Potential connectivity among American lobster fisheries as a result of larval drift across the species' range in eastern North America

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ABSTRACT

We used a bio-physical model to estimate for the first time the effect of larval drift on potential connectivity among American lobster (*Homarus americanus*) fisheries management areas over the geographic range of the species. The model predicted drift of larvae over distances of 50-805 km (mean = 129 km), which connected many management areas and caused marked spatial heterogeneity in retention and self-seeding versus import and export of larvae by different fisheries areas. Including mortality functions in the model resulted in less drift and settlement, and had complex effects on the amount, but not on the incidence, of connectivity among fisheries. The model's predictions received support from comparison of predicted settlement to landings six or seven years later in some (but not all) parts of the model domain, although improvements are needed to capture spatial variability in larval release and drift across the species' range. This information is important to lobster fisheries management, as the amount and direction of connectivity between fisheries can inform cooperative management strategies to sustain interconnected fisheries.

Key words: American lobster, larval dispersal, potential connectivity, fisheries management areas, bio-physical modeling.

Introduction

Life cycles of many marine species consist of benthic adults and planktonic larvae. In such species ocean circulation can cause larvae to be dispersed very far (e.g., 100s or 1 000s of km) from their place of origin (Kough et al. 2013; Reisser et al. 2014). This may limit the ability of populations to self-recruit and result in connectivity (i.e., exchange of individuals and genes) among populations via larval exchange (Cowen et al. 2000). The extent to which benthic populations self-recruit or depend on larval supply from other areas influences their growth rate and persistence (Cowen and Sponaugle 2009). The amount of connectivity also determines whether such units represent separate, independent populations or are instead interdependent components of a larger population structure (Dadswell, 1979; Yakubu and Fogarty 2006).

The American lobster, *Homarus americanus*, supports the most important fishery in terms of landed value in Atlantic Canada (DFO 2016) and eastern North America (Wahle et al. 2004). The lobster's range spans the Atlantic Shelf of North America from Cape Hatteras, North Carolina (35.25˚N latitude), to Labrador (51.73˚N) (Lawton and Lavalli 1995), although all major fisheries and areas of significant lobster abundance are located north of Cape Cod, Massachusetts (38.6°N) (Pezzack 1992; Fogarty 1995). Lobster fisheries are divided into management areas (hereafter MAs) called Lobster Fishing Areas (LFAs) in Atlantic Canada and with different names in different parts of the United States, such as Lobster Management Zones (LMZs) in the state of Maine. Each lobster MA has its own regulations, which aim to ensure a sufficient proportion of adult lobsters survive fishing long enough to reproduce and maintain the species' stocks. This form of management is complicated by the fact that the American lobster has a life cycle comprising benthic adults and larvae that inhabit the water column (Factor 1995).

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After hatching, lobster larvae develop through four stages (I, II, III, and IV) that drift in surface waters (Factor 1995). These larval stages are not particularly strong swimmers (Factor, 1995; Stanley et al. 2016), so they likely disperse passively with currents, although swimming ability of stage IV is higher (Cobb et al. 1989a; Stanley et al. 2016) and may impact dispersal and connectivity (Katz et al. 1994). Settlement occurs about halfway through stage IV, once suitable substrate is found, at which point the benthic phase begins (Botero and Atema 1982; Cobb et al. 1989a, b). As the larval phase can last 24-110 days or more (MacKenzie 1988), there is much potential for lobsters in different areas to be connected via larval drift and represent components of larger interconnected stocks or populations. Indeed, work by Miller (1997) along the coast of southern Nova Scotia (NS) suggested that recruitment to adult lobster populations may be influenced more by supply of larvae from other areas than by local larval production. Cooperative efforts and co-construction of regulations by lobster fishers working in areas that are strongly connected by larval supply may thus be important to management of the fishery.

Because of the importance of the lobster fishery and the potential for fisheries areas to be interconnected by larval dispersal, physical oceanographic data and computer models have been used to estimate drift and dispersal of lobster larvae. For example, winds, currents, and swimming by stage IV lobsters were demonstrated to potentially transport larvae over distances of ~150-300 km from offshore to the coast of Rhode Island (Katz et al. 1994). Similarly, physical data and models of the Gulf of Maine (GM) demonstrated potential transport of larvae between offshore banks and inshore fisheries (Harding and Trites 1988; Harding et al. 2005), as well as among inshore fisheries separated by 20 to 400 km (Incze and Naimie 2000; Xue et al. 2008). Potential connectivity among different source-sink areas was estimated in another model of the GM (Incze et al. 2010), which showed again that settling larvae in some locations could originate from many different and distant sources (up to 400 km away), although the most important contributor to potential settlement in a given area tended to be its nearest 'upstream neighbor'. Larval drift from Prince Edward Island (PEI) to Cape Breton, NS, was predicted using drift bottle and current meter data incorporated into a physical oceanographic model (Miller and Hannah 2006). A semi-Lagrangian individual-based biophysical model of the southern Gulf of St. Lawrence (SGSL) (Chassé and Miller 2010) suggested net drift of larvae from west to east in this region, and potential loss of larvae from the SGSL to the Scotian Shelf (SS), as predicted by Miller and Hannah (2006); modest changes to existing management areas in the SGSL were suggested by predictions of that model (Chassé and Miller 2010).

The above studies demonstrated that ocean currents could transport lobster larvae over large distances and result in interdependence of fishing grounds separated by tens to hundreds of kilometers. Genetic analyses by Kenchington et al. (2009) and Benestan et al. (2015) found very small, but statistically significant, genetic differences among lobsters in different parts of the species' range, which suggested high gene flow and some weak population structuring due to isolation by distance. It is therefore likely that lobsters in different MAs are non-independent 'sub-populations' linked as sources and sinks by larval exchange, forming a metapopulation-like structure (e.g., Dadswell 1979; Yakubu and Fogarty 2006). If this is true, then certain MAs may be relatively resistant to fishing pressure and other 'stressors' within their boundaries, but more vulnerable to depletion of source areas that supply them with larvae, and *vice versa* (Dadswell 1979; Yakubu and Fogarty 2006); such information is relevant to fisheries management.

Importantly, previous modeling work of larval dispersal in American lobster has mostly been done within a single basin or stretch of coastline representing a relatively small portion of the species' geographic range; the largest-scale studies thus far have covered areas of approximately 19 321 km^2 (Chassé and Miller 2010) and 110 486 km^2 (Incze et al. 2010), which represented only ~7 and 40 %, respectively, of the lobster's range (~272 770 km^2; Pezzack 1992; Lawton and Lavalli 1995). This incomplete spatial coverage is important for two main reasons. First and most obviously, it results in incomplete characterization of source-sink linkages between lobster management areas, including for MAs that were included in these studies but are connected to areas outside these studies' domain. Second, physical processes occurring outside the spatial domain of these studies are likely to influence dispersal within these domains. For example, circulation within the SGSL is strongly influenced by physical processes outside of this region exerted by the Labrador Current and St. Lawrence River (Koutitonsky and Bugden 1991) and circulation within the GM is impacted by the Gulf Stream (Xue et al. 2008; Incze et al. 2010). Therefore, a larger-scale model including such effects may reveal patterns not detected to date.

In the present study, a new large-scale biophysical model that included most of the species' range was used to calculate drift of lobster larvae from hatch to settlement and estimate potential connectivity among lobster in different geographic areas. The physical domain of this model included regions not previously modeled - the northern Gulf of St. Lawrence (NGSL), southern and western Newfoundland (NL), and the Scotian Shelf (SS) (Fig. 1, 2). It was also overall much larger (area = ~201 551 km^2, which is ~74 % of the species geographic range, and 100% of the range of high abundance [see above]) than domains used in prior studies (~7-40 % of species' range) of lobster larval drift. We used the model to predict connectivity by larval drift among lobster in different fisheries management areas, and examined these predictions in the context of lobster population dynamics and fisheries management. We also made some initial attempts at validating the model's predictions.

Materials and Methods

Physical model

We used a variant of the NEMO-OPA (Nucleus for European Modelling of the Ocean – Ocean Parallisé) ocean circulation modeling system (Madec 2008). The NEMO-OPA system was designed to simulate global circulation in deep offshore waters, but the variant we used was developed by Brickman and Drozdowski (2012a) for shallower coastal waters of Atlantic Canada and the northeastern United States. Several biophysical dispersion-retention studies have used this basic hydrodynamic model (Maps et al., 2013; Ouellet et al., 2013; Lavoie et al., 2015; Maps et al., 2015; Benestan et al. 2016) or a variant of it (Daigle et al., 2016). The model domain (longitude: 71.5°-54.9°W; latitude: 38.6°-52.0°N) spans part of the Northwest Atlantic Shelf including the Gulf of Maine (GM), Scotian Shelf (SS) and Gulf of St. Lawrence (GSL) (Fig. 1). This domain covers 74% of the American lobster's range and includes all portions of the species' distribution where lobsters are most abundant and where major fisheries are concentrated (Pezzack 1992; Fogarty 1995). The model has a spatial resolution of approximately 1/12° (~9 km x 6 km). Horizontal eddy diffusivity and viscosity coefficients are calculated using a Smagorinski (1963) scheme, with a 'no slip' condition to allow for lateral friction along the coasts. The model is three-dimensional and includes 46 vertical layers with a resolution of 6 m near the surface to resolve the surface mixed layer.

Physical data from 2005 onwards are used to force the oceanographic model, including temperature and salinity fields from the Department of Fisheries and Oceans' hydrographic climate database, as well as tides and river runoff data from Maurice Lamontagne Institute. Winds and air temperature obtained from the Canadian Meteorological Center (CMC) are used in conjunction with bulk formulas to simulate the surface of the ocean. The physical model has been validated against observed currents and temperatures, transport of experimental drifters, and results from independent models including the Global Ocean-Atmosphere Prediction and Predictability model (Brickman and Drozdowski 2012a; Lavoie et al., 2015; Daigle et al., 2016).

We ran model simulations for each of eight years (2005-2012) using only the summer months (June 1 – September 30) of each year, when lobster larvae are expected to be released and drifting in the water column (Aiken and Waddy 1986). We used the physical oceanographic model output to drive a semi-Lagrangian individual-based bio-physical model for lobster larvae based on the code developed by Chassé and Miller (2010), but with some modifications (described below). The physical model was forced with three-hourly physical inputs and we used a 5-minute time step to calculate the displacement of drifting particles. Outputs were generated by the lobster dispersal model every 12 hours of drift.

Biological inputs: larval release

Lobster catch data for specific regions have been used to estimate annual egg production, and thus to provide larval inputs, in previous modeling studies of the GM (Incze et al. 2010) and SGSL (Chassé and Miller 2010). However, catch and egg production data is currently unavailable for certain regions in the expanded model domain, particularly the NGSL and parts of NS. Furthermore, female size structure, size at maturity, size-specific fecundity, and timing of larval release all differ markedly over the large geographic domain of our model (Aiken and Waddy 1986; Miller 1997), but this information is unavailable for many of its regions. Therefore, as a first step we examined the potential effects of physical forces and larval development on spatial connectivity of lobsters without accounting for spatial variability in larval production. Connectivity estimates in the present study therefore represent ‘potential connectivity’, defined by Watson et al. (2010) as the likelihood of larval transport from source to sink areas, as opposed to 'realized connectivity', the actual amount of larval exchange among sources and sinks which combines potential connectivity with factors such as larval productivity and mortality to estimate linkages and settlement patterns (Watson et al. 2010).

We set the amount and timing of larval release to be constant throughout the model domain where adult lobsters occur. Locations of hatch (Fig. 1) were based on the historical distribution of lobsters (from 1947-1986) summarized by Pezzack (1992), with the exception that areas > 100 m depth in the Gulf of Maine were excluded because recent work (Incze et al. 2010) found low abundance of ovigerous female lobsters, and thus larval input, in these areas. Larval production in any grid cells outside of this distribution was set to zero. To ensure a large sample size of larvae on which to base calculations, we used a magnitude of larval hatch equal to some of the highest values estimated for the SGSL by Chassé and Miller (2010). In each model grid cell that fell within the aforementioned historical range, berried female abundance was assumed to be 4 000 km^{-2} (216 000 per 9 km x 6 km grid cell), egg production (assumed to be equivalent to larval hatch) was 10 000 per female, and total annual hatch was therefore 4 x 10^7 larvae km^{-2} (Chassé and Miller 2010), or 2.16 x 10^9 larvae per grid cell.

The timing of larval release was controlled using a hatching function derived by Chassé and Miller (2010) on the basis of empirical hatch values observed from all areas ('ports') in their model of the SGSL. The function was a 3rd-order polynomial that estimated the proportion (z) of total annual hatch in each cell per two-week period (x) as $z = 0.0008*x^3 – 0.0432*x^2 + 0.2484*x – 0.1251$ ($R^2 = 0.887$), with hatch beginning on 19 June (x = 0.5), peaking between 24 July (x = 3.0) and 31 July (x = 3.5), and ending on 11 September (x = 6.0). Based on this function, a cluster of larvae representing a certain proportion of the total larval hatch in each model grid cell was released every 12 hours at a depth of 1.0 m in the centre of each cell, for a total of 182 clusters released per year over a 91-day period from each cell in which hatch occurred.

Larval development and mortality

We included temperature-dependent development functions in the model to account for the fact that water temperature affects the development rate of lobster larvae (Hadley 1906; Templeman 1936; Hughes and Matthiessen 1962; Hudon and Fradette 1988). Three different functions can be found in the literature that describe this relationship: (1) equations derived from a lab study of larvae from warmer-water regions in the SGSL and GM (MacKenzie 1988), (2) field-based estimates from the GM suggesting 60 % faster development than in the previous lab study (Annis et al. 2007), and (3) lab-derived equations for larvae originating from a colder-water region in the NGSL (Quinn et al. 2013). Chassé and Miller (2010) used the equations of MacKenzie (1988) in their model of the SGSL, while Xue et al. (2008) and Incze et al. (2010) used equations based on the results of Annis et al. (2007) in their models of the GM. We performed preliminary simulations with each of these three functions in our model, which showed that drift and connectivity patterns predicted in the large-scale model were markedly impacted by which function was included; detailed results of these exercises will be published in a separate paper (see also preliminary results in Quinn 2014). Briefly, the field-based estimates of Annis et al. (2007) resulted in the most different predictions, but due to the possibility that these development estimates were based on different cohorts (see Quinn et al. 2013) we did not use this function in the present study. However, significant differences in predicted connectivity were also observed depending on whether the model used lab-derived development equations from MacKenzie (1988) versus those from Quinn et al. (2013). Given that these differences may be the result of real local adaptation, we divided the model domain into a predominantly colder-water 'northern' region and a predominantly warmer-water 'southern' region, based on large-scale trends in summer sea surface temperatures most likely to be encountered by larvae in each region (Ouellet et al. 2003; Quinn et al. 2013; Fig. 1). Larval stages were incremented using the cold-source equations from Quinn et al. (2013) for clusters released in 'northern regions' (NGSL and NL) and using warm-source equations of MacKenzie (1988) for those released from 'southern regions' (GM, SS, and SGSL) (Fig. 1, Table 1). As stage IV was not observed by Quinn et al. (2013), we estimated an equation for the duration of this stage (Table 1) from the duration of larval stage III assuming that larvae of this species spend 20.3% of the total larval phase in stage III and 50.7% in stage IV, as reported by MacKenzie (1988).

Because larval mortality can strongly limit potential connectivity by larval drift (Chassé and Miller 2010; Watson et al. 2010), we ran model simulations with and without a larval mortality function and assessed the impact of mortality on model predictions. In simulations that included mortality, we used a spatially-uniform mortality rate of 20% day^{-1}, as was done by Chassé and Miller (2010) based on a historical plankton tow time series of Scarratt (1964) for the SGSL. Spatially-uniform mortality was used in the present study because few empirical estimates exist of larval mortality across the species' range.

Larval drift and settlement

Once released, clusters of larvae were simulated to drift according to currents calculated by the physical model. Larvae were kept at a depth of 1 m during simulations, as lobster larvae tend to remain in surface waters above local thermoclines in the surface mixed layer (Hudon et al. 1986; Harding et al. 1987; Ennis 1995). A Runge-Kutta fourth-order tracking algorithm calculated the trajectories of drifting clusters. To simulate physical processes occurring at scales smaller than the model's 9 km x 6 km grid cells, a random walk algorithm (e.g., Visser 1997; Xue et al. 2008) was used. This random walk included a baseline horizontal diffusivity of 2.0 $m^2 s^{-1}$, generated a random direction and proportional (0-1) multiplier of this value with RANLUX (James 1994), and randomly moved larvae within (or occasionally between) model cells after movements were calculated based on advection due to currents.

When larvae reached stage IV, we used a settlement function similar to that used by Chassé and Miller (2010) to simulate the pelagic-benthic transition. This function assumed that larvae were competent to settle after passing through 50 % of stage IV, with the peak of larval settlement occurring 2/3 through this stage, based on laboratory observations by Cobb et al. (1989b). Whether larvae could settle in a given cell was controlled by bottom temperature to effectively prevent settlement in deep, cold offshore areas where it is not thought to occur in nature (Incze and Naimie, 2000). Chassé and Miller (2010) allowed larvae to settle only where bottom temperature was ≥ 12°C, based on low survival of larvae at temperatures < 12°C (MacKenzie 1988). However, recent work has demonstrated that larvae are capable of settling at temperatures at least as low as 10°C (Chiasson et al. 2015), and in many parts of our model domain (e.g., parts of NL) water temperature never exceeds 10°C during the period when larvae must develop and settle in nature (Ma et al. 2012; Quinn and Rochette 2015). Therefore, in the present study larvae were allowed to settle if bottom temperature was ≥ 10°C. Larvae that did not encounter waters ≥ 10°C before the end of their competence phase (end of stage IV) 'died'.

The number of larvae settling in each model grid cell was summed over the entire summer of each simulated year to quantify total larval settlement. Because the tracking algorithm stored information regarding larval positions at each one-hour time step, it was possible to determine the cell in which settling larvae had originally hatched, which allowed potential connectivity to be calculated among different source-sink areas. This also allowed distances drifted by larvae between hatch and settlement to be calculated. Data from model outputs of all eight years (2005-2012) were averaged and then used in all subsequent analyses, as was done by Chassé and Miller (2010). This was done because relative connectivity values did not vary much among years; specifically, pairwise connectivity values among management areas (see below) in one year were always strongly, positively, and significantly correlated with values in each other year ($+0.612 \leq R \leq +0.930$, $n = 2209$, all $p < 0.001$).

Potential connectivity calculations

Average annual settlement per model cell was used to calculate average potential connectivity values between pairs of source and sink areas between 2005 and 2012, for model simulations done without (0 % day^{-1}) or with (20 % day^{-1}) larval mortality. We calculated potential connectivity from two complementary perspectives. First, 'source-to-sink' connectivity was calculated as the proportion of all larvae released from each source area that settled somewhere that were predicted to drift to and settle in each sink area; the proportion of settling larvae released from a given area that settled in the same area (self-connectivity) represented larval 'retention'. Then, 'sink-from-source' connectivity was calculated as the proportion of all larvae settling in each sink area that originated from each source area; self-connectivity calculated from this perspective (i.e., proportion of settlers in an MA that hatched there) represented 'self-seeding'. It should be noted that though both retention and self-seeding were calculated on the same numerator (number of larvae remaining in the same MA), denominators differed, so these values can be quite different for the same MA. The source and sink areas used for these calculations were 47 lobster fisheries management areas (MAs) in the US and Canada, which included Canadian Lobster Fishing Areas (LFAs) 11-27, 29-38, and 40-41, Maine Lobster Management Zones (LMZs) A-G, several geographic areas in the southern GM (see Incze et al. 2010) and George's Bank (GB) (Fig. 1A, B). These MAs ranged in size from approximately 1 200 to 275 000 km^2, with an average area ± standard deviation (SD) of 23 851 ± 36 260 km^2. We also carried out analyses among smaller source-sink areas of ~equal size (~54 00 km^2), but because spatial connectivity patterns among these were not markedly different from those observed among MAs, which are of greater relevance to fisheries, results for these smaller units are not presented in this paper (but see preliminary results in Quinn 2014).

Drift distances, settlement and settlement success per MA, and effects of mortality

In addition to relative connectivity, we calculated drift distances, settlement, and settlement success of larvae and compared these between model simulations with and without larval mortality. In each year, for each simulated larva the Euclidean distance (± 1 km) from location of hatch to that of settlement was calculated. These distances were averaged across years and these averages were summarized with descriptive statistics (average ± SD, 5th and 95th percentiles, and frequency distribution in 50-km bins). The average annual (2005-2012) number of larvae potentially settling in each MA was determined based on the total number of yearly settlers in all model cells that fell within each MA (see Fig. 1B). Settlement success per each MA was similarly calculated as the total number of larvae released from all model cells within a MA that settled somewhere within the model domain divided by the total number of larvae released from that MA. To assess whether spatial patterns in settlement and settlement success per MA were functions of MA size, which varied considerably, Pearson's correlation coefficients (R, $\alpha \leq 0.05$) were calculated between MA size and both settlement per MA and settlement success.

We compared drift distances between simulations with and without larval mortality using an independent samples *t*-test with degrees of freedom (*df*) adjusted to account for unequal variances. We used paired *t*-tests to compare settlement, settlement success, export, retention, import, and self-seeding by each MA between simulations with and without mortality. Finally, we used Pearson's correlation coefficients ($\alpha \leq 0.05$) to assess the degree to which overall spatial patterns in these measures agreed or not between simulations with and without mortality.

Determining the role of each MA as a source or sink for other MAs' larvae

We further used source-to-sink and sink-from-source connectivity values to estimate the 'role' of each MA as a source or sink of larvae to or from other MAs. The role of a particular MA as a source to other MAs was calculated by summing its relative (i.e., percent) contribution to settlement (sink-from-source connectivity) in all MAs other than itself (sinks); this was analogous to the 'relative importance of source areas' reported by Chassé and Miller (2010). The role of a particular MA as a sink to other MAs was calculated by summing the proportion of each MAs' settling larvae that settled in a particular MA (source-to-sink connectivity). Each MA's self-seeding and retention values were also examined and equated, respectively, to its role as a larval source and sink to itself. If MAs were not connected as sources and sinks to each other, then the roles of all MAs would be zero; the greater the deviance from this 'null expectation', the greater the importance of connectivity to source-sink dynamics among MAs. Roles calculated from model results without and with mortality were compared using paired *t*-tests. Because MAs

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ranged markedly in size, Pearson's correlation coefficients ($\alpha \leq 0.05$) were also calculated to assess whether MA size influenced each area's role, as done for settlement data above.

Model Validation

As a first test of the model's predictive ability, we compared the supply of competent stage IV larvae to different MAs predicted by the model to fisheries landings observed in those MAs several years later, similar to Chassé and Miller (2010). We obtained fisheries landings data for Canada from the Department of Fisheries and Oceans (DFO 2016) and for the USA from the Atlantic States Marine Fisheries Commission (AMFSC 2015). We used estimates, based on the new aging technique of Kilada et al. (2013), of the relationship between age and size of lobsters across the species' range to determine when larvae predicted to settle in a given year would be expected to start recruiting to the fishery. These size-age relationships suggest that the earliest age at which lobsters attain the minimum legal size across our model domain is six years, but can be greater (up to nine years) depending on region (Davis, Kilada, and Rochette, University of New Brunswick, unpublished data). Because we could not obtain landings data for MAs in some or all regions from 2013 onward, we were only able to compare model-predicted total annual settlement per MA in 2005 to total annual landings in 2011 and 2012, and settlement in 2006 to landings in 2012 We first made these three comparisons across the entire model domain, then across the Canadian and American portions of the domain separately, and then finally within four broad geographic regions with distinct oceanographic characteristics (Brickman and Drozdowski, 2012a, b; Fig. 2): NL, the GSL (NGSL and SGSL), the SS and BF, and the GM (ME and SGM). The only American portion of the lobster's range included in our model domain was the GM, so the American and GM comparisons were equivalent; thus, a total of six trios of regional comparisons were made. For each of these, we calculated Pearson's correlation coefficients ($\alpha \leq 0.05$) between predicted settlement and reported landings when these settlers were expected to start recruiting to the fishery. This was done separately for model predictions with 0 % and 20 % day^{-1} mortality, resulting in a total of 36 comparisons.

Assessing the importance of large-scale modeling

To assess the extent to which simulating larval drift across the species' range led to patterns not captured by smaller-scale regional modeling, we created two subdivisions of our model domain mimicking the SGSL model of Chassé and Miller (2010) and the GM model of Incze et al. (2010), and then estimated i) the percentage of larvae released from each MA within these sub-domains that settled outside of the sub-domains (export) as well as ii) the percentage of larvae settling within these sub-domains that originated from outside of them (import). This was done for model outputs from simulations with (20 % day^{-1}) and without (0 %) larval mortality.

Results

Larval drift distances

Model simulations predicted that distances drifted by larvae between hatch and settlement ranged from 'zero' (actual drift ≤ 5-9 km, but settlement in the model grid cell from which the larva was released) to a maximum of 805.2 km (no mortality) or 633.2 km (20 % mortality day^{-1}) (Fig. 3A, B). In the absence of mortality, larvae drifted on average 128.8 km ± 124.5 (SD), with peak drift occurring between 50 and 100 km (Fig. 3A). Including mortality in model simulations resulted in significantly ($t_{df = 14098} = -10.180$, $p < 0.001$) shorter drift distances, averaging 108.6 ± 126.8 km and with the peak of the distribution shifting from 50-100 km to <

50 km (Fig. 3B). Similarly, 95 % of larvae drifted less than 410 km without mortality (Fig. 3A) compared to less than 375 km with mortality (Fig. 3B).

Settlement of larvae from and in each fisheries management area (MA)

Predicted annual settlement per MA averaged 85 126 ± 135 285 competent stage IV larvae without mortality and 992 ± 2 050 with mortality of 20 % day^{-1} (Fig. 4A, B). Settlement varied widely among MAs, ranging from 120 (LFA 40) to 536 502 larvae (GB) without mortality (Fig. 4A), or from 0 (LFAs 15 and 16) to 12 050 larvae (GB) with mortality (Fig. 4B). Settlement was predicted to be highest in MAs within southwestern Newfoundland (NL) (LFAs 13A-14B), the southern Gulf of St. Lawrence (SGSL) (LFAs 23-26A), and southern Gulf of Maine (SGM) (OCC and GB), and lowest along the northern GSL (NGSL) (LFAs 15-19), Scotian Shelf (SS) (LFAs 29-33), and Maine (ME) coast (LMZs A-G) (Fig. 4A, B). The percentage of larvae released from an MA that successfully settled somewhere within the model domain (i.e., settlement success) was overall low (average ± SD without mortality: $5.9*10^{-4}$ ± $7.1*10^{-4}$ %; with mortality: $15.8*10^{-6}$ ± $6.4*10^{-6}$ %), with the vast majority of particles released drifting into offshore areas too cold for settlement (Fig. 4C, D). Settlement success of released larvae also varied markedly among MAs, ranging from $2.8*10^{-6}$ (LMZ B) to $2.7*10^{-3}$ % (LFA 21) without mortality (Fig. 3C) or from $1.3*10^{-7}$ (LMZ C) to $2.4*10^{-5}$ % (LFA 25) with mortality (Fig. 4D). Highest settlement success was predicted for larvae released from MAs in western NL (LFAs 13A and 13B), the GSL (LFAs 19-26B), and SGM (MB, OCC, BIS, and GB), and lowest settlement success for larvae released along the NGSL (LFAs 15-18), SS (LFAs 30-34, and 40-41), and parts of ME (LMZs A-G) (Fig. 4C, D). There was no significant correlation between MA size and settlement per MA (no mortality: R = +0.083, p = 0.579; 20 % day^{-1} mortality: R =

+0.250, $p = 0.091$; both $n = 47$) or settlement success of larvae from each MA (no mortality: $R = -0.140$, $p = 0.347$; 20 % day^{-1} mortality: $R = -0.127$, $p = 0.395$).

There was a tendency for larvae released from MAs with high settlement to also have high settlement success (no mortality: $R = +0.491$, $p < 0.001$; 20 % day^{-1} mortality: $R = +0.416$, $p = 0.004$; both $n = 47$), although there were notable exceptions to this trend (Fig. 4A-D). For example, a high percentage of the larvae released from LFAs 12, 13A, 13B, 20A, 20B, and 21, and BIS successfully settled somewhere within the model domain, but these MAs received relatively low numbers of settlers themselves (Fig. 4A-D), while LFAs 14B and 41 and GB had very low settlement success but comparably good settlement (Fig. 4A-D).

Both settlement per MA ($t_{df = 46} = -4.320$, $p < 0.001$) and settlement success of larvae from each MA ($t_{df = 46} = -5.745$, $p < 0.001$) were significantly lower overall when mortality was included in simulations (Fig. 4A-D). However, larval mortality did not markedly affect spatial patterns of settlement, as strong correlations in settlement ($R = +0.861$, $p < 0.001$, $n = 47$) and settlement success ($R = +0.888$, $p < 0.001$, $n = 47$) were found among MAs in simulations with and without larval mortality (Fig. 4A-D).

Potential connectivity among fisheries MAs

The model predicted considerable drift of larvae among lobster MAs of eastern North America (Fig. 5-7). Estimates of source-to-sink connectivity suggest that 27.7 % (13/47 areas, without mortality) or 25.5 % (with mortality) of MAs retain the majority (≥ 50 %, up to 95 %) of their own larval production (high retention), while the remaining 72.3 or 74.5 % of MAs export the majority of their larvae to other MAs (Fig. 5A, B). Similarly, the majority of the settlement in 26.1 % (without mortality) or 47.8 % (with mortality) of MAs resulted from retention of local larval production (high self-seeding), while the remaining 73.9 or 52.2 % of MAs depended on other MA sources to supply them with the majority of their settlers (Fig. 6A, B). MAs predicted to have relatively high retention and/or self-seeding were broadly distributed throughout the species' range (e.g., LFAs 11 and 14B in NL, LFAs 15, 25, and 26A in the GSL, LFAs 27 and 34 on the Scotian Shelf, LFAs 35 and 36 in the inner Bay of Fundy (BF), and LMZ D and OCC in the Gulf of Maine (GM)), and came in a wide range of sizes (as small as LFA 14B [~7 669 km^2], and as large as LFA 41 [~235 881 km^2]; see Fig. 2B) (Fig. 5, 6).

All MAs, even those with high retention and/or self-seeding, sent and received larvae to and from at least one other MA, and sometimes as many as 6-12 others (Fig. 5, 6). Larvae were also predicted to drift among MAs in different geographic regions, including from NL to the NGSL, from the NGSL to the SGSL, from the SGSL to the SS, from the SS to the BF and GM, and between the BF and the GM (Fig. 5, 6). Direct connectivity among MAs in the GSL and GM regions was not observed, however (Fig. 5, 6). More limited larval export was also predicted from the SGSL to the northeastern SS, as well as from the Magdalen Islands (SGSL, LFA 22) and Cape Breton, NS (SS, LFA 27) to parts of NL (Fig. 5, 6). Quite a few MAs exported > 90 % of their larval production to other areas (34.8 or 39.1 % of MAs without (Fig. 5A) or with mortality (Fig. 5B), respectively) and/or received > 90 % of their settlers from other MAs (28.3 or 30.4 % of MAs without (Fig. 6A) or with mortality (Fig. 6B), respectively). Such highly-connected MAs with low retention and/or self-seeding included many in NL (LFA 11, 12, and 14A-14C), the NGSL (LFAs 15, 16, 18, 20B, and 21), the Scotian Shelf (LFAs 30, 31B, 32, and 40), the outer BF (LFAs 37 and 38), and the GM (LMZs A, B, and E (Fig. 5, 6).

Mortality effects on larval exchange

Including mortality in model simulations reduced the numbers of larvae exchanged by all connected pairs of MAs (average reduction = 97.5 ± 47.8 %, range = 0.1-99.9 %), with the number of larvae exchanged by the majority (66.7 %) of MA pairs being reduced by $\geq$ 90 % with mortality. Reductions to larval exchange did not follow a simple pattern (e.g., greater reductions for MAs located further apart than for those closer together; Fig. 5, 6, 7). Connectivity patterns predicted with and without mortality were mostly similar, but not identical (source-to-sink connectivity: $R = +0.777$, $n = 950$, $p < 0.001$; sink-from-source: $R = +0.697$, $n = 950$, $p < 0.001$) (Fig. 5, 6). In particular, including mortality in model simulations resulted in significantly greater relative contributions of local larval production to settlement in each MA (8.9 ± 27.3 % greater self-seeding: $t_{df = 46} = +2.239$, $p = 0.030$) and lower contributions of larvae from external sources (0.7 ± 0.1 % less sink-from-source connectivity among different MAs: $t_{df = 902} = -2.385$, $p = 0.017$). However, because self-seeding and retention need not be the same for a particular MA (see details of calculations in Methods), mortality did not have a significant effect on the proportion of settling larvae retained by their MA of origin (retention: $t_{df = 46} = +0.659$, $p = 0.513$) or on the proportion of larvae exported to external sinks from each MA ($t_{df = 902} = -0.317$, $p = 0.752$) (Fig. 5A vs. 5B). However, patterns differed among MAs and there were many cases in which self-connectivity actually decreased with mortality and relative connectivity to another MA(s) increased; specifically, retention increased by 0.5-89.6 % in 52.2 % of MAs but decreased by 0.03-32.9 % in the remaining 47.8 % of MAs (Fig. 5A vs. 5B) and self-seeding increased by 1.2-76.0 % in 39.1 % of MAs but decreased by 0.1-68.5 % in 60.9 % of MAs (Fig. 6A vs. 6B). This was especially noticeable for MAs along the Scotian Shelf (LFAs 27, 29-34, and 40), southern ME (LMZs C-G), and the SGM (NH, MB, OCC, and BIS), for which larvae exported to offshore MAs (LFA 41 or GB) actually represented a greater proportion of their larvae that successfully recruited to the bottom when mortality was included (Fig. 5B) than when it was not (Fig. 5BA). The majority (73.5 %) of MA pairs were connected when either 0 % or 20 % day^{-1} mortality were included in model simulations (Fig. 5, 6). A minority (26.5 %) of MA pairs that exchanged larvae without mortality were no longer connected when mortality was included (Fig. 5, 6), but these were MA pairs that had very low connectivity in general even with 0 % mortality (average source-to-sink connectivity = 2.2 ± 4.9 %, average sink-from-source connectivity = 3.1 ± 7.7 %). Therefore, incidence of connectivity among pairs of MAs (i.e., whether each pair of MAs exchanged any larvae) was nearly identical between model simulations with and without mortality (Fig. 5, 6).

Roles of MAs as sources and sinks

Most management areas had some role as both a source and a sink to other MAs, sending or receiving a certain proportion of their larvae, although many played a greater role as one than the other (Fig. 7). MAs with particularly large roles as both sources and sinks were located in the SGSL (LFAs 23-26A), SS (LFAs 27, 34, and 41) and BF (LFA 36) (Fig. 7). These MAs played roles as sinks or sources totalling 300-400 %, thereby exceeding the ability of any MA to act as a source or sink to itself by 3-4 times. However, several MAs had little role as sources or sinks to other areas, or even to themselves, including LFAs 14C (NL), 20B and 21 (NGSL), 30, 31B, 32 (SS) and 37 (BF), and LMZs B and E (ME) (Fig. 7A, B). Roles of MAs as sinks to themselves and to others did not differ between simulations with and without mortality (paired *t*-tests: $t_{46} \leq 0.811$, $p \geq 0.422$; Fig. 7A, B). A notable exception to this trend was the offshore areas previously alluded to in section 3.3 (LFA 41 and GB), the roles of which as larval sinks nearly doubled in simulations with mortality (Fig. 7B). Roles of MAs as sources to themselves significantly increased overall (paired *t*-test: $t_{46} = 2.165$, p = 0.033) and roles as sources to other MAs decreased overall (paired *t*-test: $t_{46} = - 2.199$, p = 0.036) as a result of including mortality in simulations (Fig. 7A, B). Correlations between MA size and nearly all MA roles were non-significant both without mortality (role as source to self: R = +0.105, p = 0.481; role as source to others: R = +0.146, p = 0.326; role as sink to self: R = -0.237, p = 0.108; all n = 47) and with 20 % day^{-1} mortality included in the model (role as source to self: R = +0.089, p = 0.552; role as source to others: R = +0.141, p = 0.345; role as sink to self: R = -0.270, p = 0.058). However, there were significant correlations between MA size and the roles of MAs as sinks of larvae to other MAs (no mortality: R = -0.489, p < 0.001; with 20 % day^{-1} mortality: R = -0.688, p < 0.001), meaning that larger MAs did tend to receive proportionally more larvae than smaller ones.

Model validation results

In 14 of the 36 comparisons attempted (38.9 %) involving six different spatial domains, different hatch years (2005 and 2006), landings years (2011 and 2012), and mortality estimates (0% and 20% day^{-1}), predicted settlement in different MAs was positively and significantly correlated to landings (in 2011 and/or 2012) when these settlers were expected to start recruiting to the fishery in each of these MAs (see Methods and Table 2). At the regional scale, these correlations were significant for the Scotian Shelf/Bay of Fundy system with 0 % larval mortality in the model (3/3 comparisons), and in the Gulf of St. Lawrence system with 0% and 20% day^{-1}mortality (6/6 comparisons) in the model, but they were not significant in the Gulf of Maine or in Newfoundland, with or without mortality (0/6 significant comparisons each). In Canadian waters the correlation was positive and significant in 2/3 comparisons with 20 % mortality and in 3/3 comparisons with 0% mortality in the model (3/3 comparisons). The correlation was not significant in the US (GM system) or over the full domain of the model, whether daily larval mortality in the model was 0 % or 20 % (0/6 significant comparisons each).

Importance of large-scale modeling

The large-scale model used in the present study allowed us to estimate connections between MAs inside regions modeled in previous studies (SGSL: Chassé and Miller, 2010; GM: Incze et al., 2010) and other MAs outside these regions (Tables 3, 4). Overall the SGSL exported 2.5 % (no mortality) or 3.5 % (with mortality) of its larvae that successfully settled somewhere in the model domain to other regions (NL, the NGSL, and SS) and it received 10.8 % (no mortality) or 12.1 % (with mortality) of its settlers from sources outside the region (Table 3). Different MAs within the SGSL exported 0.1-19.0 % (no mortality) or 0.3-15.6 % (with mortality) of their settling larvae and received 2.3-40.4 % (no mortality) or 5.1-42.1 % (with mortality) of their settlers from MAs outside of the SGSL domain of Chassé and Miller (2010) (Table 3). The GM exported 17.4 % (no mortality) or 35.1 % (with mortality) of its larvae overall, and received 2.9 (no mortality) or 3.0 % (with mortality) of its settlers from outside sources (Table 4). Different MAs in the GM exported 0-84.1 % (no mortality) or 0-97.3 % (with mortality) of their larvae and received 0-80.3 % (no mortality) or 0-39.0 % (with mortality) of their settlers from MAs (mainly on the SS) outside of the GM domain modeled by Incze et al. (2010) (Table 4).

Discussion

Large-scale spatial patterns of potential connectivity

In this study, we used a new modeling system covering ~74 % of the American lobster's range (100 % of the area with high lobster abundance and major fisheries) to estimate potential connectivity among lobster fisheries management areas (MAs) in eastern North America at a larger scale than has been attempted before. The model predicted considerable exchange of larvae among MAs; for instance, all MAs exchanged larvae with 1-12 others and 32.5 % (with 20 % d^{-1} mortality) or 40.6 % (no mortality) of all settling larvae settled in a different MA than that in which they hatched. These results demonstrate that current management divisions are likely not independent 'units' or 'stocks'. The extensive connectivity among MAs predicted in the present study agrees with overall low genetic differences among lobsters in localities within the GSL and GM (Kenchington et al., 2009; Benestan et al., 2015). In fact, a recent study involving the same large-scale bio-physical modeling system and over 10,000 single nucleotide polymorphisms estimated that current-mediated larval dispersal accounts for 21 % of neutral genetic structure among lobsters sampled from 19 locations across the species' range (Benestan et al., 2016). In other studies, analyses of historical fluctuations in lobster landings (Dadswell, 1979; Campbell and Mohn, 1983; Harding et al., 1983; Bo, 2016) and genetics (Kenchington et al., 2009; Benestan et al., 2015, 2016) have suggested a large-scale division of lobsters into 2 large 'stocks' (GSL versus GM stocks), the boundary of which is located approximately midway along the Scotian Shelf (i.e., ~LFA 31B, 32, or 33). Our results showed considerable connectivity within the GSL and GM, but more limited connectivity between these regions, which is consistent with this hypothesis.

MAs vary greatly in size (from ~1 200 to 275 000 km^2 in area), and hence in the number of model cells from which larvae hatched and in which they could settle, and it might be expected that larger MAs would have relatively high settlement, settlement success, and "roles" as sources or sinks compared to smaller MAs. However, this was not generally the case, as settlement, settlement success, and 3/4 types of MA roles were not significantly correlated with

MA size. Therefore, high settlement and settlement success of particular MAs reflect favourable circulation patterns and sea surface temperatures experienced by larvae in and around these MAs, rather than the size of these MAs. The one exception was the role of each MA as a sink for larvae from others, which was significantly correlated with MA size. However, this size effect appears to have been inconsistent across most MAs and was driven by a few very large MAs, such as LFA 41, which contain much more area to receive settling larvae than most others. Indeed, if LFA 41 is removed from consideration the correlations between MA size and MA role as a sink to others become non-significant (0 % mortality: R = -0.268, p = 0. 069; 20 % day^{-1} mortality: R = -0.219, p = 0.139).

Larval mortality did not generally affect whether or not MAs were connected by larval exchange. However, larval mortality did have significant, and at times complex, effects on predicted larval drift. Overall settlement and drift distances were lower with mortality than without, and many MAs showed less larval export or import with mortality, as would be expected. Interestingly, however, we found that the relative importance of certain (11/47) MAs (e.g., LFA 41 offshore of NS) to settlement of larvae from other MAs actually increased with mortality. This presumably resulted from the non-linear relation between development and mortality rates across the model domain, along with strong currents at certain locations (see Fig. 2) taking most larvae away from their place of origin and depositing them in a neighbouring MA. Given the overall reduction in drift and connectivity resulting from including mortality in model simulations, along with the emergence of some complex patterns, future work should attempt to quantify larval mortality rates in nature, including how these vary over space (Chassé and Miller 2010; Watson et al. 2010) and over time.

Comparisons to previous modeling studies

We found that most (95 %) larval exchange occurred over distances from 5-9 km up to 375-410 km, which is comparable to the 20-400 km range of distances observed in previous studies (Chassé and Miller, 2010; Incze et al., 2010). Our results agreed with the predictions of Harding et al. (2005) that larvae drift between offshore Georges Bank (GB and part of LFA 41) and Browns Bank (LFA 40) in the GM and inshore fisheries (e.g., Maine LMZs, NH, and Massachusetts). They also agree with those of Xue et al. (2008) and Incze et al. (2010) in predicting drift of larvae to the southwest along the Maine coast, including from the Bay of Fundy and southwest NS to Maine LMZs, or areas further southwest in the southern GM. Models of Xue et al. (2008) and Incze et al. (2010) predicted the greatest contributors to settlement in each MA to be its nearest neighbours, with relatively high settlement in most Maine LMZs, and results of the present study generally agree with this. Drift and connectivity patterns in the present study also agree with those documented by Chassé and Miller (2010) for the SGSL, where dominant circulation mainly connected source areas in the western SGSL to sinks in the eastern SGSL, with some infrequent east-to-west connectivity between some contiguous MAs (e.g., from LFA 26A to LFA 25).

There were, however, some notable differences between modeling results of this and earlier studies. In the GM, in particular, the larger-scale model used in this study predicted that Maine LMZs A and B receive most of their settlers from Canadian LFAs (especially LFAs 34 and 38), and there was overall more and further drift and less retention of larvae along the Maine coast, particularly for larvae released from LMZs B and E. Importantly, the model in this study used lab-derived warm-source equations of MacKenzie (1988) to increment larval development in the GM, whereas Xue et al. (2008) and Incze et al. (2010) used estimates derived by Annis et

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al. (2007) on the basis of field sampling, which provided markedly faster development than observed in any lab study to date and favoured greater larval retention. However, field estimates by Annis et al. (2007) may have been derived from different larval cohorts (see Methods and Quinn et al. 2013), which is why we did not use them in this study. A separate modeling exercise (Quinn, 2014) revealed that these field-based and lab-based development functions (see Methods) lead to differences in drift distance and connectivity comparable to those observed between these earlier studies and ours. This finding speaks to the importance of this biological component of dispersal models and the need for further research to accurately estimate these development functions, including their potential variability over space and time.

Other differences from previous studies also occurred in the relative (i.e., percent) connectivity among areas. Previous studies of the GM (Incze et al. 2010) and GSL (Chassé and Miller 2010) did not consider exchange of larvae by areas within their domains and with those outside of them, and larvae that were predicted to leave their model domain were removed from calculations. In contrast, in the present study we also included external sources and sinks of larvae from GM and SGSL areas, reducing the overall estimates of connectivity among MAs within each of these regions. For example, our model allowed quantification of larval exchange between the GM and the Scotian Shelf, input of larvae from source areas in the NGSL to sinks in the SGSL, and some export of larvae from sources in the SGSL to external sinks on the Scotian Shelf and in southern Newfoundland. In some cases during our study, MAs in previously-modeled regions were connected, sometimes strongly (mean ± SD = 13.7 ± 23.0 %, range = 0-97 %), as sources or sinks to MAs in other regions (NL, NGSL, SS, and each other). Inter-regional connectivity was maintained, and in some cases was high, even when larval mortality was included in model simulations, which reduced long-distance dispersal. These findings illustrate the importance of modeling drift at a large spatial scale to estimate stock structure and spatial connectivity patterns of lobsters within more circumscribed regions.

Our large-scale model may also have led to differences in estimates of retention, self-seeding and connectivity relative to previous smaller-scale studies due to its i) somewhat coarser spatial resolution (~5-9 km versus 4 km in Chassé and Miller 2010 and 3-5 km in Incze et al. 2010) and ii) ability to account for remote forcing, such as the influence of the St. Lawrence River on the SGSL (Koutitonsky and Bugden 1991). It is unclear how important these effects were, as we lacked the means to quantify them in the present study, which would have required use of multiple oceanographic models within a common time frame and bio-physical dispersal model.

Model validation: successes, failures and future improvements of the model

Our validation results compare favourably to those of previous modeling studies of larval dispersal in American lobster (Chassé and Miller 2010; Incze et al. 2010) or other lobster species (e.g., Kough et al. 2013), which have had poor or mixed (i.e., model validated in some locations but not others) success validating their settlement predictions. Predicted settlement per MA was not significantly correlated to time-lagged landings over the entire model domain, but it did correlate significantly with landings for some subdivisions of the domain, especially when mortality was not included in simulations (Canada overall, SS, and GSL), suggesting that the model better captures realistic physical and biological aspects of lobster larval drift in some areas than in others (NL and the GM, USA). The only region for which predictions were validated when mortality was included was the GSL, which was also the location where the 20 % day^{-1} used in this study was estimated (Scarrat 1964; Chassé and Miller 2010). This may have occurred because larval mortality in other regions is much different from this, suggesting it may be important to quantify geographic variation in larval mortality for future modeling work. The best correlations were also obtained in relatively low-retention regions (e.g., GSL) with stronger advective currents (Fig. 2) and less complex coastlines (Brickman and Drozdowski, 2012b), while regions with poorer correlations were those with more complex coastlines (e.g., GM) and perhaps greater influences of smaller-scale diffusion than advection (e.g., Largier 2003; Xue et al. 2008). Future work with a finer-resolution version of this model may better capture the effects of local bathymetry, eddy diffusion, and tidal stirring that are thought to exert greater influences on nearshore drift and circulation than larger-scale advection due to currents and winds (Largier 2003). These smaller-scale models should also work towards integrating more realistic behaviours of lobster larvae and postlarvae, which may markedly affect realized settlement and connectivity, such as i) ‘horizontal’ swimming of stage IV larvae in relation to currents, which may alter drift trajectories (Katz et al. 1994), ii) diel vertical migrations by stages I, II, and III (Harding et al. 1987; Stanley et al. 2016), which may increase retention in areas with high velocity offshore currents, such as the Gaspé region (Hill 1991; Brickman and Drozdowski 2012b; Galbraith et al. 2013), and iii) settlement decisions of stage IV lobsters in relation to substrate, which can markedly affect search behaviours and likelihood of settlement in the lab (Botero and Atema 1982) and varies markedly over the species’ range.

Some of the disagreements between model predictions and landings may be due to spatial differences in abundance of adult lobsters not accounted for in model simulations; low ‘potential connectivity’ between two areas can be associated with high ‘realized connectivity’ if larval production in the source area is particularly high, and *vice versa* (Watson et al. 2010). Several MAs in western NL were predicted to have relatively high settlement and to play relatively large roles to other MAs as larval sources or sinks. However, NL has very low lobster abundances (and presumably settlement, though this has rarely been measured in NL) compared to many other parts of the species’ range (Pezzack 1992; DFO 2016). Therefore including actual egg production data in future modeling work is expected to reduce predicted settlement and roles for MAs in NL. Conversely, abundances, catches, and settlement of lobster in the GM, especially along the ME coast, have been increasing to extremely high levels in recent years (Boudreau et al. 2014; AMFSC 2015), but the high larval release potential of such abundant lobster stocks was not accounted for in our simulations. Our model predicted that, based on physics, this region might have relatively low settlement, but if larval release was adjusted to account for high abundances and egg production, the observed disconnect between model predicted settlement and observed landings would likely decrease considerably. Thus, future work with this model should attempt to account for spatiotemporal variability in in the magnitude and timing of hatch (Harding et al. 1983; Aiken and Waddy 1986; Ennis 1995; Chassé and Miller 2010).

Whereas our model validation tests produced mixed results, these are arguably quite encouraging because of some of the improvements that can be anticipated to physical and biological components of the model (see above), but also because the data against which model predictions of settlement were validated, fisheries landings, are far-removed from settlement itself. Our model predicts supply of stage IV larvae competent to settle, so the best metric against which to compare model predictions would be abundances of newly-settled stage IV and/or juvenile lobsters (‘early benthic recruitment’ *sensu* Wahle et al. 2004; Incze et al. 2010). The American Lobster Settlement Index (Wahle et al. 2004) is the most promising source for such data, but at present this database does not have data for several regions of our model (e.g., NL and NGSL). The only data available for use across the large domain of our model are fisheries landings, which are a reasonable surrogate for lobster abundances (Boudreau et al. 2014). Landings are obviously of considerable interest to the fishery, and being able to predict spatial patterns of landings based on larval supply would be extremely useful (Wahle et al. 2004). However, using landings as endpoint in our tests means that more than just the dispersal model was being validated; poor matches are ambiguous, and could be related to i) deficiencies of our model, ii) post-settlement processes such as mortality of juvenile lobsters or movement of adults before fisheries ‘recruitment’ (Lawton and Lavalli, 1995), and/or iii) differences between spatial patterns in landings and abundances (e.g., fishing intensity, catchability). Another limitation to our use of landings for model validation is that all settlers were assumed to recruit to the fishery in the same one or two years, whereas in reality different individuals of a same cohort of settlers will recruit to the fishery over a period of several years. Interestingly, recent work has shown that comparisons between settlement quantified *in situ* and landings can yield strong correlations, but only if an appropriate and variable (i.e., with settlers growing at different rates and recruiting to the fishery at different ages) temporal lag between settlement and recruitment is used (Wahle et al. 2004; Noah Oppenheim, University of Maine, Darling, ME, Pers. Comm.).

Implications of results to lobster populations and fisheries

This study identified MAs within the lobster’s range that may be particularly important to the supply of larvae to other MAs due to their role as sources and sinks to other MAs. We also identified some MAs that may rely heavily on other MAs for their own supply of larvae. Management areas with high retention and self-seeding, and therefore low export to and import from other MAs, included some of those in the southern GM (e.g., OCC, BIS, and GB), Bay of

Fundy (LFA 35), and southwest NS (LFA 34); these lobster MAs might be relatively self-sufficient. Areas in Newfoundland, the NGSL, and SGSL had high retention, but low self-seeding, meaning they keep much of their own production but also receive many larvae from external sources; such locations might function primarily as 'sink populations', the size and stability of which would depend on external productivity (Cowen and Spounagle 2009). Some MAs, including LFAs 18 (NGSL), 29 and 41 (SS) had low retention, which implies that few local larvae were retained by them but they provided large proportions of settlers to other MAs; these MAs may thus act primarily as 'sources' to other areas. Preservation of important areas such as these could be important to maintaining lobster fisheries.

As described above, MAs that are important sources but have little role as sinks, may depend on what little larvae they produce and can retain, and as a result might be fairly small in size and temporally less stable (Dadswell 1979; Cowen and Spounagle 2009). Alternatively, lobster populations in such areas may be maintained by movement of adults (Dadswell 1979; Lawton and Lavalli 1995). Indeed, the similarity in 'potential larval connectivity' among years (this study, see Methods), despite marked inter-annual variability in lobster abundance (Boudreau et al. 2014; DFO 2016), suggests that ocean currents and temperatures alone don't control changes in 'realized connectivity' (Watson et al. 2010) in the real ocean, but rather benthic processes affecting juveniles (e.g., growth and mortality) and adults (e.g., movements and egg production) play a large role too. The integration of benthic and pelagic processes in connectivity studies represents a challenging but likely worthwhile undertaking to achieve a more holistic understanding of the population structure of lobster and other marine species with a biphasic life history.

Conclusions

The new model we used in this study, which covers most of the American lobster's range, predicted considerable connectivity by larval drift among fisheries management areas, supporting the notion that lobster in eastern North America have a large-scale population structure, or structure(s), consisting of interconnected 'subpopulations' linked by complex dynamics (Cowen et al. 2000; Yakubu and Fogarty 2006). Our results suggest that vulnerability to depletion (*sensu* Cowen and Sponaugle 2009) varies considerably among MAs, with some being largely self-sufficient (high self-seeding), and others appearing to depend primarily on external sources for larvae and recruitment. The impacts of the same conservation practices and levels of fishing mortality could therefore differ considerably among MAs, depending on their larval recruitment dynamics, and changes to the fishery in one area might impact recruitment to lobster fisheries in other areas that depend upon the former as a larval source (Ennis 1986). Such connectivity could significantly impact fisheries recruitment and sustainability, so understanding the extent to which different MAs are connected by larval drift is highly important and can inform cooperative management strategies to sustain interconnected fisheries.

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Table 1. Lab-derived equations relating development time (D, in days) of 'warm origin' and 'cold origin' larval stages I-IV to temperature (T, in °C), which we used in our bio-physical model to estimate larval dispersal. Warm-source equations for stages I-III came from MacKenzie (1988), and that for stage IV came from Incze et al. (1997; 2010), based on data in MacKenzie (1988). Cold-source equations for stages I-III came from Quinn et al. (2013), and that for stage IV was derived in this study (see description in text, and in Quinn 2014).

Stage	**Warm-source equations (MacKenzie 1988)**	**Cold-source equations (Quinn et al. 2013)**
I	$D = 851(T-0.84)^{-1.91}$	$D = 0.031T^2 – 1.525T + 22.704$
II	$D = 200(T-4.88)^{-1.47}$	$D = 0.001T^2 – 0.425T + 16.469$
III	$D = 252(T-5.30)^{-1.45}$	$D = 0.033T^2 – 1.674T + 30.219$
IV	$D = 0.358833T^2 – 14.316T + 156.895$	$D = 0.029T^2 – 2.354T + 49.368$

Table 2. Comparison between model-predicted settlement per lobster management area (MA) in 2005 and 2006 and observed fisheries landings in same MA six or more years later (see Methods for details). Values shown are Pearson's correlation coefficients (R) resulting from these comparisons, using 0% or 20 % day^{-1} mortality (values separated by a comma) in model simulations, considering different settlement-landing year combinations and different parts of the model domain: full model domain, Canada only, four geographic regions with different oceanographic characteristics (Brickman and Drozdowski 2012a, b; see also Fig. 2) (GM: Gulf of Maine; NL: Newfoundland; GSL: Gulf of St. Lawrence; SS+BF: Scotian Shelf and Bay of Fundy). The number of MAs included in each comparison is listed in parentheses. P-values for each correlation are indicated as follows: *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$; no label: $p > 0.05$ (non-significant). An 'n/a' indicates that settlement in 2006 was not compared to landings in 2011 because enough time has not elapsed for settlers to have recruited to fisheries within the intervening five years.

Region	**Settlement year**	**Landings year**	
		2011	2012
Full Domain	2005	0.147, -0.012 (43)	0.179, 0.009 (43)
	2006	n/a	0.224, -0.091 (43)
Canada	2005	0.416*, 0.278 (32)	0.444*, 0.391* (32)
	2006	n/a	0.478**, 0.369* (32)
USA (GM)	2005	-0.398, -0.352 (11)	-0.384, -0.343 (11)
	2006	n/a	-0.372, -0.363 (11)

NL	2005	-0.260, -0.104 (7)	-0.252, -0.102 (7)
	2006	n/a	-0.231, -0.072 (7)
GSL	2005	0.719**, 0.592* (13)	0.772**,0.612* (13)
	2006	n/a	0.842***, 0.612* (13)
SS+BF	2005	0.584*, 0.232 (12)	0.581*, 0.242 (12)
	2006	n/a	0.828***, 0.182 (12)

Table 3. Significance of large-scale modeling to predicting connectivity among lobster MAs within the portion of the SGSL (including LFAs 23-26B, but not LFA 22) modeled by Chassé and Miller (2010). Values shown are the percentage of larval production lost by each MA to areas outside of the SGSL (% export), and the percentage of settlement within each MA that originated from areas outside of the SGSL (% import), under model simulations involving larval mortality of 0% or 20 % day^{-1}.

	No mortality (0 % day^{-1})		**Spatially-uniform mortality (20 % day^{-1})**	
MA	% Export	% Import	% Export	% Import
LFA 23	1.066	40.353	3.540	42.116
LFA 24	11.140	19.444	14.959	31.277
LFA 25	0.105	8.571	0.324	6.837
LFA 26A	1.038	2.272	0.498	5.155
LFA 26B	18.989	2.436	15.638	5.104
SGSL Overall	2.492	10.784	3.515	12.147

Table 4. Significance of large-scale modeling to predicting connectivity among lobster MAs within the portion of the GM (including LFAs 35-38 in the BF and LFAs 34 and 40 on the SS, but not offshore areas GB or LFA 41) modeled by Incze et al. (2010). Values shown are the percentage of larval production lost by each MA to areas outside of the SGSL (% export), and the percentage of settlement within each MA that originated from areas outside of the SGSL (% import), under model simulations involving larval mortality of 0% or 20 % day^{-1}.

	No mortality (0 % day^{-1})		**Spatially-uniform mortality (20 % day^{-1})**	
MA	% Export	% Import	% Export	% Import
LFA 34	19.191	27.014	41.599	10.074
LFA 40	84.131	63.976	97.310	38.992
LFA 35	0.000	0.231	0.000	0.215
LFA 36	0.000	1.984	0.000	0.076
LFA 37	0.000	7.074	0.000	0.000
LFA 38	0.000	4.480	0.000	2.477
LMZ A	0.065	0.127	0.000	4.313
LMZ B	0.487	0.001	0.000	0.000
LMZ C	0.241	0.000	29.826	0.000
LMZ D	0.823	0.000	7.741	0.000
LMZ E	8.074	0.000	92.766	0.000
LMZ F	9.189	0.000	27.247	0.000

LMZ G	24.513	0.000	74.049	0.000
NH	15.521	0.000	52.245	0.000
MB	20.416	7.173	51.108	0.000
OCC	10.061	3.928	47.994	1.919
BIS	0.000	80.297	0.000	3.381
GM Overall	17.428	2.856	38.508	2.980

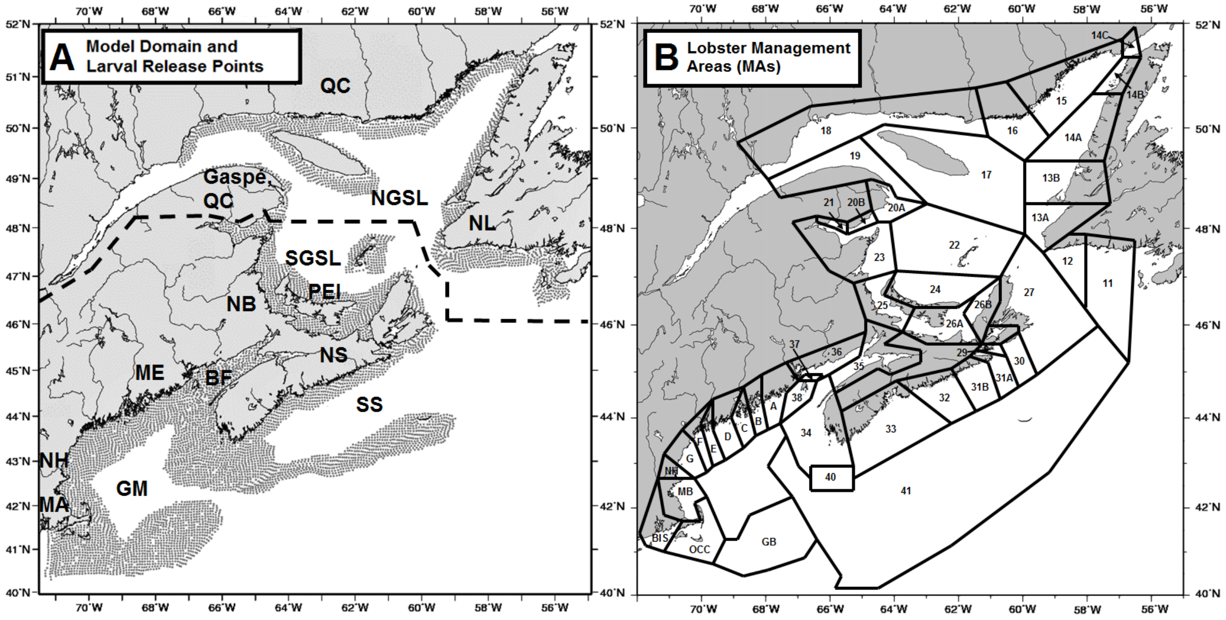

Fig. 1. Geographic domain of the large-scale oceanographic model used in this study showing (A) larval release points (dots), the division of the model into 'northern' and 'southern' domain (black dash line) where different larval development functions were used (see Methods) and regions on land (QC = Quebec, NL = Newfoundland, PEI = Prince Edward Island, NB = New Brunswick, NS = Nova Scotia, ME = Maine, NH = New Hampshire, MA = Massachusetts) and in the ocean (NGSL and SGSL = northern and southern Gulf of St. Lawrence, SS = Scotian Shelf, BF = Bay of Fundy, GM = Gulf of Maine) discussed in the text and (B) fisheries management areas (MAs) from Canada (LFAs 11-41) and the US (Maine LMZs A-G, NH = New Hampshire, MB = Massachusetts Bay, OCC = Outer Cape Cod, BIS = Block Island Sound, GB = Georges Bank) that were used as source-sink areas among which connectivity was estimated.

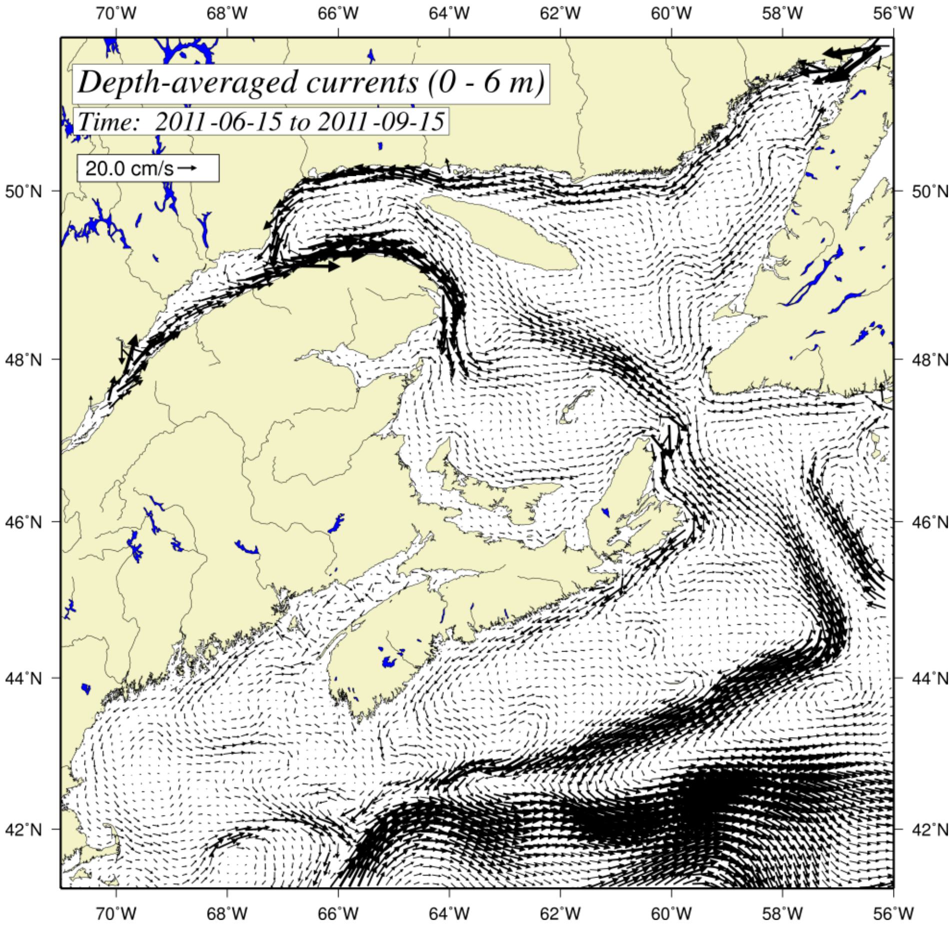

Fig. 2. Representative circulation patterns during the summer across the model domain. Mean modeled surface currents (averaged over the top 0-6 m of the water column) derived from the physical oceanographic model (Brickman and Drozdowski 2012a, b) used in this study are plotted for 15 June to 15 September 2011, which was an 'average year' in terms of settlement, dispersal, and current data (results not shown). The size of arrows plotted indicates the magnitude of mean currents per every fourth 9 km x 6 km model cell.

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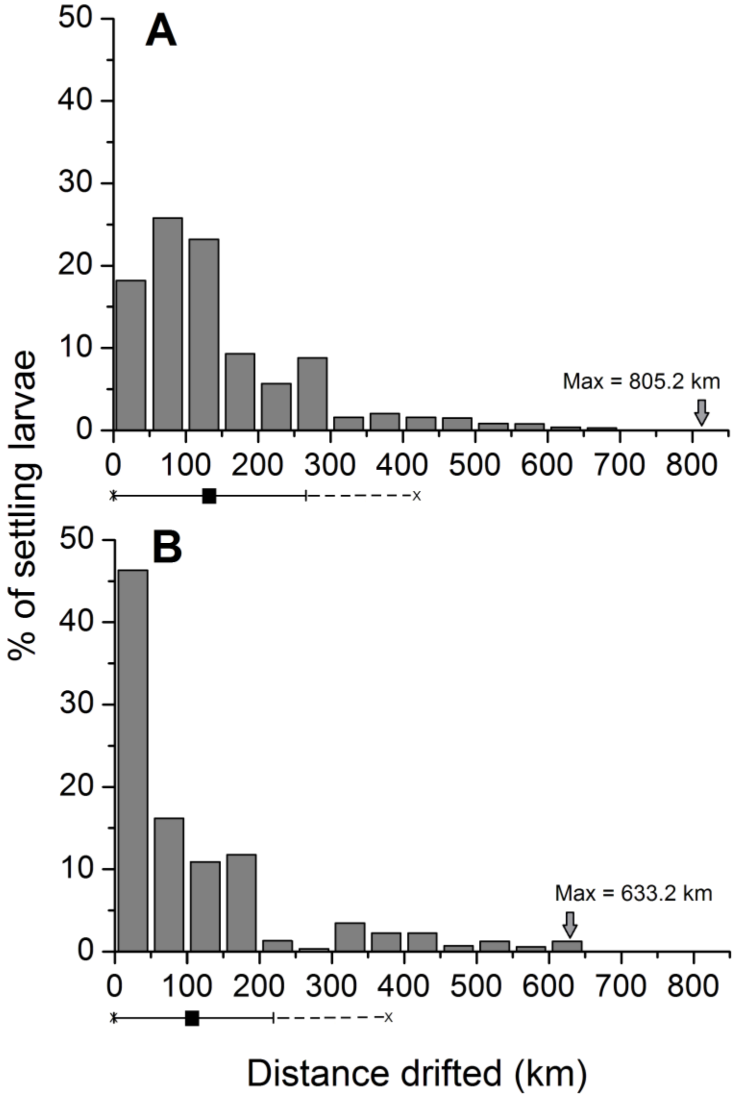

Fig. 3. Frequency distribution of distances drifted by larvae between hatch and settlement in model simulations with larval mortality of (A) 0% or (B) 20% day^{-1}. Values were calculated based on model outputs averaged across 2005-2012 (see Methods). The maximum distance drifted is indicated by an arrow. The black square and solid bars below each x-axis indicate the average distance drifted ± SD, and the 'x' symbols with dashed line show the 5th and 95th percentiles of the data.

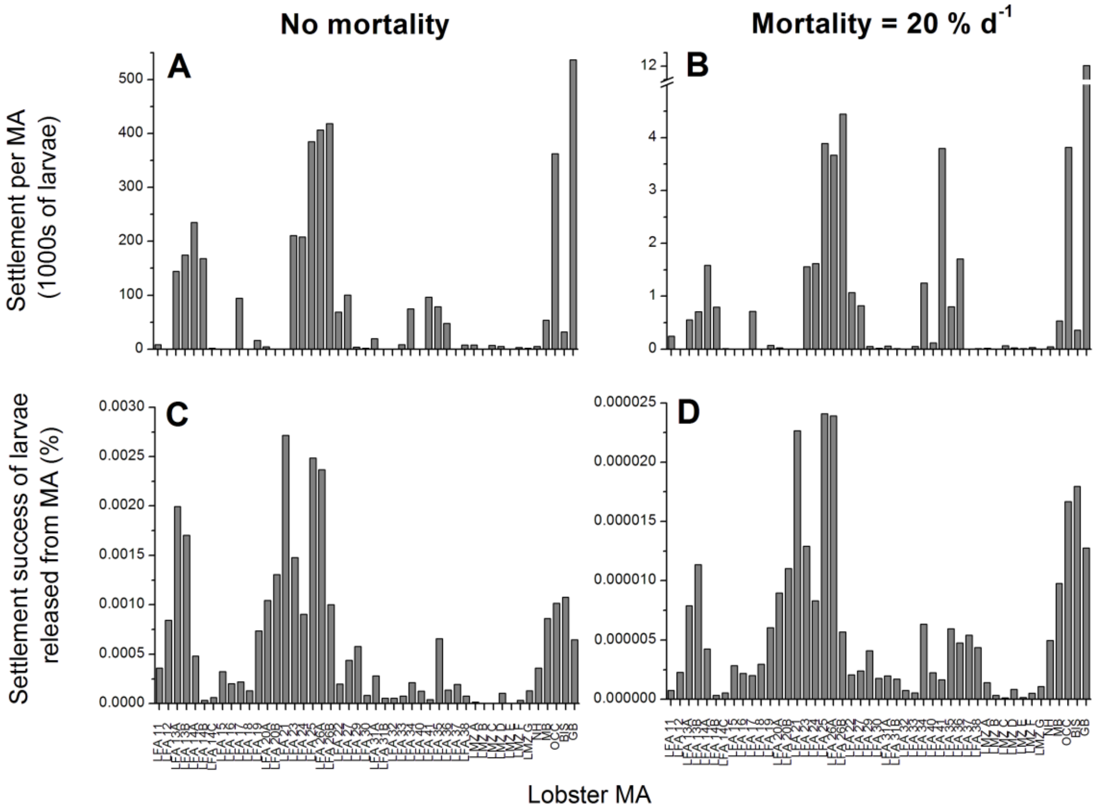

Fig. 4. Average annual settlement (A, B) within and average settlement success of larvae (C, D) from each lobster MA across all simulated years (2005-2012), assuming larval mortality of (A, C) 0% or (B, D) 20% day^{-1}. Annual settlement success was calculated as the total number of larvae released from an MA that settled somewhere within the model domain, divided by the total number of larvae released from that MA * 100 %.

Fig. 5. Matrix showing relative source-to-sink connectivity among lobster management areas (MAs) predicted by the model, based on average settlement across eight years (2005-2012) of simulations assuming (A) larval mortality of 0% or (B) 20% day^{-1}. Each cell shows the percentage of successfully settling larvae released (hatched) from a given source area (columns) predicted to settle in a given sink area (rows); darker shading indicates higher percentages, and the values in each column add to 100 %. Areas are labeled with Canadian LFA numbers, Maine (USA) LMZ letters, or other abbreviations in the southern GM (SGM, USA) (see Fig. 1B and Methods). The larger geographic regions in which MAs are located are also labeled, with abbreviations as in Fig 1A.

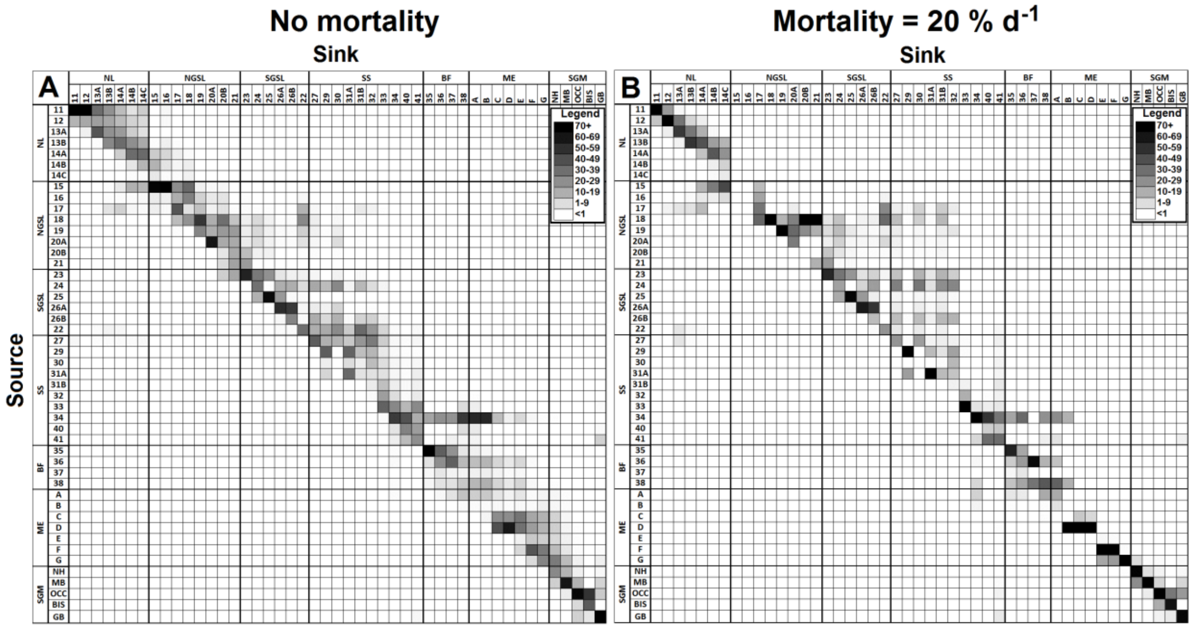

Fig. 6. Connectivity matrix showing relative sink-from-source connectivity among lobster management areas (MAs) predicted by the model, based on averaged settlement across eight years (2005-2012) of simulations that either (A) did not include larval mortality (mortality = 0 %) or (B) included 20 % day^{-1} mortality throughout the model domain. Each cell shows the percentage of larvae predicted to settle in a particular sink area (columns) that were released (hatched) from a given source area (rows); darker shading indicates higher percentages, and the values in each column add to 100 %. Labels for regions and MAs are the same as described in the caption to Fig. 5.

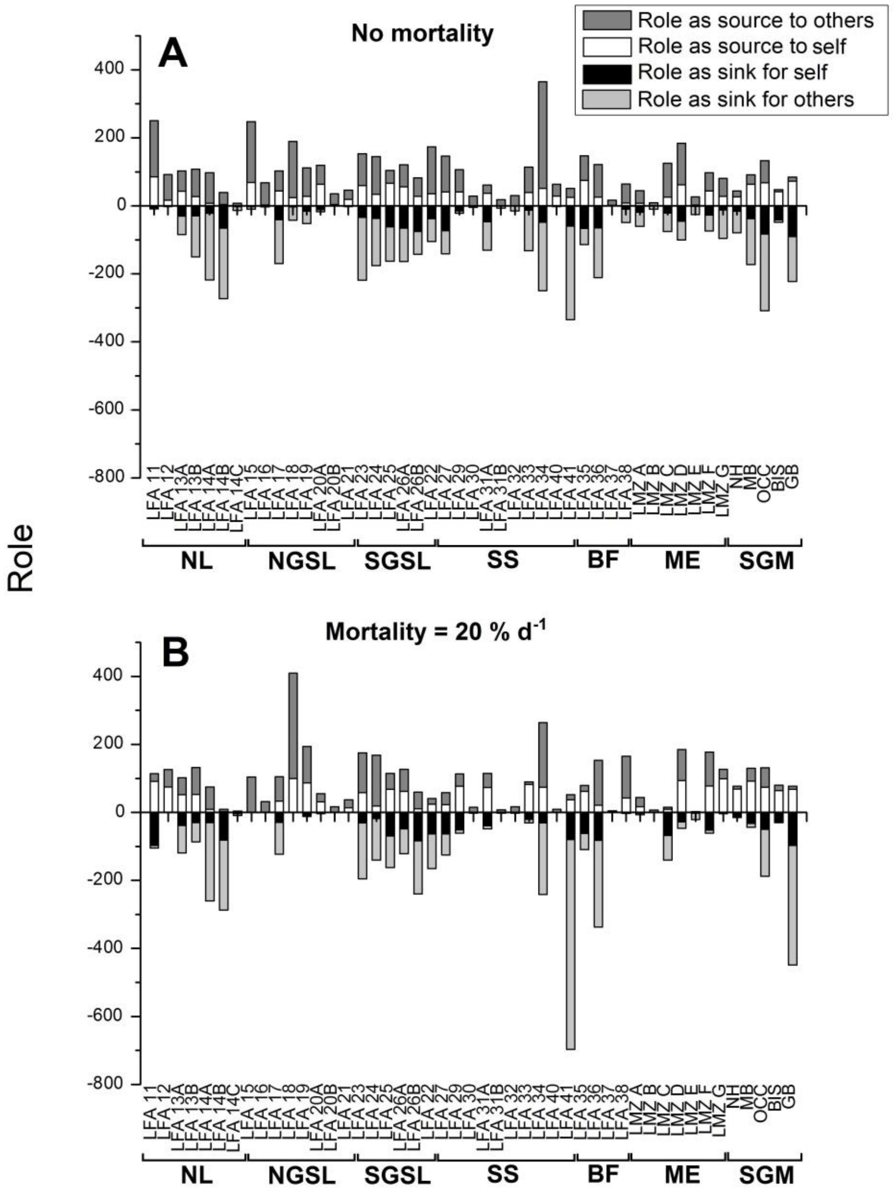

Fig. 7. ‘Role’ of each lobster management area (MA) as a source (positive values) and sink (negative values) of larvae to other MAs (dark and light gray bars) and to itself (white and black bars). Roles were calculated based on model simulations assuming (A) larval mortality of 0% and (B) 20% day^{-1}. Role as a source was assigned a positive value for clarity of plotting, and was calculated for each MA by summing the values in different columns of a particular row of the sink-from-source connectivity matrix (Fig. 6A, B). Similarly, role as a sink was given a negative

value, and was calculated by summing the values in different columns of a particular row of the source-to-sink connectivity matrix (Fig. 5A, B). The magnitude of an area's role indicates to what extent it is predicted to be connected with other areas, and the predominant direction(s) of its role indicates the nature of this interaction (e.g., prominent source, sink, both, or neither). Areas are arranged from left-to-right in the approximate order of prevailing currents and larval drift across the model domain (see Fig. 2).