the start of the simulation and then every 7 days during model runs to simulate continuous release. The larvae, as well as the drift cards, could be in the ocean for varying amounts of time, both in reality and in the model, since it is a probabilistic process of reaching the coast. Then, the predicted recruitment data were recorded and compared with the actual recruitment data. Only the 18 northern recruitment study sites were within the domain of the model in the June/July dataset, so only these sites were used for parameterization. For comparison, the coast was divided into 18 bins between the midpoints of the 18 sites where the collectors were deployed. This segmented the coast based on the data (Fig. 4). The number of propagules predicted to arrive at the 18 sites was counted and divided by the coast length for that section. For the July/August data, only 16 of the sites where collectors were deployed were within the model, so the methodology was executed in an identical manner but with only 16 bins. Then, we examined whether the observed recruitment was positively correlated with the predicted recruitment. Each species was analyzed in a separate regression. The statistics and model were written and executed using FORTRAN.

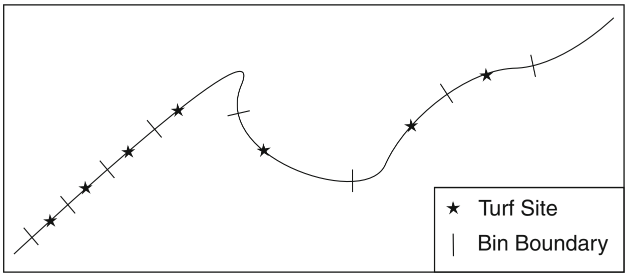

Fig. 4 A conceptual diagram to explain how the coast was divided for statistical analysis. The coastline is divided into bins (delineated by *perpendicular lines*) at the midpoint between study sites (as denoted by *stars*). The first bin boundary (as seen from *left* to *right*) is located at a distance before the first study site at a distance equivalent to half the distance from the first study site to the second study site. Similarly, the last bin is placed to the right of the last study site at a distance equivalent to half the distance from the last study site to the second to the last study site

Results

Drift card study

Of the 2,490 cards deployed, 1,005 (40.36%) were recovered and reported. The majority of the cards were found along the coast of Massachusetts, New Hampshire, and Maine (Fig. 5). The majority of drift cards were recovered in close proximity to the deployment site with a tendency to be recovered south of the deployment site (Figs. 1, 5). There was some long-distance dispersal—some cards reached locations far north of where they were deployed and some reached the Canadian coast of New Brunswick and Nova Scotia (Fig. 5). One card was detected in England and another along the coast of Norway within a year of their release.

Recruitment study

After approximately 30 days, over 90% of the settlement collectors were recovered from the June/July (97/100) and July/August (82/90) deployments. Over 80% of the sites were colonized by non-native decapods in both datasets (Tables 2, 3). The recruitment of both species generally declined with increasing latitude but to different extents. We observed that *C. maenas* recruited from the most southern site to the second most northern site, while the recruitment of *H. sanguineus* was limited to southern sites (Fig. 6). The most northern site where *H. sanguineus* was detected was Kittery, Maine in the June/July data (Table 2) and South Portland, Maine in the July/August dataset (Table 3). The most northern site, Machias, ME, was not colonized by either native or introduced decapod species. Recruitment of non-native species was higher in the June/July (4.1 recruits/collector, SE = 1.2) than July/August period (1.1 recruits/collector, SE = 0.3).

Oceanographic model

For drift cards, the stochastic oceanographic spread model consistently produced better fits to the observed data than CSR at all three sites (Figs. 7, 8). Depending on the scale, the r ranged from 0.35 to 0.82 for Marshfield, MA, 0.38–1.00 for Matinicus Island, ME, and 0.11–0.87 for Schoodic Peninsula, ME (Fig. 9). However, the model was

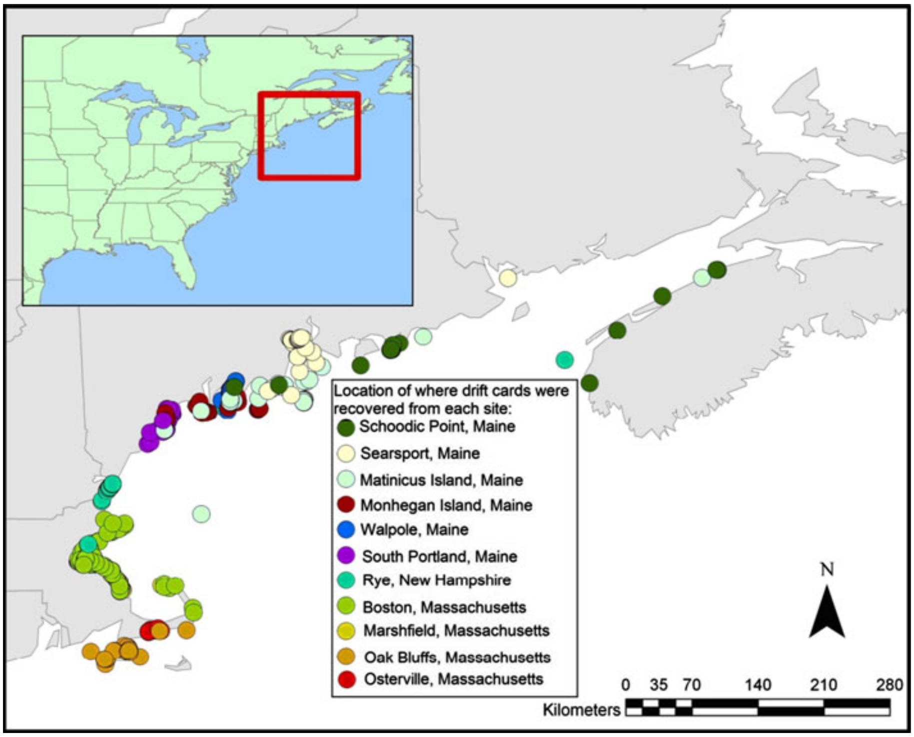

Fig. 5 The recovery locations of the drift cards, color-coded by the site where they were deployed

Table 2 Average number of *C. maenas* and *H. sanguineus* recruits per collector deployed at 20 sites from mid-June to mid-July, 2007

Latitude	Longitude	# of *C. maenas*	# of *H. sanguineus*	# of collectors recovered
41.595	−70.911	1.8	0.8	5
41.715	−70.637	9.8	3.4	5
41.927	−70.543	2.0	0.8	4
42.119	−70.672	1.8	5.0	5
42.355	−70.969	10.8	3.6	5
42.417	−70.907	3.8	0.8	5
42.500	−70.838	2.2	0.0	5
42.524	−70.884	14.2	1.0	5
42.674	−70.665	9.2	2.2	5
43.041	−70.713	0.6	0.0	5
43.081	−70.709	1.2	0.2	5
43.651	−70.227	1.3	0.0	4
43.935	−69.577	0.2	0.0	5
43.960	−69.213	0.4	0.0	5
44.394	−68.084	0.3	0.0	4
44.439	−68.932	4.8	0.0	5
44.481	−68.423	0.0	0.0	5
44.499	−67.854	0.0	0.0	5
44.607	−67.560	0.2	0.0	5
44.628	−67.385	0.0	0.0	5

not able to consistently predict the spread of *C. maenas* and *H. sanguineus*. We found that for the recruitment data of collectors retrieved in mid-July (Table 2), on which the model's diffusion parameter (Table 1) was fitted, the model prediction was significant for *H. sanguineus* ($r = 0.544$, $P = 0.020$) but was not significant for *C. maenas* ($r = 0.254$, $P = 0.309$). For validation, the model parameters generated from the June/July data (Table 2) were used to predict the July/August recruitment data (Table 3). This resulted in an r of 0.389 and −0.227 for *H. sanguineus* and

Table 3 Average number of *C. maenas* and *H. sanguineus* recruits per collector deployed at 18 sites from mid-July to mid-August, 2007

Latitude	Longitude	# of *C. maenas*	# of *H. sanguineus*	# of collectors recovered
41.595	−70.911	0.8	2.8	5
41.715	−70.637	0.4	0.8	5
42.355	−70.969	1.6	0.6	5
42.417	−70.907	0.3	0.5	4
42.500	−70.838	0.8	0.5	4
42.524	−70.884	1.0	0.3	4
42.674	−70.665	3.4	1.2	5
43.041	−70.713	0.6	0.2	5
43.081	−70.709	0.2	0.2	5
43.651	−70.227	0.5	0.3	4
43.935	−69.577	0.5	0.0	4
43.960	−69.213	0.3	0.0	4
44.394	−68.084	0.5	0.0	4
44.439	−68.932	1.4	0.0	5
44.481	−68.423	0.0	0.0	4
44.499	−67.854	0.0	0.0	5
44.607	−67.560	0.2	0.0	5
44.628	−67.385	0.0	0.0	5

C. maenas, respectively. For *H. sanguineus*, an outlier was identified and when removed resulted in an r of 0.791.

Discussion

Accurate and predictive coupled physical-biological models are important for managing both non-native and native species and their populations. For native species, this type of model can possibly forecast annual recruitment of economically important species, such as crabs, lobsters, mollusks, and fish, and also help set quotas to make a fishery sustainable (Jamieson 1993; Pauly et al. 2002). While the model could provide many benefits, we were interested in the spread of intertidal decapods and validating it on a large-scale standardized dataset. If successful, this theoretical predictive model could make monitoring feasible within real-world limitations by identifying where to optimally allocate limited sampling intensity. Yet before these models can be used for this or other purposes, models need to be tested rather than assumed to be predictive.

In this study, we conducted two studies collecting different types of data on the large-scale patterns of spread that allowed us to validate a model, determine deficiencies in its ability, and identify possible directions for future research for predicting the spread of species. Since we were not able to consistently predict recruitment data, we needed to examine whether this was due to shortcomings in incorporating physical forcings into the model. To do so, we conducted a drift card study to determine whether the model could predict the physical transport of passive particles. We found that the model cannot consistently predict the recruitment of crabs, but can predict the landing positions of drift cards. This suggests that the relatively simple and accessible model used in this study, using mean hydrography, mean winds, and tides, was adequate for predicting the spread of passive particles deployed from the intertidal zone. Therefore, inaccuracies in biological predictions were not due to limitations in the oceanographic model itself.

Our coupled biological-physical oceanographic model could predict the spread of drift cards but could not consistently predict the spread of the larvae of two non-native species. While the model worked fairly well for *H. sanguineus*, it failed to predict the spread of *C. maenas*. This disparity could be explained by differences in morphology, behaviors, and/or larval ecology between the two different species. Most of our understanding of maturation and larval behaviors has been from studies conducted in laboratories and may not accurately represent natural behavior (Byers and Pringle 2006). Several other biological processes have been shown to affect post-settlement processes and patterns of recruitment (Eggleston and Armstrong 1995; Scheibling and Robinson 2008). These processes include competition, predation, and even cannibalism (Lohrer and Whitlatch 2002). Cannibalism occurs for both species, but is far more prevalent for *C. maenas* than *H. sanguineus* (Griffen and Byers 2009) and has been shown to regulate populations (Moksnes 2004). This could explain the lower than predicted larval density of *C. maenas* in northern locations, which have higher adult densities, compared with southern sites, which have low adult densities and the highest levels of observed recruitment. Both of these species have been

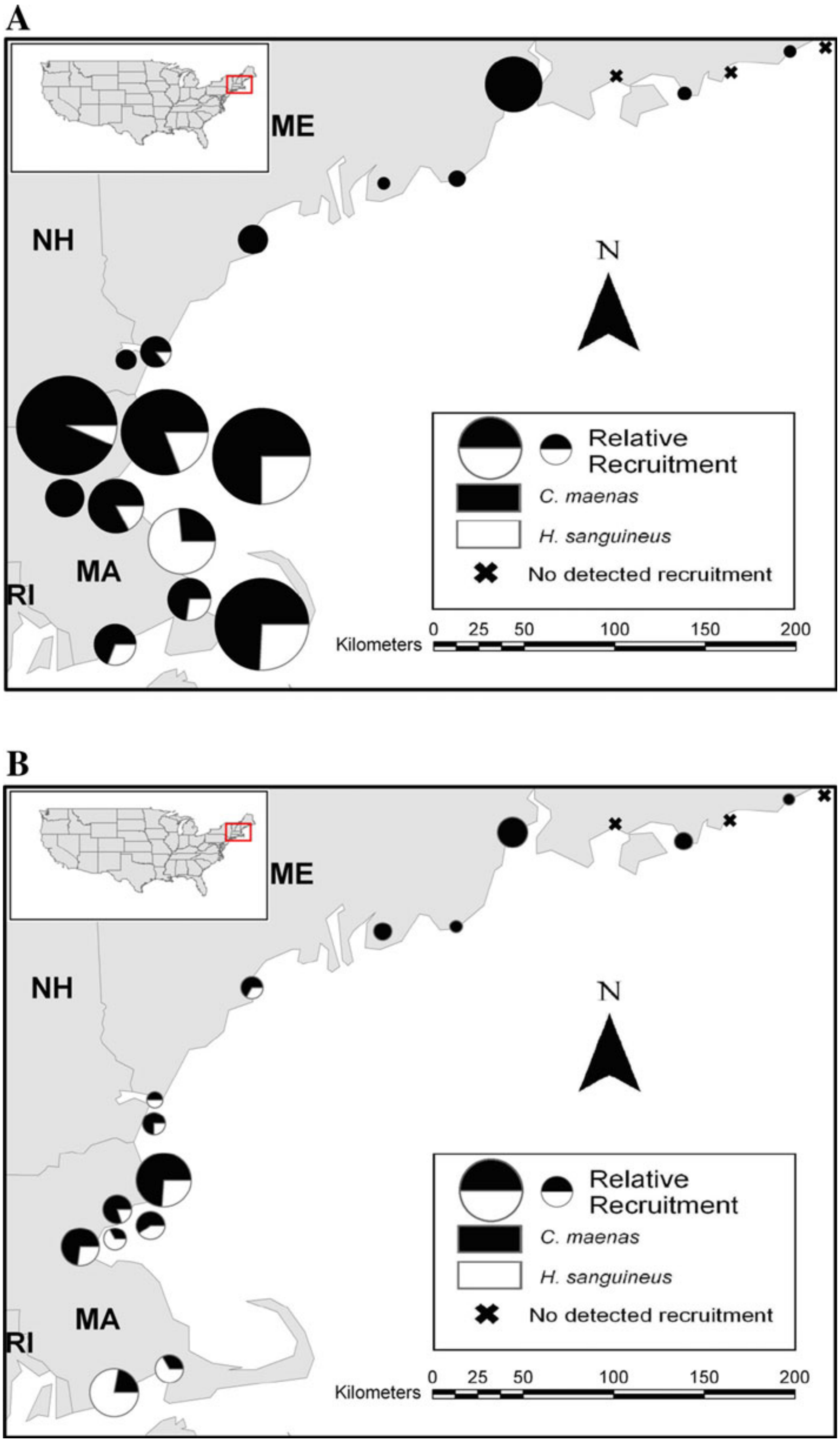

Fig. 6 The relative recruitment of invasive decapods to 20 sites from New Bedford, MA to Machias, ME. The size of the pie chart is proportional to the amount of recruitment by introduced species. The proportion of the larvae of *C. maenas* and *H. sanguineus* is displayed in *black* and *white* pie portions, respectively. **a** Collectors deployed from mid-June to mid-July during the 2007 breeding season. **b** Collectors deployed from mid-July to mid-August during the 2007 breeding season

observed in the subtidal zone, but we were only able to model intertidal densities. If subtidal populations are a substantial source of propagules, this may explain discrepancies we found in biological predictions. *Carcinus maenas* more commonly inhabits the subtidal than *H. sanguineus* (D. Delaney, pers. obs.). Populations of *C. maenas*, including large, reproductively mature individuals are still found throughout southern New England. This

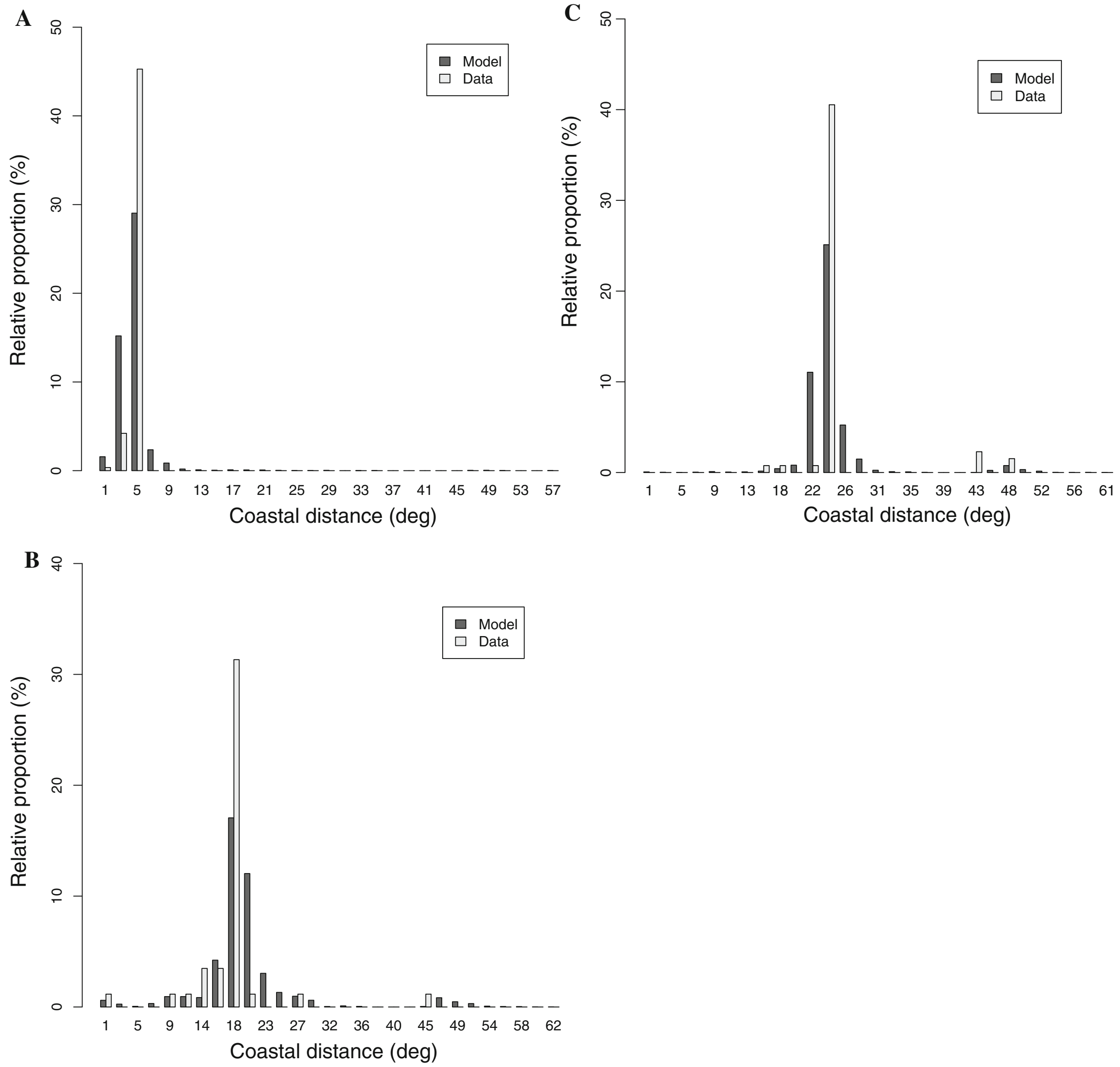

Fig. 7 A probability density function of the actual recovery locations of drift cards ("Data") and the model's predicted locations of drift cards ("Model"). The diffusion coefficient of the model was estimated by fitting all drift cards released from 3 sites (Deer Island, MA; Monhegan Island, ME; and Searsport, ME). Then, the estimated diffusion coefficient was used to predict recovery locations of drift cards deployed from the 3 validation sites (Marshfield, MA; Matinicus Island, ME; Schoodic Peninsula, ME). The coastline was discretized to quantify the data into 30 bins of equal size. For each bin, the percent of the cards found within was quantified as the "Relative proportion". We plotted this data separately for each of the three validation sites. **a** Marshfield, MA. **b** Matinicus Island, ME. **c** Schoodic Peninsula, ME. The coastline was divided up into approximately 111-km-long segments (i.e., 1 degree of coastal distance)

unsampled population could be a possible explanation for why the model predicts the spread of *H. sanguineus* better than the spread of *C. maenas.* We recommend that future studies sample both the intertidal and subtidal habitat for the density of these non-native species. When examining whether we can predict the spread for the July/August period, we used the fitted diffusion parameter (i.e., α) from the June/July dataset. If diffusion varies between months, this could explain the model's poor fits for July/August. Gallego (2011) found that predictive abilities of a similar model were particular sensitive to changes in horizontal diffusion. Deviations from predicted patterns may have strong abiotic influence that was not modeled. This could have great implications, especially for those species inhabiting areas on the edge of their physiological tolerances and distribution (Byers and Pringle 2006). For both species, we found an inverse relationship between their recruitment and latitude. This could be due to declining water temperature with latitude that is known to increase the duration of time that the organism spends as planktonic larvae (Dawirs 1985) and that increased time in plankton decreases the probability of larvae spreading and retaining upstream (Byers and Pringle 2006). This could explain greater observed recruitment at southern sites compared

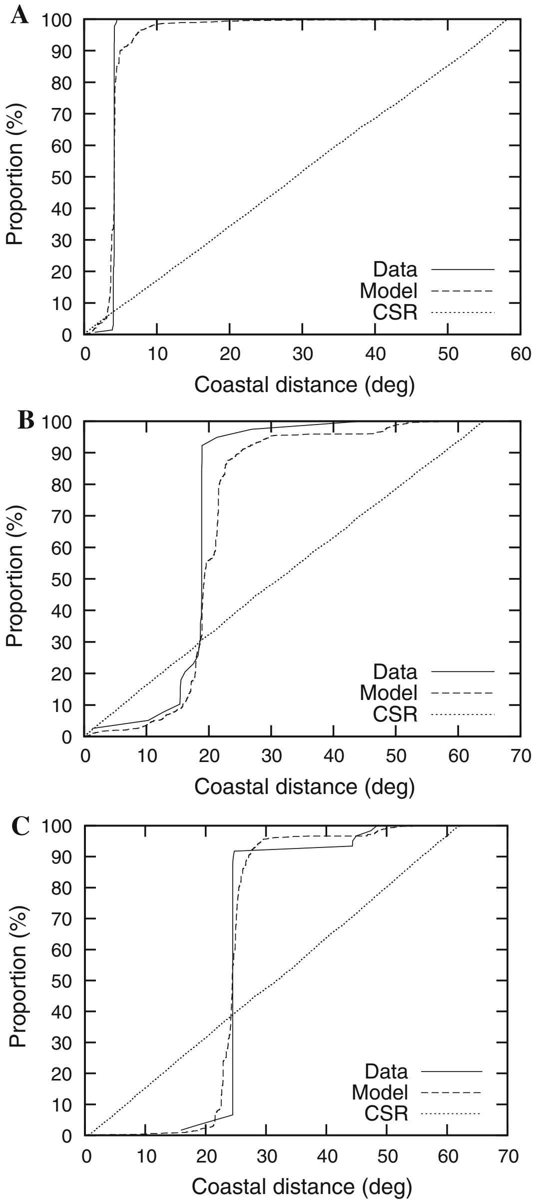

Fig. 8 The cumulative, proportional distribution of drift cards ("Data"), the predicted recovery locations ("Model"), and the null model ("CSR") along the coast line at three deployment sites. **a** Marshfield, MA. **b** Matinicus Island, ME. **c** Schoodic Peninsula, ME

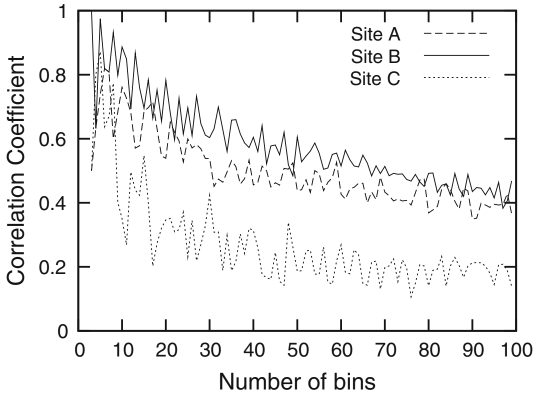

Fig. 9 The multi-scale rank Spearman correlation coefficient between the observed recovery locations for the drift cards and the locations predicted by the model for the three validation sites: *Site A* Marshfield, MA. *Site B* Matinicus Island, ME. *Site C* Schoodic Peninsula, ME. Correlations were done with various sizes from 3 to 99 equal size bins

with northern sites, which have colder water temperatures, a prolonged duration of larvae in the water column, and a later peak time of settlement (Berrill 1982; Behrens Yamada 2001). Alternatively, this could be due to much larger larval supply for *H. sanguineus* in the southern end of the model domain and/or it could simply be that southern sites are downstream from sites with high density of adult *C. maenas* and waters rich with their propagules are driven southward by the cold Labrador Current from the north.

To better be able to predict the spread of the larvae of intertidal species, we recommend several future research directions, in addition to consideration of competition and predation discussed above. Since larval behavior can have a profound effect on the spread of larvae, we recommend a migration away from research that treats them as passive particles (Metaxas and Saunders 2009 and references therein). Instead, research should focus on behavior and settlement cues, informed by studies conducted under natural conditions (Steinberg et al. 2008; Anderson and Epifanio 2010). By collecting and incorporating this type of data into the models should increase their predictive abilities. Further, the temperature of the water may not only affect the density of adults (and therefore propagule pressure) but could also modify the larval behavior of a species. For example, in regions with a sharp thermocline, the larvae may reduce the amplitude of their DVM at cold depths which could impact their overall transport. Since temperature can vary by region, larval behaviors may not be consistent for a species among disparate regions.

Second, dynamics may vary spatially as well as temporally, and thus, we recommend that recruitment studies be replicated over multiple years (subject to resource constraints), to quantify inter-annual variability. In this paper, we have used flow fields derived from climatological averages. Long-term climatological prediction is challenging so for the moment average climatologies are a practical way to proceed. Future work may better incorporate inter-annual variation. Regardless, our analysis is sufficient to indicate that the model failed to capture biological spread of one species (*C. maenas*, but not *H. sanguineus*) in the 1 year we examined; hence, at the very least, it will not be consistently predictive, and thus, caution is warranted. In comparison, it did not fail to predict drift cards as one might expect if inter-annual variability was highly dominating. Finally, the drift card and larval study were done in the same year. Thus, inter-annual variability could not account for the discrepancy between results. Still, it is possible that the drift cards were deployed in a year where flow patterns closely matched average flows and that results would not be as good in climatologically unusual years. Nevertheless, the most parsimonious interpretation of the available information is that the difference between the ability to fit biological entities and drift cards is limited by our knowledge of the biology. However, we recognize that our interpretation may be overturned as more information is collected, and therefore, we recommend additional data collection and replication of our studies. Additionally these replicated studies will reduce the chance of false negative, or Type II error. While we cannot rule out Type II error, in our study, there is no evidence that our model can predict *C. maenas*.

Third, we recommend conducting a full sensitivity analysis of our model. While conceptually this is desirable, operationally it goes beyond the scope of this project for the following reasons. First, given the complexity of oceanographic models, each single simulation takes significant computational time to run. Even fitting and analyzing the dispersal parameter took substantial time. Second, and more importantly, it is not just the parameter values that need to be considered, but also the structure of the biological model, for which little data currently exist.

Fourth, while we have built the simplest, most parsimonious biological submodel given the available information, we believe that substantially more work will need to be done to determine how each component interacts and how they vary across space and time. Our results suggest that further refining a physical model in isolation may not improve spread predictions; modelers interested in predicting the spread of planktonically dispersed species, such as the intertidal invasive species we examined in this study, need to shift their current focus to refining the biological component of biophysical models and collecting the biological datasets needed to parameterize and validate these models. Importantly, our work does not negate the relevance of refining physical oceanographic models in general, which remains important for many reasons beyond invasive species. Indeed, better physical oceanographic models may capture non-biological propagules with even greater accuracy. However, for the purpose of predicting spread of intertidal biological organisms, the main limitation appears to be in the biological component, given the difference in fit between drift cards and larvae. North et al. (2008) found the dispersal distance or transport success was due to differences in swimming behavior between the species, rather than environmental variability. So, even subtle differences in behavior can have large consequences for the survival chance of the organisms and modeled results (Vikebø et al. 2007; North et al. 2008; Peck and Hufnagl in press). Therefore, much work remains but our study helps us understand where to focus our future efforts and that is on collecting data on larval behaviors, life history characteristics, and on developing more advanced biological components of biophysical models.

In summary, we conducted two studies collecting different types of data on the large-scale patterns of spread that allowed us to validate a model, determine gaps in its ability, and identify directions for future research in predicting the spread of species. We found that we could predict the spread of passively transported particles (drift cards) but we could not predict the recruitment of active larvae for at least one species. These biological shortcomings seem not to be due to the physical model, given the predictive ability of drift card data. Thus, until biologists have quantified and better understand larval ecology in natural settings, we expect difficulty in predicting the spread of marine species. Until then, however, these relatively simple oceanographic models can be used to predict passive particles such as marine debris (Barnes 2002), oil spills (Crawford et al. 1996), or seeds from native and non-native plants (Ayres et al. 2004; Highsmith 1985). Our findings also highlight the importance of validating physical models with recruitment data. As we demonstrate, despite the appeal and logic of using oceanographic models, one should not presume that they will accurately predict biological patterns.

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