

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

Brady K. Quinn*, Joël Chassé, and Rémy Rochette

B.K. Quinn: Department of Biological Sciences, University of New Brunswick, Saint John, NB, Canada E2L 4L5; bk.quinn@unb.ca.

J. Chassé: Department of Fisheries and Oceans Canada, Gulf Region, Maurice Lamontagne Institute, Mont-Joli, QC, Canada G5H 3Z4; Joel.Chasse@dfo-mpo.gc.ca

R. Rochette: Department of Biological Sciences, University of New Brunswick, Saint John, NB, Canada E2L 4L5; rochette@unb.ca.

***Corresponding author:** Brady K. Quinn, bk.quinn@unb.ca, 1-506-343-7676

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 export and import 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 the incidence, of potential 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 still needed to capture larval behaviours and spatial variability in larval release and mortality across the species' range, this information is important to lobster fisheries management because 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

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) (Pezzack 1992; Fogarty 1995; Lawton and Lavalli 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.

The pelagic larval phase of lobsters is a challenge to discrete spatial fishery management. After hatching, lobster larvae develop through four stages (I, II, III, and IV) that drift in surface waters (Factor 1995). The larval stages, especially stages I-III, are not particularly strong swimmers (Factor 1995; Stanley et al. 2016) and are usually assumed to 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 if sea bottom with suitable substrate and temperature is found, at which point the benthic phase begins (Botero and Atema 1982; Cobb et al. 1989a, b). The larval phase of lobsters can last 24-110 days or more (MacKenzie 1988), so there is much potential for larvae to drift among lobster MAs. In many other marine species with planktonic larvae, ocean circulation can cause larvae to be dispersed widely (e.g., 100s or 1 000s of km) from their place of origin (Kough et al. 2013; Reisser et al. 2014), which may limit the ability of 'populations' to self-

recruit and result in connectivity (i.e., exchange of individuals and genes) among populations (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), and determines whether they represent separate populations or are instead interdependent components of a larger population structure (Dadswell, 1979; Yakubu and Fogarty 2006). 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 weak population structuring due to isolation by distance but also gene flow among putative populations. Further, 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. Different lobster MAs may therefore be 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). 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.

Physical oceanographic data and computer models have been used to estimate dispersal of lobster larvae and resultant connectivity. For example, winds, currents, and swimming by stage IV lobsters were shown to potentially transport larvae over distances of ~150-300 km from offshore to the coast of Rhode Island (Katz et al. 1994), and bio-physical 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 contributors to potential settlement in a given area tended to be itself and its nearest ‘upstream neighbor’. Larval drift from Prince Edward Island (PEI) to Cape Breton, NS, was predicted using drifters and current data incorporated into a physical oceanographic model (Miller and Hannah 2006). An 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 export of larvae from the SGSL to the Scotian Shelf (SS); only modest changes to management areas in the SGSL were suggested by predictions of that model (Chassé and Miller 2010).

The above studies demonstrated that ocean currents can potentially transport lobster larvae over large distances and result in interdependence of fishing grounds separated by tens to hundreds of kilometers. Importantly, previous modeling work of larval dispersal in American lobster has been done within single regions representing relatively small portions of the species’ range; the largest-scale studies conducted thus far covered about 19 321 km² (Chassé and Miller 2010) and 110 486 km² (Incze et al. 2010), representing only ~7 and 40 %, respectively, of the lobster’s range (~272 770 km²; Pezzack 1992; Lawton and Lavalli 1995). This incomplete spatial coverage is an important limitation for two main reasons. First, and most obviously, it results in incomplete characterization of source-sink linkages between lobster management areas. Second, physical processes occurring outside the spatial domain of these studies are likely to influence

dispersal within these domains (e.g., GM: Xue et al. 2008; Incze et al. 2010; SGSL: Koutitonsky and Bugden 1991). Therefore, a larger-scale model will 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 and estimate potential connectivity among lobster in different management areas. This study was conducted to address objectives identified under research theme #2 (larval dispersal) of the Canadian Fisheries Research Network's *Lobster Node* (Rochette et al., under review). 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 (~201 551 km², or ~74 % of the species geographic range and most areas of high abundance [see Fogarty 1995]) than domains used in prior studies (~7-40 % of species' range) of lobster larval drift. We used the model to estimate potential connectivity by larval drift among different fisheries management areas. We then attempted to validate model predictions and examined them in the context of lobster population dynamics and fisheries management.

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 simulates global circulation in deep offshore waters. The variant we used was developed by Brickman and Drozdowski (2012a) for use in shallower coastal waters. 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 most of the species' distribution in which lobsters are most abundant and major fisheries are concentrated (Pezzack 1992; Fogarty 1995). The model has a spatial resolution of 1/12° (~9 km x 6 km). Horizontal eddy diffusivity and viscosity coefficients are calculated using the Smagorinski (1963) scheme, with a 'no slip' condition to allow for lateral friction along the coast. 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 runoff data from Maurice Lamontagne Institute for all major rivers in the model domain. Winds and air temperature obtained from the Canadian Meteorological Center are used in conjunction with bulk formulas to force simulations of the ocean surface. 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) of June 1 – September 30, when the majority of lobster larvae are expected to be released and drifting in the water column in most regions (Aiken and Waddy 1986; Incze et al. 2010). 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 daily averaged outputs re-interpolated to 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 and larval production in previous modeling studies of the GM (Incze et al. 2010) and SGS (Chassé and Miller 2010), but these data are currently unavailable at a useful resolution for certain regions in the expanded domain of our model, such as the NGSL and parts of NS. Furthermore, female size structure, size at maturity, size-specific fecundity, and timing of larval release vary 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’, which is the actual amount of larval exchange among sources and sinks.

We set the amount and timing of larval release to be uniform throughout the model domain where adult lobsters are present. Locations of hatch (Fig. 1) were based on the geographic range of lobsters summarized by Pezzack (1992) (see also Fogarty 1995; Pinsky et al. 2013; DFO 2016), with the exception that areas deeper than 100 m in the GM were excluded due to low abundance of ovigerous female lobsters, and thus larval input, observed in these areas (Incze et al. 2010). Larval production in any grid cell 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 species' range, berried female abundance was assumed to be 4 000 km⁻² (216 000 per 9 km x 6 km grid cell), larval hatch (assumed to be equivalent to egg production; but see Tang 2016; Tang et al., under review) was 10 000 per female, and total annual hatch was therefore 4 x 10⁷ larvae km⁻² (Chassé and Miller 2010), or 2.16 x 10⁹ 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 $z = 0.0008x^3 - 0.0432x^2 + 0.2484x - 0.1251$ ($R^2 = 0.887$), 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 for each larval stage in the model to account for the fact that water temperature affects the development rate of lobster larvae (MacKenzie 1988; Ennis 1995). Three such sets of functions can be found in the literature: (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, which suggest 60 %

faster development than 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 from Annis et al. (2007) in their models of the GM. We performed preliminary simulations with each of these three sets of functions, which greatly impacted predicted drift and connectivity patterns (Quinn 2014). The field-based estimates of Annis et al. (2007) resulted in the most different predictions, but due to the possibility that these estimates were based on different cohorts (see Quinn et al. 2013) we did not use them in the present study. However, significant differences in predicted connectivity were also observed between models using lab-derived development equations from MacKenzie (1988) and Quinn et al. (2013). Given that the latter differences may be the result of local adaptation (Quinn et al. 2013), 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 reported duration of larval stage III and assuming that larvae of this species spend 20.3% of the total larval phase in stage III and 50.7% in stage IV (MacKenzie (1988)).

Because larval mortality can limit potential connectivity (Chassé and Miller 2010; Watson et al. 2010), especially when low temperatures lengthen larval development and drift

time, we ran and compared model simulations with and without a larval mortality function. 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 calculations

Once released, clusters of larvae were simulated to drift according to currents calculated by the physical model. Prior to settlement, larvae were kept at a depth of 1 m 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 was used to calculate 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, with small-scale diffusivity set to 2.0 m² s⁻¹ and random numbers obtained from the function RANLUX (James 1994). The random walk was applied to larvae within the model domain 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 prevent settlement in offshore areas (depth > 200 m) 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 $\geq 12^{\circ}\text{C}$, based on low survival of larvae at temperatures $< 12^{\circ}\text{C}$ (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 $\geq 10^{\circ}\text{C}$. Larvae that did not encounter waters $\geq 10^{\circ}\text{C}$ before the end of their competence phase (end of stage IV) ‘died’.

The tracking algorithm stored larval position data at each one-hour time step, which we used to calculate distances drifted by larvae between hatch and settlement and to determine potential connectivity among different source-sink areas. Results presented here are average values of the eight modeled larval periods (2005-2012), similarly to Chassé and Miller (2010).

Potential connectivity calculations

Average annual settlement predicted per model cell was used to calculate average potential connectivity values between pairs of source and sink areas between 2005 and 2012, for simulations done without ($0\% \text{ day}^{-1}$) or with ($20\% \text{ day}^{-1}$) larval mortality. We calculated potential connectivity from two complementary perspectives. First, ‘source-to-sink’ connectivity was calculated as the proportion of all settling larvae released from each source area predicted to settle in each sink area, with the proportion that settled in the same source area (self-connectivity) representing larval ‘retention’. Source-to-sink connectivity may alternatively have been calculated based on all larvae released from each source, not just those that settled, but due to high offshore losses and very low overall percent settlement of larvae within the model domain (see Results) these values would all be extremely low, not add up to 100% for each area,

and be difficult to interpret and discuss. Patterns of source-to-sink connectivity (i.e., export and retention) among management areas were essentially the same for both methods of calculating these values (results not shown), however, so for ease of discussion we present those values calculated based on settling larvae only. Second, we also calculated ‘sink-from-source’ connectivity as the proportion of all larvae settling in each sink area that originated from each source area, with the proportion of settlers in an area that hatched there (self-connectivity) representing ‘self-seeding’. It should be noted that though retention and self-seeding have the same numerator value (number of larvae remaining in a same area), they have different denominators, and can thus differ markedly for the same area. 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 km² (average = 23 851 km², SD = 36 260 km²).

Potential drift distances, settlement, and effects of mortality

We calculated potential drift distances and settlement of larvae in model simulations with and without larval mortality. In each year, the distance (± 1 km) from location of hatch to that of predicted settlement was calculated for each simulated larva, and the resulting values were summarized across all years with descriptive statistics. Then we estimated the average annual number of larvae potentially settling in each MA, based on the total number of yearly settlers in all model cells that fell within each MA (see Fig. 1B), as well as the average annual percentage (%) of larvae released from each MA that settled somewhere within the model domain. Because

MA range markedly in size, Pearson's correlation coefficients ($\alpha \leq 0.05$) were also calculated to assess whether MA size influenced settlement of larvae in and from each MA.

We compared potential drift distances of larvae released from each MA 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 of larvae in and from each MA, 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 importance of each MA as a potential source or sink to other MA

We calculated an index of the potential importance of a particular MA as a source to other MAs by summing its predicted relative (i.e., percent) contribution to settlement (sink-from-source connectivity) in all MAs (sinks) other than itself (as done by Chassé and Miller 2010), and an index of the potential importance of a particular MA as a sink to other MAs by summing the proportion of each MAs' settling larvae that settled in a particular MA (source-to-sink connectivity). These indices were calculated for each MA based on model simulations without and with mortality, and results of these simulations were compared using paired *t*-tests.

Model validation

As a first test of our model's predictive ability, we compared its estimated supply of competent stage IV larvae to different MAs 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 a novel aging technique (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 varies between six and nine years across our model domain (Davis, Kilada, and Rochette, University of New Brunswick, unpublished data). Because we could not obtain landings data for some MAs from 2013 onward, we were only able to compare model-predicted 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 (LFAs 11-41) and American (LMZs A-G and other geographic areas in the SGM; see Fig. 1B) portions of the domain separately, and finally within four broad geographic regions with distinct oceanographic characteristics (Brickman and Drozdowski, 2012a, b; Fig. 2): NL (LFAs 11-14C), the GSL (LFAs 15-26B), the SS and BF (LFAs 27-41), and the GM. As the GM and American domains were identical, a total of six different trios of regional comparisons were made. For each of these, we calculated Pearson's correlation coefficients ($\alpha \leq 0.05$) between predicted potential settlement and reported landings when these settlers were expected to start recruiting to the fishery. This was done separately for model predictions with 0 % day⁻¹ and 20 % day⁻¹ mortality, resulting in a total of 36 comparisons.

Assessing the effects 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). We then estimated i) the percentage of larvae released from each MA within these sub-domains predicted to settle outside of the sub-domains (export) as well as ii) the percentage of larvae settling in these sub-domains that potentially originate from outside (import). This was done for simulations with (20 % day⁻¹) and without (0 % day⁻¹) larval mortality.

Results

Potential larval drift distances

Model simulations predicted that distances drifted by larvae before settlement could range from ‘zero’ (actual drift ≤ 5 -9 km = settlement in model cell where larva hatched) to a maximum of 805.2 km (no mortality) or 633.2 km (mortality rate of 20 % day⁻¹) (Fig. 3A, B). In the absence of mortality, larvae were predicted to drift on average 128.8 km \pm 124.5 (SD), with peak drift frequency between 50 and 100 km (Fig. 3A). Including mortality in simulations resulted in significantly ($t_{df=14098} = -10.180$, $p < 0.001$) shorter predicted drift distances, averaging 108.6 \pm 126.8 km with peak frequency < 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).

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

Predicted annual settlement per MA averaged 85 126 \pm 135 285 competent stage IV larvae without mortality and 992 \pm 2 050 with mortality of 20 % day⁻¹ (Fig. 4A, B), and it varied widely among MAs, from 120 (LFA 40) to 536 502 larvae (GB) without mortality (Fig. 4A), and 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 a MA that were predicted to successfully settle somewhere within the model domain was overall very low (average \pm SD without mortality: $5.9 \times 10^{-4} \pm 7.1 \times 10^{-4}$ %; with mortality: $15.8 \times 10^{-6} \pm 6.4 \times 10^{-6}$ %), with the vast majority of particles released drifting into offshore areas too cold for settlement (Fig. 4C, D). Settlement 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) and from 1.3×10^{-7} (LMZ C) to 2.4×10^{-5} % (LFA 25) with mortality (Fig. 4D). Larvae released from MAs in western NL (LFAs 13A and 13B), the GSL (LFAs 19-26B), and SGM (MB, OCC, BIS, and GB) were predicted to have the highest percent settlement, while larvae released from MAs along the NGSL (LFAs 15-18), SS (LFAs 30-34, and 40-41), and parts of ME (LMZs A-G) had the lowest predicted percent settlement (Fig. 4C, D). There was no significant correlation between MA size and settlement in each per MA (no mortality: $R = +0.083$, $p = 0.579$; 20 % day⁻¹ mortality: $R = +0.250$, $p = 0.091$; both $n = 47$) or percent settlement of larvae released from each MA (no mortality: $R = -0.140$, $p = 0.347$; 20 % day⁻¹ mortality: $R = -0.127$, $p = 0.395$).

Potential settlement in each MA ($t_{df=46} = -4.320$, $p < 0.001$) and percent settlement of larvae from each MA ($t_{df=46} = -5.745$, $p < 0.001$) were both significantly lower when mortality was included in simulations (Fig. 4A-D), and as described above there were large differences in connectivity among particular pairs of MAs due to including mortality in model simulations. However, larval mortality did not have an overall statistically significant effect on spatial

patterns of settlement, as strong correlations in potential settlement of larvae in each MA ($R = +0.861$, $p < 0.001$, $n = 47$), as well as of larvae from each MA ($R = +0.888$, $p < 0.001$, $n = 47$), were found in simulations with and without larval mortality (Fig. 4A-D).

Potential connectivity among fisheries MAs

Source-to-sink connectivity estimates suggest that 27.7 % (13/47, without mortality) or 25.5 % (12/47, with mortality) of MAs may retain the majority (≥ 50 %, up to 95 %) of their own larval production (high retention) that eventually settle, while the remaining 72.3 or 74.5 % of MAs may 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 could result from retention of local larval production (high self-seeding), while the remaining 73.9 or 52.2 % of MAs potentially depend on other MA sources to supply them with the majority of their settlers (Fig. 5C, D). MAs predicted to have relatively high potential 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 ranged from as small as LFA 14B (~7 669 km²) to as large as LFA 41 (~235 881 km²) (Fig. 2B, 5).

All MAs, even those with high predicted retention and/or self-seeding, were predicted to send and receive larvae to and from at least one, and sometimes as many as 6-12, other MAs (Fig. 5). 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 MAs on the northeastern SS (LFAs 27-31A), from the southwestern SS (LFAs 31B-41) to the BF and GM, and between the BF and the GM (Fig. 5). Direct connectivity among MAs in the GSL and GM regions was

not predicted, however, and connectivity between the northeastern and southwestern SS was very limited (Fig. 5). 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). Many MAs were predicted to export > 90 % of their larval production to other areas (34.8 and 39.1 % of MAs without (Fig. 5A) and with mortality (Fig. 5B), respectively) and/or receive > 90 % of their settlers from other MAs (28.3 and 30.4 % of MAs without (Fig. 5C) and with mortality (Fig. 5D), respectively). MAs with low potential retention and/or self-seeding, but high connectivity to other MAs, 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).

Effect of mortality on predicted larval exchange

The majority (73.5 %) of MA pairs were potentially connected when either 0 % or 20 % day⁻¹ mortality was included in model simulations (Fig. 5). A minority (26.5 %) of MA pairs that exchanged larvae without mortality were no longer connected when mortality was included (Fig. 5), but these were MA pairs that had predicted connectivity very low and close to zero even with 0 % mortality (average source-to-sink connectivity = 2.2 ± 4.9 %, average sink-from-source connectivity = 3.1 ± 7.7 %; see Fig. 5). Including mortality in model simulations did reduce the specific numbers of larvae predicted to be 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 ≥ 90 % with mortality. Reductions to larval exchange did not follow a simple pattern, such as greater reductions for MAs located further apart than for those closer together (Fig. 5, 6). Potential 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). In particular, including mortality in model simulations resulted in significantly greater relative contributions of local larval production to potential 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, mortality did not have a significant overall effect on the proportion of settling larvae that were potentially 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 potential connectivity of MAs to themselves actually decreased with mortality; specifically, potential retention increased with mortality 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. 5C vs. 5D). 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).

Importance of MAs as potential sources and sinks

Management areas varied considerably in their potential importance as sources and/or sinks to other MAs (Fig. 6). MAs predicted to be particularly important as both sources and sinks were LFAs 23-26A located in the SGSL, LFAs 27, 34, and 41 on the SS, and LFA 36 in the BF

(Fig. 6), whereas other MAs only had marginal importance as sources or sinks to other areas, or even to themselves, including LFAs 14C in NL, LFAs 20B and 21 in the NGSL, LFAs 30, 31B, and 32 on the SS., LFA 37 in the BF, and LMZs B and E along the ME coast (Fig. 6A, B). The importance of MAs as sinks to themselves and to other MAs did not differ between simulations with and without mortality (paired t -tests: $t_{46} \leq 0.811$, $p \geq 0.422$; Fig. 6A, B). A notable exception to this trend was the offshore areas alluded to in the previous section (LFA 41 and GB), the importance of which as potential larval sinks nearly doubled in simulations with mortality (Fig. 6B). The potential importance of MAs as sources to themselves significantly increased overall (paired t -test: $t_{46} = 2.165$, $p = 0.033$), and their importance as sources to other MAs decreased overall (paired t -test: $t_{46} = -2.199$, $p = 0.036$), as a result of mortality (Fig. 6A, B).

Model validation results

In 14 of the 36 comparisons attempted (38.9 %), predicted settlement (in 2005 and/or 2006) was positively and significantly correlated to landings (in 2011 and/or 2012) when settlers were expected to start recruiting to the fishery in different MAs (see Methods and Table 2). At the regional scale, these correlations were significant for the Scotian Shelf/Bay of Fundy system with 0 % day⁻¹ larval mortality in the model, and in the Gulf of St. Lawrence system with 0 % day⁻¹ and 20 % day⁻¹ mortality in the model, but they were not significant in the Gulf of Maine or in Newfoundland, with or without mortality. In Canadian waters the correlation was positive and significant in 2/3 comparisons with 20 % mortality and in all comparisons with 0 % day⁻¹ mortality in the model. 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 % day⁻¹.

Effects of large-scale modeling

The large-scale model used in the present study allowed us to estimate potential 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 was predicted to potentially export 2.5 % (no mortality) or 3.5 % (with mortality) of its larvae that successfully settle somewhere in the model domain to other regions (NL, the NGSL, and SS) and receive 10.8 % (no mortality) or 12.1 % (with mortality) of its settlers from sources outside the region (Table 3). Different MAs within the SGSL potentially export 0.1-19.0 % (no mortality) or 0.3-15.6 % (with mortality) of their settling larvae, and receive 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 was predicted to export 17.4 % (no mortality) or 35.1 % (with mortality) of its larvae overall, and receive 2.9 (no mortality) or 3.0 % (with mortality) of its settlers from outside sources (Table 4). Different MAs in the GM potentially export 0-84.1 % (no mortality) or 0-97.3 % (with mortality) of their larvae and receive 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 (and most areas with high lobster abundances 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 the potential for considerable

exchange of larvae among MAs; for instance, all MAs were predicted to exchange larvae with 1-12 others and 32.5 % (with 20 % d⁻¹ mortality) or 40.6 % (no mortality) of all settling larvae were predicted to settle 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 potential 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 are consistent with this hypothesis, showing considerable potential connectivity within but limited connectivity between the GSL and GM.

MAs vary greatly in size (from ~1 200 to 275 000 km² 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 potential settlement or importance as sources or sinks compared to smaller MAs. However, this was not generally the case, as settlement, settlement of larvae in and from each MA was not significantly correlated with MA size and MAs strongly connected to others and with large potential importance as sources or sinks varied considerably in size. While results of such correlations are admittedly tentative

given the limited biological information (e.g., homogeneous egg production) in our simulations, they do suggest that the potential for high settlement and connectivity of certain MAs likely reflects favourable circulation patterns and sea surface temperatures for larval development in and around these MAs, rather than the size of these MAs.

A constant larval mortality rate did not generally have a statistically significant effect on whether or not MAs were potentially connected by larval exchange. However, larval mortality did have significant, and at times complex, effects on predicted larval drift. Overall predicted settlement and drift distances were lower with mortality than without, and many MAs showed less potential larval export and 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, GB in the offshore SGM) to potential settlement of larvae from other MAs actually increased with mortality. In all modeled years (2005-2012), with or without larval mortality included in simulations, the specific MAs that were more connected to offshore MAs with mortality had quite low retention and/or self-seeding and strong one-way connections to other specific MAs. This presumably resulted from strong currents at these locations (see Fig. 2) taking most larvae away from their place of origin and depositing them in neighbouring MAs, such that the self-connectivity was very unlikely and perhaps resulted mainly from dispersal back from other intermediate areas (thus representing longer drift than export to other MAs). Given the overall reduction in potential drift and connectivity resulting from including mortality in model simulations, along the complex patterns found, future work should quantify larval mortality rates in nature, including how these vary over space (Chassé and Miller 2010) and time.

Comparisons to previous modeling studies

Our model predicted that nearly all (95 %) larval exchange occurs over distances of 5-9 km to 375-410 km, which is comparable to the 20-400 km range of distances predicted in previous studies (Chassé and Miller, 2010; Incze et al., 2010). Our results agreed with the predictions of Harding et al. (2005) that larvae may 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 GM. Models of Xue et al. (2008) and Incze et al. (2010) predicted the greatest contributors to settlement in each MA to be itself or its nearest neighbours, with relatively high settlement in most Maine LMZs, and results of the present study generally agree with this (but see below). Potential 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 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 may receive most of their settlers from Canadian LFAs (especially LFAs 34 and 38), and there was overall more and further drift and less retention or settlement of larvae predicted 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 al. (2007) on the basis of field sampling, which

provided markedly faster development than observed in any lab study to date and thus 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 potential 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., percentage) connectivity estimated among areas. Previous studies of the GM (Incze et al. 2010) and GSL (Chassé and Miller 2010) did not consider exchange of larvae between areas within and outside their model domains, and larvae that were predicted to leave these domains 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 overall the relative estimates of connectivity among MAs within each of these regions. For example, in our study we found that MAs in previously-modeled regions were potentially connected, sometimes strongly (mean \pm SD = 13.7 ± 23.0 %, range = 0-97 %) as sources or sinks, to MAs in other regions (NL, NGSL, SS). Potential inter-regional connectivity was maintained, and in some cases was high, even when larval mortality was included in model simulations and reduced the possibility of long-distance dispersal. 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 better account for effects of remote forcing, such as the influence of the St. Lawrence River on the SGSL and atmospheric events outside of the immediate area of interest (Koutitonsky and Bugden 1991). Our 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. Perhaps in the future work over an even larger domain than ours may be attempted and reveal further patterns of interest to the study of lobster connectivity. For example, including eastern NL, a possible source to some MAs in western NL, could reduce predicted self-seeding of the NL MAs (LFAs 11-14) we modeled. Including southern New England, a probable sink for larvae from MAs in the GM and maybe SS, could also reduce the percent ‘losses’ of larvae from these MAs predicted when they drifted outside the model domain.

Model validation and future improvements to 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) and 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 may better capture 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 an increased influence of smaller-scale diffusion relative to 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). Models should also work towards integrating more realistic behaviours of lobster larvae, 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.

Disagreements between model predictions and landings may also have been caused by spatial differences in the abundance and egg production of adult lobsters not accounted for in model simulations. Indeed, 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 be relatively important as potential larval sources or sinks to other MAs.

However, NL has very low lobster abundances compared to many other parts of the species' range (Pezzack 1992; DFO 2016), and including actual egg production data in future modeling work is expected to reduce the predicted importance of NL as a source and/or sink. 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 type of model should attempt to account for spatiotemporal variability in the magnitude (and timing) of hatch (Harding et al. 1983; Aiken and Waddy 1986; Ennis 1995; Chassé and Miller 2010), perhaps including losses of embryos that occur between spawn and hatch (Tang 2016; Tang et al. In review).

Whereas our model validation tests produced mixed results, these are arguably quite encouraging because of improvements that can be anticipated to physical and biological components of the model (see above), and because the data against which model predictions of settlement were validated (i.e., fisheries landings) are far-removed from settlement itself. In particular, our model did not account for the (likely considerable) spatial variability in abundance of adult lobster that arises as a result of post-settlement mortality, benthic movements, and uncertain time lags between benthic and fisheries recruitment. The best metric against which to compare our model's predictions would be abundances of newly-settled stage IV (settlers) and/or young 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). If data can be obtained for additional regions, then comparisons to observed abundances of settlers and juveniles should ultimately be attempted, and would be better than validation of predicted potential settlement against landings.

Implications of results to the future study of lobster populations and fisheries

This study identified several MAs within the lobster's range that, based on current-driven larval dispersal, seem to be strongly linked to other MAs as sources and/or sinks, and others that seem relatively independent. Specifically, several MAs in Newfoundland, the NGSL, and SGSL had high retention, but low self-seeding, which if true would mean that they are important larval 'sinks', keeping much of their own production and also receive many larvae from external sources. Other MAs, including LFAs 18 (NGSL), 29 and 41 (SS) had low retention but provided large proportions of settlers to other MAs, which if true implies that these are important 'sources' to other areas. Finally, MAs with relatively high potential self-sufficiency, meaning high predicted retention and self-seeding, and therefore low export to and import from other MAs, included some MAs in the southern GM (e.g., OCC, BIS, and GB), Bay of Fundy (LFA 35), and southwest NS (LFA 34). This information is of clear relevance to fisheries management, as for example protection of MAs that act as important sources to other areas could be important to maintaining lobster fisheries. Further work is of course needed, though, to validate and improve our model and its predictions, which includes acquiring data on egg production and settlement over more of the species' range. Our results also implicate the Scotian Shelf, which has not previously been examined in studies of lobster larval dispersal, as a priority for future research.

Results suggested that MAs in certain portions of this large area may be strongly connected to those in the highly-productive and well-studied GSL and GM, but not to each other. We also noted a potential disconnect in larval dispersal across the middle (~LFA 31) of the SS, and much work suggests limited gene flow across this region (e.g., Dadswell, 1979; Kenchington et al. 2009; Benestan et al. 2015); the factors (e.g., surface circulation) responsible for a potential barrier to gene flow in this area, including limits to larval dispersal, should be further examined.

Conclusions

The new model used in this study, which covers most of the American lobster's range, predicted considerable potential connectivity by larval drift among fisheries MAs, 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 considerable variability among MAs in terms of potential self-sufficiency versus dependence 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 (Ennis 1986). Before predictions made by this model can be used to inform fisheries management further work is needed to improve and validate it, most importantly by obtaining and incorporating realistic egg production data. Once this is achieved, information obtained concerning the extent to which different MAs are connected by larval drift can inform cooperative management strategies to sustain interconnected fisheries.

Acknowledgements

Computing support for this project was provided by the DFO Gulf Region, and by ACENET, the regional advanced research computing consortium for universities in Atlantic Canada. ACENET is funded by the Canada Foundation for Innovation, the Atlantic Canada Opportunities Agency, and the provinces of Newfoundland & Labrador, Nova Scotia, and New Brunswick. The authors wish to thank Christopher Baker, Laura Benestan, Marthe Larsen Haarr, Jeff Houlahan, Heather Hunt, Raouf Kilada, Bruce MacDonald, Noah Oppenheim, Patrick Ouellet, Bernard Sainte-Marie, Michel Comeau, and John Tremblay for advice during project planning and analyses, and for sharing data. We also thank the many lobster harvesters and association leaders involved in the *Lobster Node* of the NSERC Canadian Fisheries Research Network (CFRN) for their involvement in planning and discussions of modeling work and outputs. Funding for this project was provided by NSERC through the CFRN and companion DFO funds, as well as an NSERC Discovery grant and a New Brunswick Innovation Foundation (NBIF) Research Innovation Fund grant to RR. BKQ was supported by an NSERC Canada Graduate Scholarship, an NBIF Graduate Student Scholarship, and a UNB School of Graduate Studies Research Assistantship. We also thank two anonymous reviewers for providing comments that improved the manuscript.

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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 the same MA six or more years later (see Methods for details). Values shown are Pearson's correlation coefficients (R) resulting from these comparisons, using a 0 % day⁻¹ or 20 % day⁻¹ mortality rate (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 (USA); NL: Newfoundland (LFAs 11-14C); GSL: Gulf of St. Lawrence (LFAs 15-26B); SS+BF (LFAs 27-41): Scotian Shelf and Bay of Fundy (LFAs 27-41)). 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)

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Table 3. Effect of large-scale modeling on predicted 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 % day⁻¹ or 20 % day⁻¹.

MA	No mortality		Spatially-uniform mortality	
	(0 % day ⁻¹)		(20 % day ⁻¹)	
	% 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	2.492	10.784	3.515	12.147
Overall				

Table 4. Effect of large-scale modeling on predicted 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 % day⁻¹ or 20 % day⁻¹.

MA	No mortality		Spatially-uniform mortality	
	(0 % day ⁻¹)		(20 % day ⁻¹)	
	% 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	17.428	2.856	38.508	2.980
Overall				

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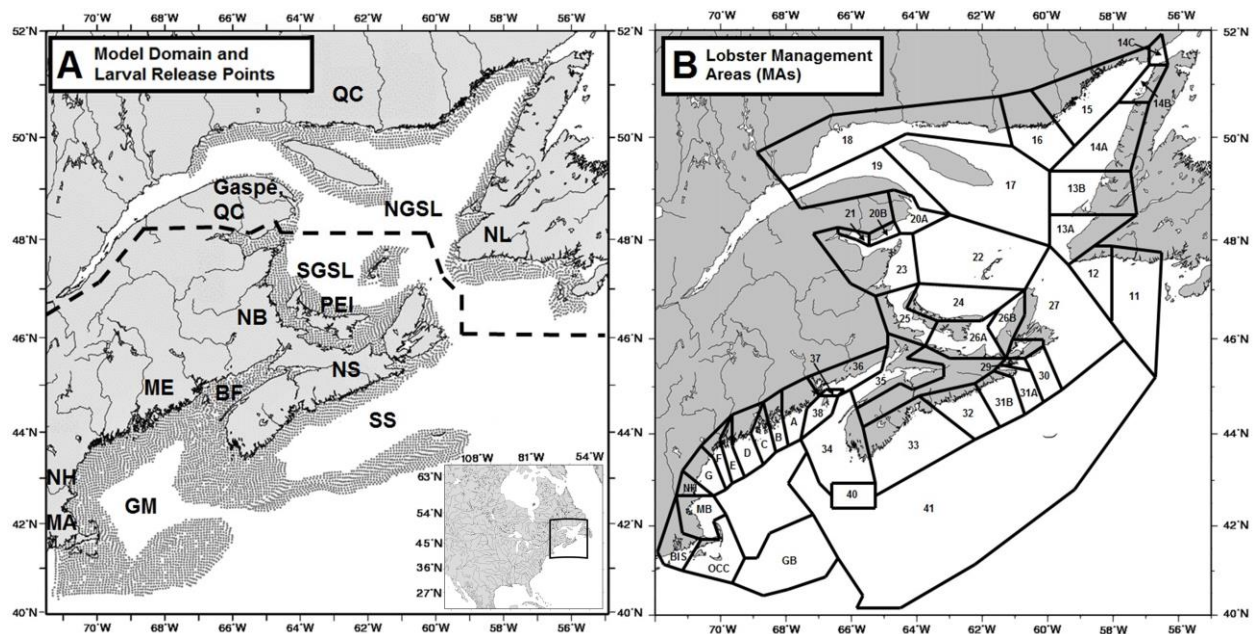


Fig. 1. Geographic domain of the large-scale oceanographic model used in this study showing (A) larval release points (dots), the division of the model into ‘northern’ and ‘southern’ domain (black dash line) where different larval development functions were used (see Methods) and regions on land (QC = 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. The inset in (A) shows the Atlantic coast of North America, with the model domain outlined in black.

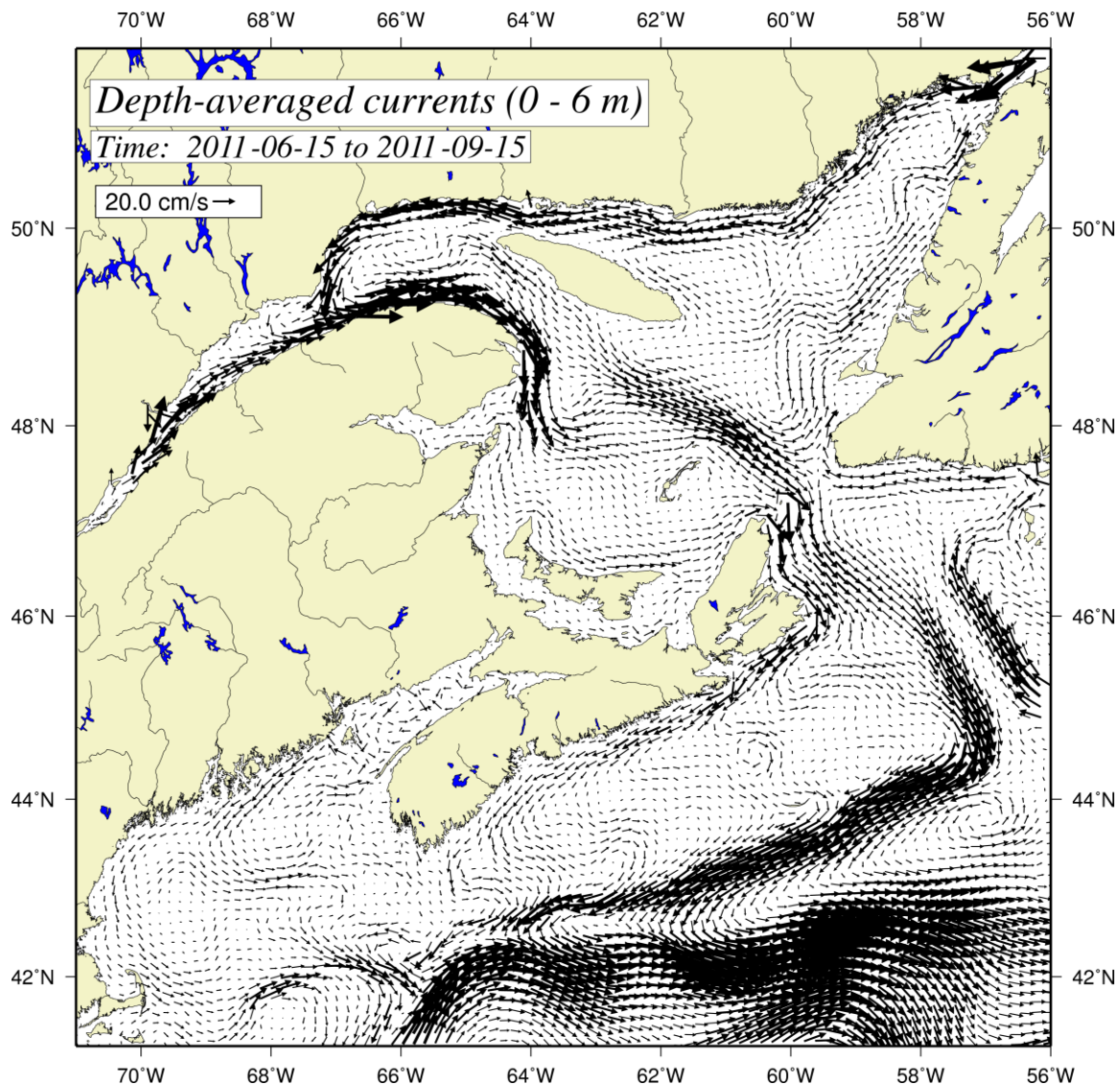


Fig. 2. Representative circulation patterns during the summer across the model domain. Mean modeled surface currents (averaged over the top 0-6 m of the water column) derived from the physical oceanographic model (Brickman and Drozdowski 2012a, b) used in this study are plotted for 15 June to 15 September 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.

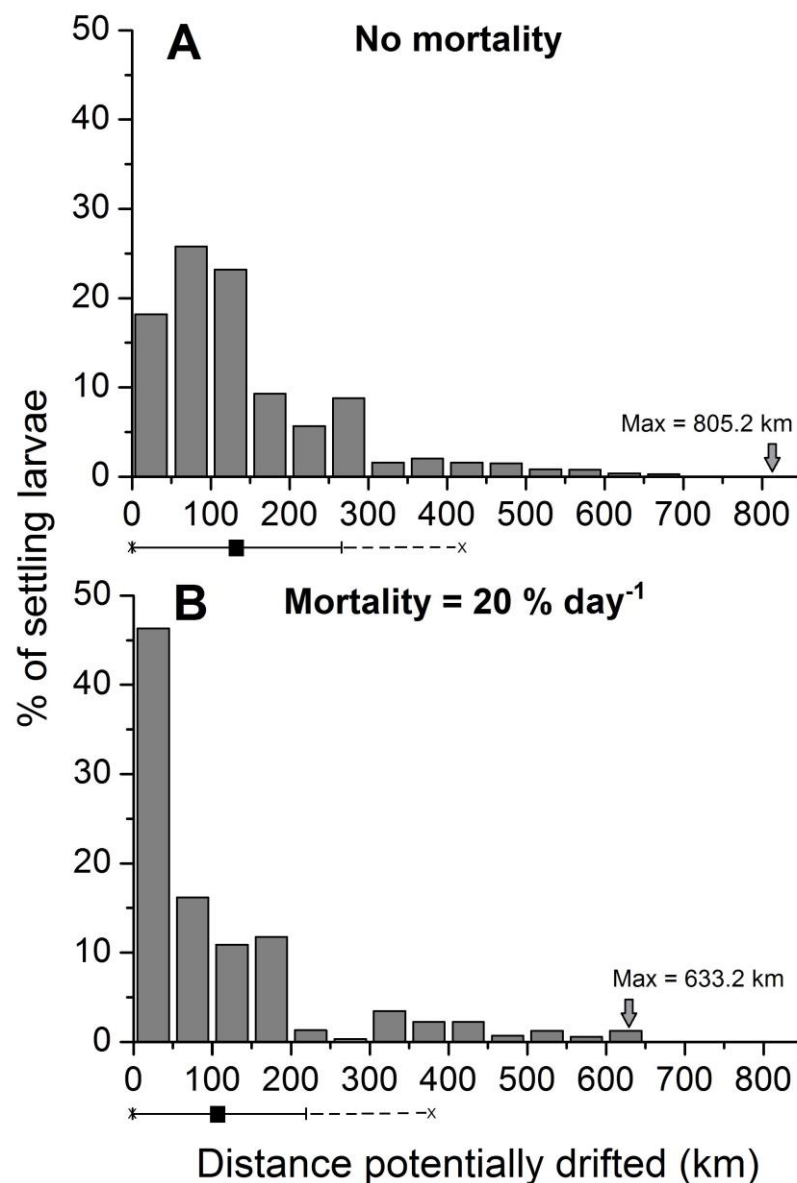


Fig. 3. Frequency distribution of distances drifted by larvae between hatch and settlement in model simulations with larval mortality of (A) 0 % day⁻¹ or (B) 20 % day⁻¹. Values were calculated based on model outputs averaged across 2005-2012 (see Methods). The maximum distance drifted is indicated by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

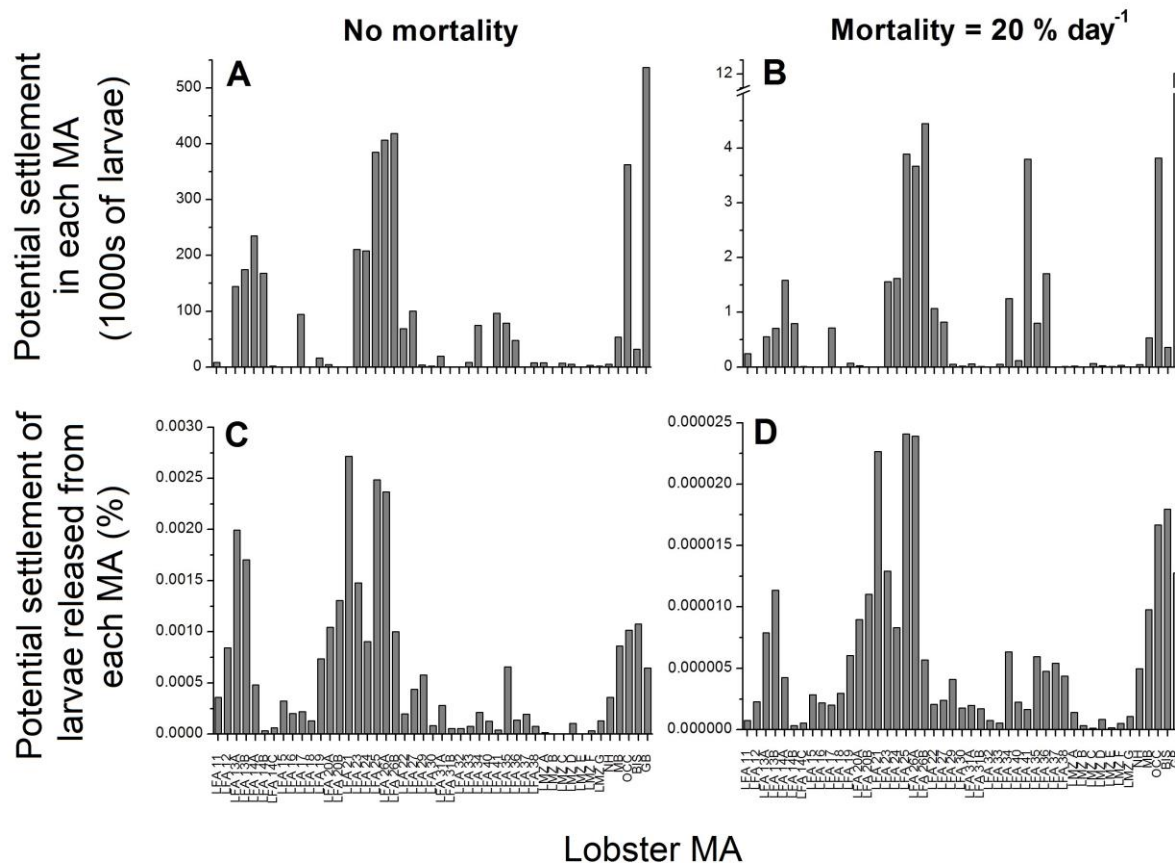


Fig. 4. Average annual potential settlement of larvae in each MA (1000s of larvae) (A, B) and percent settlement of larvae released from each MA (%) (C, D) across all simulated years (2005-2012), assuming larval mortality of (A, C) 0 % day⁻¹ or (B, D) 20 % day⁻¹.

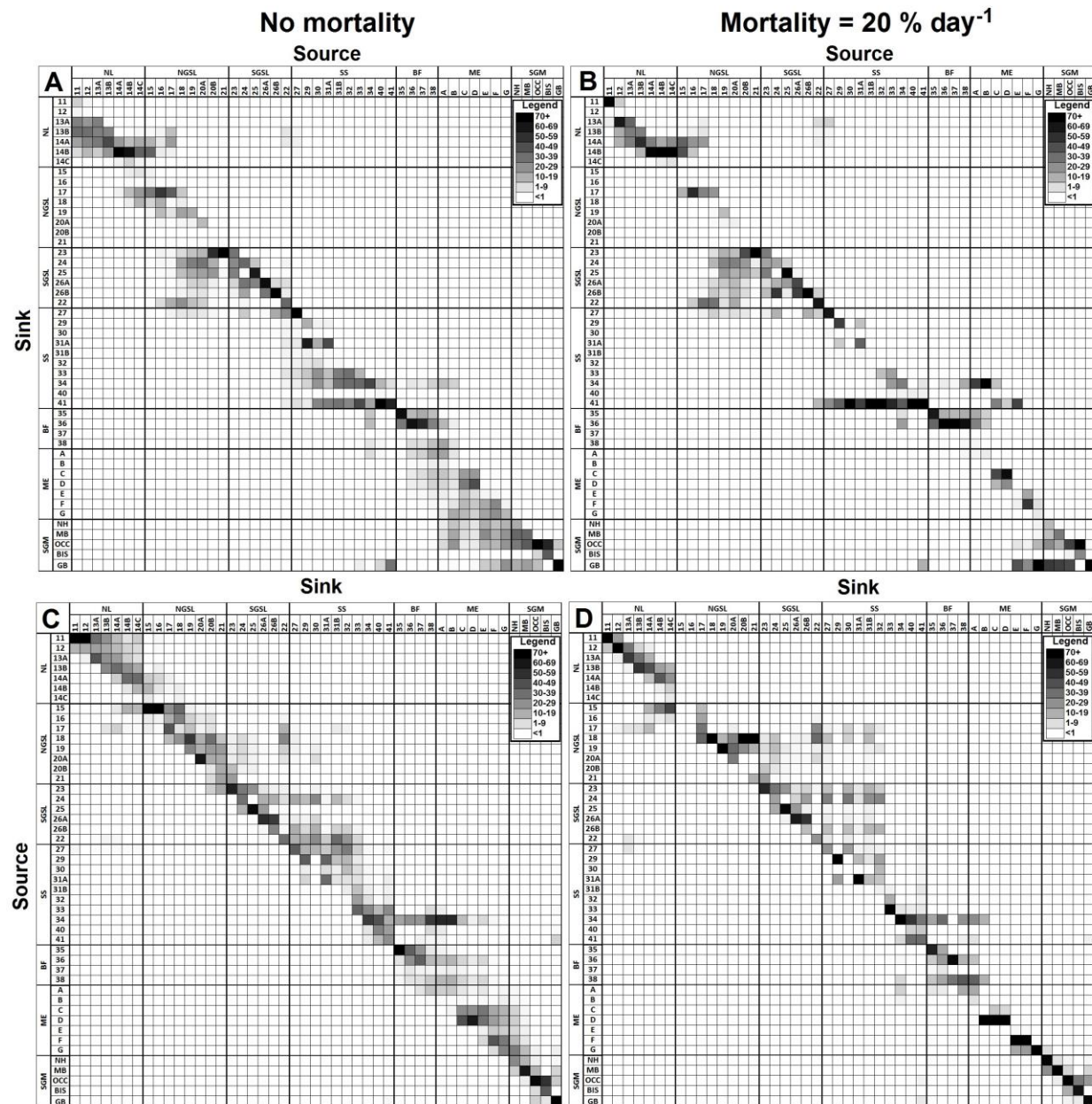


Fig. 5. Matrices showing relative potential (A, B) source-to-sink and (C, D) sink-from-source connectivity among lobster management areas (MAs) predicted by the model, based on average settlement across eight years (2005-2012) of simulations assuming (A, C) larval mortality of 0 % day⁻¹ or (B, D) 20 % day⁻¹. Each cell shows the percentage of successfully settling larvae (A, B) released (hatched) from a given source area (columns) predicted to settle in a given sink area

1039 (rows) or (C, D) predicted to settle in a particular sink area (columns) that were released
 1040 (hatched) from a given source area (rows). Darker shading indicates higher percentages, and the
 1041 values in each column add to 100 %. Areas are labeled with Canadian LFA numbers, Maine
 1042 (USA) LMZ letters, or other abbreviations in the southern GM (SGM, USA) (see Fig. 1B and
 1043 Methods). The larger geographic regions in which MAs are located are also labeled, with
 1044 abbreviations as in Fig 1A.

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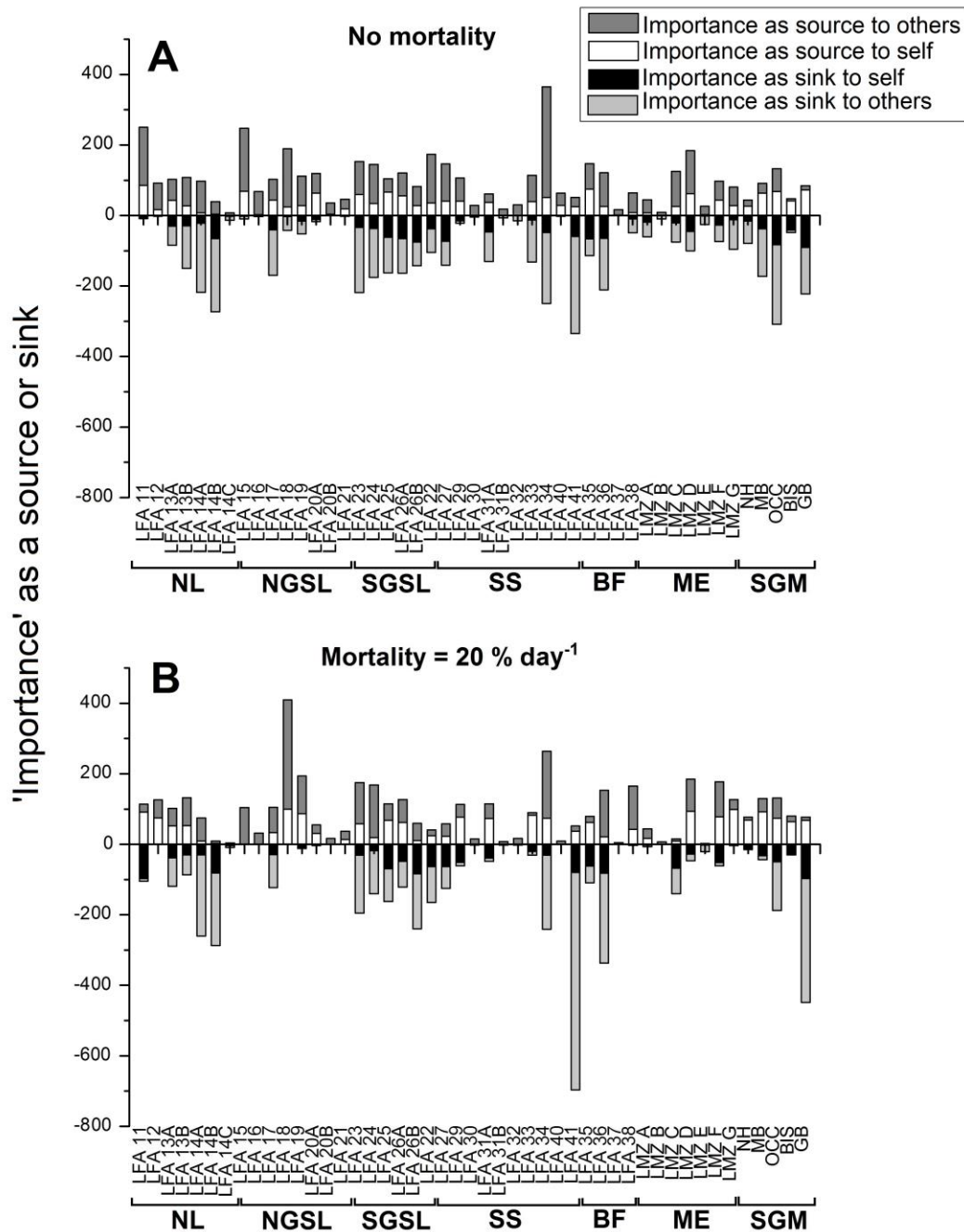


Fig. 6. 'Importance' of each lobster management area (MA) as a potential source (positive values) and sink (negative values) of larvae to other MAs (dark and light gray bars) and to itself (white and black bars). Importance indices were calculated based on model simulations assuming

1052 (A) larval mortality of 0 % day⁻¹ and (B) 20 % day⁻¹. Importance as a source was assigned a
 1053 positive value and importance as a sink a negative value for clarity of plotting. The magnitude of
 1054 an area's importance is an index of to what extent it is predicted to be connected with other
 1055 areas; for details of the calculation of these values, see Methods. Areas are arranged from left-to-
 1056 right in the approximate order of prevailing currents across the model domain (see Fig. 2).

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