

1 **Potential connectivity among American lobster fisheries as a result of larval drift across the**  
2 **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 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.

## 47 **Introduction**

48           The American lobster, *Homarus americanus*, supports the most important fishery in  
49 terms of landed value in Atlantic Canada (DFO 2016) and eastern North America (Wahle et al.  
50 2004). The lobster's range spans the Atlantic Shelf of North America from Cape Hatteras, North  
51 Carolina (35.25°N latitude), to Labrador (51.73°N) (Pezzack 1992; Fogarty 1995; Lawton and  
52 Lavalli 1995). Lobster fisheries are divided into management areas (hereafter MAs) called  
53 Lobster Fishing Areas (LFAs) in Atlantic Canada and with different names in different parts of  
54 the United States, such as Lobster Management Zones (LMZs) in the state of Maine. Each  
55 lobster MA has its own regulations, which aim to ensure a sufficient proportion of adult lobsters  
56 survive fishing long enough to reproduce and maintain the species' stocks.

57           The pelagic larval phase of lobsters is a challenge to discrete spatial fishery management.  
58 After hatching, lobster larvae develop through four stages (I, II, III, and IV) that drift in surface  
59 waters (Factor 1995). The larval stages, especially stages I-III, are not particularly strong  
60 swimmers (Factor 1995; Stanley et al. 2016) and are usually assumed to disperse passively with  
61 currents, although swimming ability of stage IV is higher (Cobb et al. 1989a; Stanley et al. 2016)  
62 and may impact dispersal and connectivity (Katz et al. 1994). Settlement occurs about halfway  
63 through stage IV if sea bottom with suitable substrate and temperature is found, at which point  
64 the benthic phase begins (Botero and Atema 1982; Cobb et al. 1989a, b). The larval phase of  
65 lobsters can last 24-110 days or more (MacKenzie 1988), so there is much potential for larvae to  
66 drift among lobster MAs. In many other marine species with planktonic larvae, ocean circulation  
67 can cause larvae to be dispersed widely (e.g., 100s or 1 000s of km) from their place of origin  
68 (Kough et al. 2013; Reisser et al. 2014), which may limit the ability of 'populations' to self-

69 recruit and result in connectivity (i.e., exchange of individuals and genes) among populations  
70 (Cowen et al. 2000).

71         The extent to which benthic populations self-recruit or depend on larval supply from  
72 other areas influences their growth rate and persistence (Cowen and Sponaugle 2009), and  
73 determines whether they represent separate populations or are instead interdependent  
74 components of a larger population structure (Dadswell 1979; Yakubu and Fogarty 2006).  
75 Genetic analyses by Kenchington et al. (2009) and Benestan et al. (2015) found very small, but  
76 statistically significant, genetic differences among lobsters in different parts of the species' range,  
77 which suggested weak population structuring due to isolation by distance but also gene flow  
78 among putative populations. Further, work by Miller (1997) along the coast of southern Nova  
79 Scotia (NS) suggested that recruitment to adult lobster populations may be influenced more by  
80 supply of larvae from other areas than by local larval production. Different lobster MAs may  
81 therefore be non-independent 'sub-populations' linked as sources and sinks by larval exchange,  
82 forming a metapopulation-like structure (e.g., Dadswell 1979; Yakubu and Fogarty 2006). If this  
83 is true, then certain MAs may be relatively resistant to fishing pressure and other 'stressors'  
84 within their boundaries, but more vulnerable to depletion of source areas that supply them with  
85 larvae, and *vice versa* (Dadswell 1979; Yakubu and Fogarty 2006). Cooperative efforts and co-  
86 construction of regulations by lobster fishers working in areas that are strongly connected by  
87 larval supply may thus be important to management of the fishery.

88         Physical oceanographic data and computer models have been used to estimate dispersal  
89 of lobster larvae and resultant connectivity. For example, winds, currents, and swimming by  
90 stage IV lobsters were shown to potentially transport larvae over distances of ~150-300 km from  
91 offshore to the coast of Rhode Island (Katz et al. 1994), and bio-physical models of the Gulf of

92 Maine (GM) demonstrated potential transport of larvae between offshore banks and inshore  
93 fisheries (Harding and Trites 1988; Harding et al. 2005), as well as among inshore fisheries  
94 separated by 20 to 400 km (Incze and Naimie 2000; Xue et al. 2008). Potential connectivity  
95 among different source-sink areas was estimated in another model of the GM (Incze et al. 2010),  
96 which showed again that settling larvae in some locations could originate from many different  
97 and distant sources (up to 400 km away), although the most important contributors to potential  
98 settlement in a given area tended to be itself and its nearest ‘upstream neighbor’. Larval drift  
99 from Prince Edward Island (PEI) to Cape Breton, NS, was predicted using drifters and current  
100 data incorporated into a physical oceanographic model (Miller and Hannah 2006). An individual-  
101 based biophysical model of the southern Gulf of St. Lawrence (SGSL) (Chassé and Miller 2010)  
102 suggested net drift of larvae from west to east in this region, and export of larvae from the SGSL  
103 to the Scotian Shelf (SS); only modest changes to management areas in the SGSL were  
104 suggested by predictions of that model (Chassé and Miller 2010).

105         The above studies demonstrated that ocean currents can potentially transport lobster  
106 larvae over large distances and result in interdependence of fishing grounds separated by tens to  
107 hundreds of kilometers. Importantly, previous modeling work of larval dispersal in American  
108 lobster has been done within single regions representing relatively small portions of the species’  
109 range; the largest-scale studies conducted thus far covered about 19 321 km<sup>2</sup> (Chassé and Miller  
110 2010) and 110 486 km<sup>2</sup> (Incze et al. 2010), representing only ~7 and 40 %, respectively, of the  
111 lobster’s range (~272 770 km<sup>2</sup>; Pezzack 1992; Lawton and Lavalli 1995). This incomplete spatial  
112 coverage is an important limitation for two main reasons. First, and most obviously, it results in  
113 incomplete characterization of source-sink linkages between lobster management areas. Second,  
114 physical processes occurring outside the spatial domain of these studies are likely to influence

115 dispersal within these domains (e.g., GM: Xue et al. 2008; Incze et al. 2010; SGSL: Koutitonsky  
116 and Bugden 1991). Therefore, a larger-scale model will reveal patterns not detected to date.

117 In the present study, a new large-scale biophysical model that included most of the  
118 species' range was used to calculate drift of lobster larvae and estimate potential connectivity  
119 among lobster in different management areas. This study was conducted to address objectives  
120 identified under research theme #2 (larval dispersal) of the Canadian Fisheries Research  
121 Network's *Lobster Node* (Rochette et al. under review). The physical domain of this model  
122 included regions not previously modeled – the northern Gulf of St. Lawrence (NGSL), southern  
123 and western Newfoundland (NL), and the Scotian Shelf (SS) (Fig. 1, 2). It was also overall much  
124 larger (~201 551 km<sup>2</sup>, or ~74 % of the species geographic range and most areas of high  
125 abundance [see Fogarty 1995]) than domains used in prior studies (~7-40 % of species' range) of  
126 lobster larval drift. We used the model to estimate potential connectivity by larval drift among  
127 different fisheries management areas. We then attempted to validate model predictions and  
128 examined them in the context of lobster population dynamics and fisheries management.

129

## 130 **Materials and Methods**

### 131 Physical model

132 We used a variant of the NEMO-OPA (Nucleus for European Modelling of the Ocean –  
133 Ocean Parallisé) ocean circulation modeling system (Madec 2008). The NEMO-OPA system  
134 simulates global circulation in deep offshore waters. The variant we used was developed by  
135 Brickman and Drozdowski (2012a) for use in shallower coastal waters. Several biophysical  
136 dispersion-retention studies have used this basic hydrodynamic model (Maps et al. 2013; Ouellet  
137 et al. 2013; Lavoie et al. 2015; Maps et al. 2015; Benestan et al. 2016) or a variant of it (Daigle

138 et al. 2016). The model domain (longitude: 71.5°-54.9°W; latitude: 38.6°-52.0°N) spans part of  
139 the Northwest Atlantic Shelf, including the Gulf of Maine (GM), Scotian Shelf (SS) and Gulf of  
140 St. Lawrence (GSL) (Fig. 1). This domain covers 74% of the American lobster's range and  
141 includes most of the species' distribution in which lobsters are most abundant and major fisheries  
142 are concentrated (Pezzack 1992; Fogarty 1995). The model has a spatial resolution of 1/12° (~9  
143 km x 6 km). Horizontal eddy diffusivity and viscosity coefficients are calculated using the  
144 Smagorinski (1963) scheme, with a 'no slip' condition to allow for lateral friction along the coast.  
145 The model is three-dimensional and includes 46 vertical layers, with a resolution of 6 m near the  
146 surface to resolve the surface mixed layer.

147 Physical data from 2005 onwards are used to force the oceanographic model, including  
148 temperature and salinity fields from the Department of Fisheries and Oceans' hydrographic  
149 climate database, as well as tides and runoff data from Maurice Lamontagne Institute for all  
150 major rivers in the model domain. Winds and air temperature obtained from the Canadian  
151 Meteorological Center are used in conjunction with bulk formulas to force simulations of the  
152 ocean surface. The physical model has been validated against observed currents and  
153 temperatures, transport of experimental drifters, and results from independent models including  
154 the Global Ocean-Atmosphere Prediction and Predictability model (Brickman and Drozdowski  
155 2012a; Lavoie et al. 2015; Daigle et al. 2016).

156 We ran model simulations for each of eight years (2005-2012) of June 1 – September 30,  
157 when the majority of lobster larvae are expected to be released and drifting in the water column  
158 in most regions (Aiken and Waddy 1986; Incze et al. 2010). We used the physical oceanographic  
159 model output to drive a semi-Lagrangian individual-based bio-physical model for lobster larvae  
160 based on the code developed by Chassé and Miller (2010), but with some modifications

161 (described below). The physical model was forced with three-hourly physical inputs and we used  
162 daily averaged outputs re-interpolated to a 5-minute time step to calculate the displacement of  
163 drifting particles. Outputs were generated by the lobster dispersal model every 12 hours of drift.

164

#### 165 Biological inputs: larval release

166 Lobster catch data for specific regions have been used to estimate annual egg and larval  
167 production in previous modeling studies of the GM (Incze et al. 2010) and SGSL (Chassé and  
168 Miller 2010), but these data are currently unavailable at a useful resolution for certain regions in  
169 the expanded domain of our model, such as the NGSL and parts of NS. Furthermore, female size  
170 structure, size at maturity, size-specific fecundity, and timing of larval release vary markedly  
171 over the large geographic domain of our model (Aiken and Waddy 1986; Miller 1997), but this  
172 information is unavailable for many of its regions. Therefore, as a first step we examined the  
173 potential effects of physical forces and larval development on spatial connectivity of lobsters  
174 without accounting for spatial variability in larval production. Connectivity estimates in the  
175 present study therefore represent ‘potential connectivity’, defined by Watson et al. (2010) as the  
176 likelihood of larval transport from source to sink areas, as opposed to ‘realized connectivity’,  
177 which is the actual amount of larval exchange among sources and sinks.

178 We set the amount and timing of larval release to be uniform throughout the model  
179 domain where adult lobsters are present. Locations of hatch (Fig. 1) were based on the  
180 geographic range of lobsters summarized by Pezzack (1992) (see also Fogarty 1995; Pinsky et al.  
181 2013; DFO 2016), with the exception that areas deeper than 100 m in the GM were excluded due  
182 to low abundance of ovigerous female lobsters, and thus larval input, observed in these areas  
183 (Incze et al. 2010). Larval production in any grid cell outside of this distribution was set to zero.

184 To ensure a large sample size of larvae on which to base calculations, we used a magnitude of  
185 larval hatch equal to some of the highest values estimated for the SGSL by Chassé and Miller  
186 (2010). In each model grid cell that fell within the aforementioned species' range, berried female  
187 abundance was assumed to be 4 000 km<sup>-2</sup> (216 000 per 9 km x 6 km grid cell), larval hatch  
188 (assumed to be equivalent to egg production; but see Tang 2016; Tang et al. under review) was  
189 10 000 per female, and total annual hatch was therefore 4 x 10<sup>7</sup> larvae km<sup>-2</sup> (Chassé and Miller  
190 2010), or 2.16 x 10<sup>9</sup> larvae per grid cell.

191 The timing of larval release was controlled using a hatching function derived by Chassé  
192 and Miller (2010) on the basis of empirical hatch values observed from all areas ('ports') in their  
193 model of the SGSL. The function was a 3<sup>rd</sup>-order polynomial that estimated the proportion (z) of  
194 total annual hatch in each cell per two-week period (x) as  $z = 0.0008*x^3 - 0.0432*x^2 + 0.2484*x$   
195  $- 0.1251$  ( $R^2 = 0.887$ ), with hatch beginning on 19 June (x = 0.5), peaking between 24 July (x =  
196 3.0) and 31 July (x = 3.5), and ending on 11 September (x = 6.0). Based on this function, a  
197 cluster of larvae representing a certain proportion of the total larval hatch in each model grid cell  
198 was released every 12 hours at a depth of 1.0 m in the centre of each cell, for a total of 182  
199 clusters released per year over a 91-day period from each cell in which hatch occurred.

200

### 201 Larval development and mortality

202 We included temperature-dependent development functions for each larval stage in the  
203 model to account for the fact that water temperature affects the development rate of lobster  
204 larvae (MacKenzie 1988; Ennis 1995). Three such sets of functions can be found in the  
205 literature: (1) equations derived from a lab study of larvae from warmer-water regions in the  
206 SGSL and GM (MacKenzie 1988), (2) field-based estimates from the GM, which suggest 60 %

207 faster development than the previous lab study (Annis et al. 2007), and (3) lab-derived equations  
208 for larvae originating from a colder-water region in the NGSL (Quinn et al. 2013). Chassé and  
209 Miller (2010) used the equations of MacKenzie (1988) in their model of the SGSL, while Xue et  
210 al. (2008) and Incze et al. (2010) used equations from Annis et al. (2007) in their models of the  
211 GM. We performed preliminary simulations with each of these three sets of functions, which  
212 greatly impacted predicted drift and connectivity patterns (Quinn 2014). The field-based  
213 estimates of Annis et al. (2007) resulted in the most different predictions, but due to the  
214 possibility that these estimates were based on different cohorts (see Quinn et al. 2013) we did not  
215 use them in the present study. However, significant differences in predicted connectivity were  
216 also observed between models using lab-derived development equations from MacKenzie (1988)  
217 and Quinn et al. (2013). Given that the latter differences may be the result of local adaptation  
218 (Quinn et al. 2013), we divided the model domain into a predominantly colder-water ‘northern’  
219 region and a predominantly warmer-water ‘southern’ region, based on large-scale trends in  
220 summer sea surface temperatures most likely to be encountered by larvae in each region (Ouellet  
221 et al. 2003; Quinn et al. 2013; Fig. 1). Larval stages were incremented using the cold-source  
222 equations from Quinn et al. (2013) for clusters released in ‘northern regions’ (NGSL and NL)  
223 and using warm-source equations of MacKenzie (1988) for those released from ‘southern regions’  
224 (GM, SS, and SGSL) (Fig. 1, Table 1). As stage IV was not observed by Quinn et al. (2013), we  
225 estimated an equation for the duration of this stage (Table 1) from the reported duration of larval  
226 stage III and assuming that larvae of this species spend 20.3% of the total larval phase in stage  
227 III and 50.7% in stage IV (MacKenzie 1988).

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

230 time, we ran and compared model simulations with and without a larval mortality function. In  
231 simulations that included mortality, we used a spatially-uniform mortality rate of 20 % day<sup>-1</sup>, as  
232 was done by Chassé and Miller (2010) based on a historical plankton tow time series of Scarratt  
233 (1964) for the SGSL. Spatially-uniform mortality was used in the present study because few  
234 empirical estimates exist of larval mortality across the species' range.

235

#### 236 Larval drift and settlement calculations

237         Once released, clusters of larvae were simulated to drift according to currents calculated  
238 by the physical model. Prior to settlement, larvae were kept at a depth of 1 m as lobster larvae  
239 tend to remain in surface waters above local thermoclines in the surface mixed layer (Hudon et al.  
240 1986; Harding et al. 1987; Ennis 1995). A Runge-Kutta fourth-order tracking algorithm was used  
241 to calculate the trajectories of drifting clusters. To simulate physical processes occurring at scales  
242 smaller than the model's 9 km x 6 km grid cells, a random walk algorithm (e.g., Visser 1997;  
243 Xue et al. 2008) was used, with small-scale diffusivity set to 2.0 m<sup>2</sup> s<sup>-1</sup> and random numbers  
244 obtained from the function RANLUX (James 1994). The random walk was applied to larvae  
245 within the model domain after movements were calculated based on advection due to currents.

246         When larvae reached stage IV, we used a settlement function similar to that used by  
247 Chassé and Miller (2010) to simulate the pelagic-benthic transition. This function assumed that  
248 larvae were competent to settle after passing through 50 % of stage IV, with the peak of larval  
249 settlement occurring 2/3 through this stage (based on laboratory observations by Cobb et al.  
250 1989b). Whether larvae could settle in a given cell was controlled by bottom temperature to  
251 prevent settlement in offshore areas (depth > 200 m) where it is not thought to occur in nature  
252 (Incze and Naimie 2000). Chassé and Miller (2010) allowed larvae to settle only where bottom

253 temperature was  $\geq 12^{\circ}\text{C}$ , based on low survival of larvae at temperatures  $< 12^{\circ}\text{C}$  (MacKenzie  
254 1988). However, recent work has demonstrated that larvae are capable of settling at temperatures  
255 at least as low as  $10^{\circ}\text{C}$  (Chiasson et al. 2015), and in many parts of our model domain (e.g., parts  
256 of NL) water temperature never exceeds  $10^{\circ}\text{C}$  during the period when larvae must develop and  
257 settle in nature (Ma et al. 2012; Quinn and Rochette 2015). Therefore, in the present study larvae  
258 were allowed to settle if bottom temperature was  $\geq 10^{\circ}\text{C}$ . Larvae that did not encounter waters  $\geq$   
259  $10^{\circ}\text{C}$  before the end of their competence phase (end of stage IV) ‘died’.

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

264

#### 265 Potential connectivity calculations

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

276 and be difficult to interpret and discuss. Patterns of source-to-sink connectivity (i.e., export and  
277 retention) among management areas were essentially the same for both methods of calculating  
278 these values (results not shown), however, so for ease of discussion we present those values  
279 calculated based on settling larvae only. Second, we also calculated ‘sink-from-source’  
280 connectivity as the proportion of all larvae settling in each sink area that originated from each  
281 source area, with the proportion of settlers in an area that hatched there (self-connectivity)  
282 representing ‘self-seeding’. It should be noted that though retention and self-seeding have the  
283 same numerator value (number of larvae remaining in a same area), they have different  
284 denominators, and can thus differ markedly for the same area. The source and sink areas used for  
285 these calculations were 47 lobster fisheries management areas (MAs) in the US and Canada,  
286 which included Canadian Lobster Fishing Areas (LFAs) 11-27, 29-38, and 40-41, Maine Lobster  
287 Management Zones (LMZs) A-G, several geographic areas in the southern GM (see Incze et al.  
288 2010) and George’s Bank (GB) (Fig. 1A, B). These MAs ranged in size from approximately 1  
289 200 to 275 000 km<sup>2</sup> (average = 23 851 km<sup>2</sup>, SD = 36 260 km<sup>2</sup>).

290

#### 291 Potential drift distances, settlement, and effects of mortality

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

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

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

308

#### 309 Determining the importance of each MA as a potential source or sink to other MA

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

317

#### 318 Model validation

319 As a first test of our model's predictive ability, we compared its estimated supply of  
320 competent stage IV larvae to different MAs to fisheries landings observed in those MAs several  
321 years later, similar to Chassé and Miller (2010). We obtained fisheries landings data for Canada

322 from the Department of Fisheries and Oceans (DFO 2016) and for the USA from the Atlantic  
323 States Marine Fisheries Commission (AMFSC 2015). We used estimates, based on a novel aging  
324 technique (Kilada et al. 2013), of the relationship between age and size of lobsters across the  
325 species' range to determine when larvae predicted to settle in a given year would be expected to  
326 start recruiting to the fishery. These size-age relationships suggest that the earliest age at which  
327 lobsters attain the minimum legal size varies between six and nine years across our model  
328 domain (Davis, Kilada, and Rochette, University of New Brunswick, unpublished data). Because  
329 we could not obtain landings data for some MAs from 2013 onward, we were only able to  
330 compare model-predicted annual settlement per MA in 2005 to total annual landings in 2011 and  
331 2012, and settlement in 2006 to landings in 2012. We first made these three comparisons across  
332 the entire model domain, then across the Canadian (LFAs 11-41) and American (LMZs A-G and  
333 other geographic areas in the SGM; see Fig. 1B) portions of the domain separately, and finally  
334 within four broad geographic regions with distinct oceanographic characteristics (Brickman and  
335 Drozdowski 2012a, b; Fig. 2): NL (LFAs 11-14C), the GSL (LFAs 15-26B), the SS and BF  
336 (LFAs 27-41), and the GM. As the GM and American domains were identical, a total of six  
337 different trios of regional comparisons were made. For each of these, we calculated Pearson's  
338 correlation coefficients ( $\alpha \leq 0.05$ ) between predicted potential settlement and reported landings  
339 when these settlers were expected to start recruiting to the fishery. This was done separately for  
340 model predictions with 0 % day<sup>-1</sup> and 20 % day<sup>-1</sup> mortality, resulting in a total of 36 comparisons.

341

#### 342 Assessing the effects of large-scale modeling

343 To assess the extent to which simulating larval drift across the species' range led to  
344 patterns not captured by smaller-scale regional modeling, we created two subdivisions of our

345 model domain mimicking the SGSL model of Chassé and Miller (2010) and the GM model of  
346 Incze et al. (2010). We then estimated i) the percentage of larvae released from each MA within  
347 these sub-domains predicted to settle outside of the sub-domains (export) as well as ii) the  
348 percentage of larvae settling in these sub-domains that potentially originate from outside (import).  
349 This was done for simulations with (20 % day<sup>-1</sup>) and without (0 % day<sup>-1</sup>) larval mortality.

350

## 351 **Results**

### 352 Potential larval drift distances

353 Model simulations predicted that distances drifted by larvae before settlement could  
354 range from 'zero' (actual drift  $\leq$  5-9 km = settlement in model cell where larva hatched) to a  
355 maximum of 805.2 km (no mortality) or 633.2 km (mortality rate of 20 % day<sup>-1</sup>) (Fig. 3A, B). In  
356 the absence of mortality, larvae were predicted to drift on average 128.8 km  $\pm$  124.5 (SD), with  
357 peak drift frequency between 50 and 100 km (Fig. 3A). Including mortality in simulations  
358 resulted in significantly ( $t_{df=14098} = -10.180, p < 0.001$ ) shorter predicted drift distances,  
359 averaging 108.6  $\pm$  126.8 km with peak frequency  $<$  50 km (Fig. 3B). Similarly, 95 % of larvae  
360 drifted less than 410 km without mortality (Fig. 3A) compared to less than 375 km with  
361 mortality (Fig. 3B).

362

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

364 Predicted annual settlement per MA averaged 85 126  $\pm$  135 285 competent stage IV  
365 larvae without mortality and 992  $\pm$  2 050 with mortality of 20 % day<sup>-1</sup> (Fig. 4A, B), and it varied  
366 widely among MAs, from 120 (LFA 40) to 536 502 larvae (GB) without mortality (Fig. 4A), and  
367 from 0 (LFAs 15 and 16) to 12 050 larvae (GB) with mortality (Fig. 4B). Settlement was

368 predicted to be highest in MAs within southwestern Newfoundland (NL) (LFAs 13A-14B), the  
369 southern Gulf of St. Lawrence (SGSL) (LFAs 23-26A), and southern Gulf of Maine (SGM)  
370 (OCC and GB), and lowest along the northern GSL (NGSL) (LFAs 15-19), Scotian Shelf (SS)  
371 (LFAs 29-33), and Maine (ME) coast (LMZs A-G) (Fig. 4A, B). The percentage of larvae  
372 released from a MA that were predicted to successfully settle somewhere within the model  
373 domain was overall very low (average  $\pm$  SD without mortality:  $5.9 \times 10^{-4} \pm 7.1 \times 10^{-4}$  %; with  
374 mortality:  $15.8 \times 10^{-6} \pm 6.4 \times 10^{-6}$  %), with the vast majority of particles released drifting into  
375 offshore areas too cold for settlement (Fig. 4C, D). Settlement of released larvae also varied  
376 markedly among MAs, ranging from  $2.8 \times 10^{-6}$  (LMZ B) to  $2.7 \times 10^{-3}$  % (LFA 21) without  
377 mortality (Fig. 3C) and from  $1.3 \times 10^{-7}$  (LMZ C) to  $2.4 \times 10^{-5}$  % (LFA 25) with mortality (Fig. 4D).  
378 Larvae released from MAs in western NL (LFAs 13A and 13B), the GSL (LFAs 19-26B), and  
379 SGM (MB, OCC, BIS, and GB) were predicted to have the highest percent settlement, while  
380 larvae released from MAs along the NGSL (LFAs 15-18), SS (LFAs 30-34, and 40-41), and  
381 parts of ME (LMZs A-G) had the lowest predicted percent settlement (Fig. 4C, D). There was no  
382 significant correlation between MA size and settlement in each per MA (no mortality:  $R =$   
383  $+0.083$ ,  $p = 0.579$ ; 20 %  $\text{day}^{-1}$  mortality:  $R = +0.250$ ,  $p = 0.091$ ; both  $n = 47$ ) or percent  
384 settlement of larvae released from each MA (no mortality:  $R = -0.140$ ,  $p = 0.347$ ; 20 %  $\text{day}^{-1}$   
385 mortality:  $R = -0.127$ ,  $p = 0.395$ ).

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

391 patterns of settlement, as strong correlations in potential settlement of larvae in each MA ( $R =$   
392  $+0.861$ ,  $p < 0.001$ ,  $n = 47$ ), as well as of larvae from each MA ( $R = +0.888$ ,  $p < 0.001$ ,  $n = 47$ ),  
393 were found in simulations with and without larval mortality (Fig. 4A-D).

394

#### 395 Potential connectivity among fisheries MAs

396 Source-to-sink connectivity estimates suggest that 27.7 % (13/47, without mortality) or  
397 25.5 % (12/47, with mortality) of MAs may retain the majority ( $\geq 50$  %, up to 95 %) of their own  
398 larval production (high retention) that eventually settle, while the remaining 72.3 or 74.5 % of  
399 MAs may export the majority of their larvae to other MAs (Fig. 5A, B). Similarly, the majority  
400 of the settlement in 26.1 % (without mortality) or 47.8 % (with mortality) of MAs could result  
401 from retention of local larval production (high self-seeding), while the remaining 73.9 or 52.2 %  
402 of MAs potentially depend on other MA sources to supply them with the majority of their settlers  
403 (Fig. 5C, D). MAs predicted to have relatively high potential retention and/or self-seeding were  
404 broadly distributed throughout the species' range (e.g., LFAs 11 and 14B in NL, LFAs 15, 25,  
405 and 26A in the GSL, LFAs 27 and 34 on the Scotian Shelf, LFAs 35 and 36 in the inner Bay of  
406 Fundy (BF), and LMZ D and OCC in the Gulf of Maine (GM)), and ranged from as small as  
407 LFA 14B (~7 669 km<sup>2</sup>) to as large as LFA 41 (~235 881 km<sup>2</sup>) (Fig. 2B, 5).

408 All MAs, even those with high predicted retention and/or self-seeding, were predicted to  
409 send and receive larvae to and from at least one, and sometimes as many as 6-12, other MAs (Fig.  
410 5). Larvae were also predicted to drift among MAs in different geographic regions, including  
411 from NL to the NGSL, from the NGSL to the SGSL, from the SGSL to MAs on the northeastern  
412 SS (LFAs 27-31A), from the southwestern SS (LFAs 31B-41) to the BF and GM, and between  
413 the BF and the GM (Fig. 5). Direct connectivity among MAs in the GSL and GM regions was

414 not predicted, however, and connectivity between the northeastern and southwestern SS was very  
415 limited (Fig. 5). More limited larval export was also predicted from the SGSL to the northeastern  
416 SS, as well as from the Magdalen Islands (SGSL, LFA 22) and Cape Breton, NS (SS, LFA 27) to  
417 parts of NL (Fig. 5). Many MAs were predicted to export > 90 % of their larval production to  
418 other areas (34.8 and 39.1 % of MAs without (Fig. 5A) and with mortality (Fig. 5B),  
419 respectively) and/or receive > 90 % of their settlers from other MAs (28.3 and 30.4 % of MAs  
420 without (Fig. 5C) and with mortality (Fig. 5D), respectively). MAs with low potential retention  
421 and/or self-seeding, but high connectivity to other MAs, included many in NL (LFA 11, 12, and  
422 14A-14C), the NGSL (LFAs 15, 16, 18, 20B, and 21), the Scotian Shelf (LFAs 30, 31B, 32, and  
423 40), the outer BF (LFAs 37 and 38), and the GM (LMZs A, B, and E (Fig. 5).

424

#### 425 Effect of mortality on predicted larval exchange

426 The majority (73.5 %) of MA pairs were potentially connected when either 0 % or 20 %  
427 day<sup>-1</sup> mortality was included in model simulations (Fig. 5). A minority (26.5 %) of MA pairs that  
428 exchanged larvae without mortality were no longer connected when mortality was included (Fig.  
429 5), but these were MA pairs that had predicted connectivity very low and close to zero even with  
430 0 % mortality (average source-to-sink connectivity =  $2.2 \pm 4.9$  %, average sink-from-source  
431 connectivity =  $3.1 \pm 7.7$  %; see Fig. 5). Including mortality in model simulations did reduce the  
432 specific numbers of larvae predicted to be exchanged by all connected pairs of MAs (average  
433 reduction =  $97.5 \pm 47.8$  %, range = 0.1-99.9 %), with the number of larvae exchanged by the  
434 majority (66.7 %) of MA pairs being reduced by  $\geq 90$  % with mortality. Reductions to larval  
435 exchange did not follow a simple pattern, such as greater reductions for MAs located further  
436 apart than for those closer together (Fig. 5, 6). Potential connectivity patterns predicted with and

437 without mortality were mostly similar, but not identical (source-to-sink connectivity:  $R = +0.777$ ,  
438  $n = 950$ ,  $p < 0.001$ ; sink-from-source:  $R = +0.697$ ,  $n = 950$ ,  $p < 0.001$ ) (Fig. 5). In particular,  
439 including mortality in model simulations resulted in significantly greater relative contributions of  
440 local larval production to potential settlement in each MA ( $8.9 \pm 27.3$  % greater self-seeding:  $t_{df=46} = +2.239$ ,  $p = 0.030$ ) and lower contributions of larvae from external sources ( $0.7 \pm 0.1$  %  
441 less sink-from-source connectivity among different MAs:  $t_{df=902} = -2.385$ ,  $p = 0.017$ ). However,  
442 mortality did not have a significant overall effect on the proportion of settling larvae that were  
443 potentially retained by their MA of origin (retention:  $t_{df=46} = +0.659$ ,  $p = 0.513$ ) or on the  
444 proportion of larvae exported to external sinks from each MA ( $t_{df=902} = -0.317$ ,  $p = 0.752$ ) (Fig.  
445 5A vs. 5B). However, patterns differed among MAs and there were many cases in which  
446 potential connectivity of MAs to themselves actually decreased with mortality; specifically,  
447 potential retention increased with mortality by 0.5-89.6 % in 52.2 % of MAs but decreased by  
448 0.03-32.9 % in the remaining 47.8 % of MAs (Fig. 5A vs. 5B) and self-seeding increased by 1.2-  
449 76.0 % in 39.1 % of MAs but decreased by 0.1-68.5 % in 60.9 % of MAs (Fig. 5C vs. 5D). This  
450 was especially noticeable for MAs along the Scotian Shelf (LFAs 27, 29-34, and 40), southern  
451 ME (LMZs C-G), and the SGM (NH, MB, OCC, and BIS), for which larvae exported to offshore  
452 MAs (LFA 41 or GB) actually represented a greater proportion of their larvae that successfully  
453 recruited to the bottom when mortality was included (Fig. 5B) than when it was not (Fig. 5BA).

455

#### 456 Importance of MAs as potential sources and sinks

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

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

470

#### 471 Model validation results

472 In 14 of the 36 comparisons attempted (38.9 %), predicted settlement (in 2005 and/or  
473 2006) was positively and significantly correlated to landings (in 2011 and/or 2012) when settlers  
474 were expected to start recruiting to the fishery in different MAs (see Methods and Table 2). At  
475 the regional scale, these correlations were significant for the Scotian Shelf/Bay of Fundy system  
476 with 0 % day<sup>-1</sup> larval mortality in the model, and in the Gulf of St. Lawrence system with 0 %  
477 day<sup>-1</sup> and 20 % day<sup>-1</sup> mortality in the model, but they were not significant in the Gulf of Maine or  
478 in Newfoundland, with or without mortality. In Canadian waters the correlation was positive and  
479 significant in 2/3 comparisons with 20 % mortality and in all comparisons with 0 % day<sup>-1</sup>  
480 mortality in the model. The correlation was not significant in the US (GM system) or over the  
481 full domain of the model, whether daily larval mortality in the model was 0 or 20 % day<sup>-1</sup>.

482

### 483 Effects of large-scale modeling

484           The large-scale model used in the present study allowed us to estimate potential  
485 connections between MAs inside regions modeled in previous studies (SGSL: Chassé and Miller  
486 2010; GM: Incze et al. 2010) and other MAs outside these regions (Tables 3, 4). Overall the  
487 SGSL was predicted to potentially export 2.5 % (no mortality) or 3.5 % (with mortality) of its  
488 larvae that successfully settle somewhere in the model domain to other regions (NL, the NGSL,  
489 and SS) and receive 10.8 % (no mortality) or 12.1 % (with mortality) of its settlers from sources  
490 outside the region (Table 3). Different MAs within the SGSL potentially export 0.1-19.0 % (no  
491 mortality) or 0.3-15.6 % (with mortality) of their settling larvae, and receive 2.3-40.4 % (no  
492 mortality) or 5.1-42.1 % (with mortality) of their settlers, from MAs outside of the SGSL domain  
493 of Chassé and Miller (2010) (Table 3). The GM was predicted to export 17.4 % (no mortality) or  
494 35.1 % (with mortality) of its larvae overall, and receive 2.9 (no mortality) or 3.0 % (with  
495 mortality) of its settlers from outside sources (Table 4). Different MAs in the GM potentially  
496 export 0-84.1 % (no mortality) or 0-97.3 % (with mortality) of their larvae and receive 0-80.3 %  
497 (no mortality) or 0-39.0 % (with mortality) of their settlers from MAs (mainly on the SS) outside  
498 of the GM domain modeled by Incze et al. (2010) (Table 4).

499

## 500 **Discussion**

### 501 Large-scale spatial patterns of potential connectivity

502           In this study, we used a new modeling system covering ~74 % of the American lobster's  
503 range (and most areas with high lobster abundances and major fisheries) to estimate potential  
504 connectivity among lobster fisheries management areas (MAs) in eastern North America at a  
505 larger scale than has been attempted before. The model predicted the potential for considerable

506 exchange of larvae among MAs; for instance, all MAs were predicted to exchange larvae with 1-  
507 12 others and 32.5 % (with 20 % d<sup>-1</sup> mortality) or 40.6 % (no mortality) of all settling larvae  
508 were predicted to settle in a different MA than that in which they hatched. These results  
509 demonstrate that current management divisions are likely not independent ‘units’ or ‘stocks’.  
510 The potential connectivity among MAs predicted in the present study agrees with overall low  
511 genetic differences among lobsters in localities within the GSL and GM (Kenchington et al.  
512 2009; Benestan et al. 2015). In fact, a recent study involving the same large-scale bio-physical  
513 modeling system and over 10,000 single nucleotide polymorphisms estimated that current-  
514 mediated larval dispersal accounts for 21 % of neutral genetic structure among lobsters sampled  
515 from 19 locations across the species’ range (Benestan et al. 2016). In other studies, analyses of  
516 historical fluctuations in lobster landings (Dadswell 1979; Campbell and Mohn 1983; Harding et  
517 al. 1983; Bo 2016) and genetics (Kenchington et al. 2009; Benestan et al. 2015, 2016) have  
518 suggested a large-scale division of lobsters into 2 large ‘stocks’ (GSL versus GM stocks), the  
519 boundary of which is located approximately midway along the Scotian Shelf (i.e., ~LFA 31B, 32,  
520 or 33). Our results are consistent with this hypothesis, showing considerable potential  
521 connectivity within but limited connectivity between the GSL and GM.

522 MAs vary greatly in size (from ~1 200 to 275 000 km<sup>2</sup> in area), and hence in the number  
523 of model cells from which larvae hatched and in which they could settle, and it might be  
524 expected that larger MAs would have relatively high potential settlement or importance as  
525 sources or sinks compared to smaller MAs. However, this was not generally the case, as  
526 settlement, settlement of larvae in and from each MA was not significantly correlated with MA  
527 size and MAs strongly connected to others and with large potential importance as sources or  
528 sinks varied considerably in size. While results of such correlations are admittedly tentative

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

533 A constant larval mortality rate did not generally have a statistically significant effect on  
534 whether or not MAs were potentially connected by larval exchange. However, larval mortality  
535 did have significant, and at times complex, effects on predicted larval drift. Overall predicted  
536 settlement and drift distances were lower with mortality than without, and many MAs showed  
537 less potential larval export and import with mortality, as would be expected. Interestingly,  
538 however, we found that the relative importance of certain (11/47) MAs (e.g., LFA 41 offshore of  
539 NS, GB in the offshore SGM) to potential settlement of larvae from other MAs actually  
540 increased with mortality. In all modeled years (2005-2012), with or without larval mortality  
541 included in simulations, the specific MAs that were more connected to offshore MAs with  
542 mortality had quite low retention and/or self-seeding and strong one-way connections to other  
543 specific MAs. This presumably resulted from strong currents at these locations (see Fig. 2)  
544 taking most larvae away from their place of origin and depositing them in neighbouring MAs,  
545 such that the self-connectivity was very unlikely and perhaps resulted mainly from dispersal  
546 back from other intermediate areas (thus representing longer drift than export to other MAs).  
547 Given the overall reduction in potential drift and connectivity resulting from including mortality  
548 in model simulations, along the complex patterns found, future work should quantify larval  
549 mortality rates in nature, including how these vary over space (Chassé and Miller 2010) and time.

550

551 Comparisons to previous modeling studies

552 Our model predicted that nearly all (95 %) larval exchange occurs over distances of 5-9  
553 km to 375-410 km, which is comparable to the 20-400 km range of distances predicted in  
554 previous studies (Chassé and Miller 2010; Incze et al. 2010). Our results agreed with the  
555 predictions of Harding et al. (2005) that larvae may drift between offshore Georges Bank (GB  
556 and part of LFA 41) and Browns Bank (LFA 40) in the GM and inshore fisheries (e.g., Maine  
557 LMZs, NH, and Massachusetts). They also agree with those of Xue et al. (2008) and Incze et al.  
558 (2010) in predicting drift of larvae to the southwest along the Maine coast, including from the  
559 Bay of Fundy and southwest NS to Maine LMZs, or areas further southwest in the GM. Models  
560 of Xue et al. (2008) and Incze et al. (2010) predicted the greatest contributors to settlement in  
561 each MA to be itself or its nearest neighbours, with relatively high settlement in most Maine  
562 LMZs, and results of the present study generally agree with this (but see below). Potential drift  
563 and connectivity patterns in the present study also agree with those documented by Chassé and  
564 Miller (2010) for the SGS, where dominant circulation mainly connected source areas in the  
565 western SGS to sinks in the eastern SGS, with some infrequent east-to-west connectivity  
566 between contiguous MAs (e.g., from LFA 26A to LFA 25).

567 There were, however, some notable differences between modeling results of this and  
568 earlier studies. In the GM in particular, the larger-scale model used in this study predicted that  
569 Maine LMZs A and B may receive most of their settlers from Canadian LFAs (especially LFAs  
570 34 and 38), and there was overall more and further drift and less retention or settlement of larvae  
571 predicted along the Maine coast, particularly for larvae released from LMZs B and E.  
572 Importantly, the model in this study used lab-derived warm-source equations of MacKenzie  
573 (1988) to increment larval development in the GM, whereas Xue et al. (2008) and Incze et al.  
574 (2010) used estimates derived by Annis et al. (2007) on the basis of field sampling, which

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

584         Other differences from previous studies also occurred in the relative (i.e., percentage)  
585 connectivity estimated among areas. Previous studies of the GM (Incze et al. 2010) and GSL  
586 (Chassé and Miller 2010) did not consider exchange of larvae between areas within and outside  
587 their model domains, and larvae that were predicted to leave these domains were removed from  
588 calculations. In contrast, in the present study we also included external sources and sinks of  
589 larvae from GM and SGSL areas, reducing overall the relative estimates of connectivity among  
590 MAs within each of these regions. For example, in our study we found that MAs in previously-  
591 modeled regions were potentially connected, sometimes strongly (mean  $\pm$  SD =  $13.7 \pm 23.0$  %, range = 0-97 %) as sources or sinks, to MAs in other regions (NL, NGSL, SS). Potential inter-  
592 regional connectivity was maintained, and in some cases was high, even when larval mortality  
593 was included in model simulations and reduced the possibility of long-distance dispersal. Our  
594 large-scale model may also have led to differences in estimates of retention, self-seeding, and  
595 connectivity relative to previous smaller-scale studies due to its i) somewhat coarser spatial  
596 resolution (~5-9 km versus 4 km in Chassé and Miller 2010 and 3-5 km in Incze et al. 2010) and  
597

598 ii) ability to better account for effects of remote forcing, such as the influence of the St.  
599 Lawrence River on the SGSL and atmospheric events outside of the immediate area of interest  
600 (Koutitonsky and Bugden 1991). Our findings illustrate the importance of modeling drift at a  
601 large spatial scale to estimate stock structure and spatial connectivity patterns of lobsters within  
602 more circumscribed regions. Perhaps in the future work over an even larger domain than ours  
603 may be attempted and reveal further patterns of interest to the study of lobster connectivity. For  
604 example, including eastern NL, a possible source to some MAs in western NL, could reduce  
605 predicted self-seeding of the NL MAs (LFAs 11-14) we modeled. Including southern New  
606 England, a probable sink for larvae from MAs in the GM and maybe SS, could also reduce the  
607 percent ‘losses’ of larvae from these MAs predicted when they drifted outside the model domain.

608

#### 609 Model validation and future improvements to the model

610 Our validation results compare favourably to those of previous modeling studies of larval  
611 dispersal in American lobster (Chassé and Miller 2010; Incze et al. 2010) and other lobster  
612 species (e.g., Kough et al. 2013), which have had poor or mixed (i.e., model validated in some  
613 locations but not others) success validating their settlement predictions. Predicted settlement per  
614 MA was not significantly correlated to time-lagged landings over the entire model domain, but it  
615 did correlate significantly with landings for some subdivisions of the domain, especially when  
616 mortality was not included in simulations (Canada overall, SS, and GSL), suggesting that the  
617 model may better capture realistic physical and biological aspects of lobster larval drift in some  
618 areas than in others (NL and the GM, USA). The only region for which predictions were  
619 validated when mortality was included was the GSL, which was also the location where the 20 %  
620 day<sup>-1</sup> used in this study was estimated (Scarrat 1964; Chassé and Miller 2010). This may have

621 occurred because larval mortality in other regions is much different from this, suggesting it may  
622 be important to quantify geographic variation in larval mortality for future modeling work. The  
623 best correlations were also obtained in relatively low-retention regions (e.g., GSL) with stronger  
624 advective currents (Fig. 2) and less complex coastlines (Brickman and Drozdowski 2012b),  
625 while regions with poorer correlations were those with more complex coastlines (e.g., GM) and  
626 perhaps an increased influence of smaller-scale diffusion relative to advection (e.g., Largier  
627 2003; Xue et al. 2008). Future work with a finer-resolution version of this model may better  
628 capture the effects of local bathymetry, eddy diffusion, and tidal stirring that are thought to exert  
629 greater influences on nearshore drift and circulation than larger-scale advection due to currents  
630 and winds (Largier 2003). Models should also work towards integrating more realistic  
631 behaviours of lobster larvae, such as i) ‘horizontal’ swimming of stage IV larvae in relation to  
632 currents, which may alter drift trajectories (Katz et al. 1994), ii) diel vertical migrations by stages  
633 I, II, and III (Harding et al. 1987; Stanley et al. 2016), which may increase retention in areas with  
634 high velocity offshore currents, such as the Gaspé region (Hill 1991; Brickman and Drozdowski  
635 2012b; Galbraith et al. 2013), and iii) settlement decisions of stage IV lobsters in relation to  
636 substrate, which can markedly affect search behaviours and likelihood of settlement in the lab  
637 (Botero and Atema 1982) and varies markedly over the species’ range.

638           Disagreements between model predictions and landings may also have been caused by  
639 spatial differences in the abundance and egg production of adult lobsters not accounted for in  
640 model simulations. Indeed, low ‘potential connectivity’ between two areas can be associated  
641 with high ‘realized connectivity’ if larval production in the source area is particularly high, and  
642 *vice versa* (Watson et al. 2010). Several MAs in western NL were predicted to have relatively  
643 high settlement and be relatively important as potential larval sources or sinks to other MAs.

644 However, NL has very low lobster abundances compared to many other parts of the species'  
645 range (Pezzack 1992; DFO 2016), and including actual egg production data in future modeling  
646 work is expected to reduce the predicted importance of NL as a source and/or sink. Conversely,  
647 abundances, catches, and settlement of lobster in the GM, especially along the ME coast, have  
648 been increasing to extremely high levels in recent years (Boudreau et al. 2014; AMFSC 2015),  
649 but the high larval release potential of such abundant lobster stocks was not accounted for in our  
650 simulations. Our model predicted that, based on physics, this region might have relatively low  
651 settlement, but if larval release was adjusted to account for high abundances and egg production  
652 the observed disconnect between model-predicted settlement and observed landings would likely  
653 decrease considerably. Thus, future work with this type of model should attempt to account for  
654 spatiotemporal variability in the magnitude (and timing) of hatch (Harding et al. 1983; Aiken and  
655 Waddy 1986; Ennis 1995; Chassé and Miller 2010), perhaps including losses of embryos that  
656 occur between spawn and hatch (Tang 2016; Tang et al. under review).

657       Whereas our model validation tests produced mixed results, these are arguably quite  
658 encouraging because of improvements that can be anticipated to physical and biological  
659 components of the model (see above), and because the data against which model predictions of  
660 settlement were validated (i.e., fisheries landings) are far-removed from settlement itself. In  
661 particular, our model did not account for the (likely considerable) spatial variability in abundance  
662 of adult lobster that arises as a result of post-settlement mortality, benthic movements, and  
663 uncertain time lags between benthic and fisheries recruitment. The best metric against which to  
664 compare our model's predictions would be abundances of newly-settled stage IV (settlers) and/or  
665 young juvenile lobsters ('early benthic recruitment' *sensu* Wahle et al. 2004; Incze et al. 2010).  
666 The American Lobster Settlement Index (Wahle et al. 2004) is the most promising source for

667 such data, but at present this database does not have data for several regions of our model (e.g.,  
668 NL and NGSL). If data can be obtained for additional regions, then comparisons to observed  
669 abundances of settlers and juveniles should ultimately be attempted, and would be better than  
670 validation of predicted potential settlement against landings.

671

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

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

689 Results suggested that MAs in certain portions of this large area may be strongly connected to  
690 those in the highly-productive and well-studied GSL and GM, but not to each other. We also  
691 noted a potential disconnect in larval dispersal across the middle (~LFA 31) of the SS, and much  
692 work suggests limited gene flow across this region (e.g., Dadswell 1979; Kenchington et al.  
693 2009; Benestan et al. 2015); the factors (e.g., surface circulation) responsible for a potential  
694 barrier to gene flow in this area, including limits to larval dispersal, should be further examined.

695 Overall, the new model used in this study that covers most of the American lobster's  
696 range predicted considerable potential connectivity by larval drift among fisheries MAs,  
697 supporting the notion that lobster in eastern North America have a large-scale population  
698 structure, or structure(s), consisting of interconnected 'subpopulations' linked by complex  
699 dynamics (Cowen et al. 2000; Yakubu and Fogarty 2006). Our results suggest considerable  
700 variability among MAs in terms of potential self-sufficiency versus dependence on external  
701 sources for larvae and recruitment. The impacts of the same conservation practices and levels of  
702 fishing mortality could therefore differ considerably among MAs (Ennis 1986). Before  
703 predictions made by this model can be used to inform fisheries management further work is  
704 needed to improve and validate it, most importantly by obtaining and incorporating realistic egg  
705 production data. Once this is achieved, information obtained concerning the extent to which  
706 different MAs are connected by larval drift can inform cooperative management strategies to  
707 sustain interconnected fisheries.

708

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726

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909 **Table 1.** Lab-derived equations relating development time (D, in days) of ‘warm origin’ and  
 910 ‘cold origin’ larval stages I-IV to temperature (T, in °C), which we used in our bio-physical  
 911 model to estimate larval dispersal. Warm-source equations for stages I-III came from MacKenzie  
 912 (1988), and that for stage IV came from Incze et al. (1997; 2010), based on data in MacKenzie  
 913 (1988). Cold-source equations for stages I-III came from Quinn et al. (2013), and that for stage  
 914 IV was derived in this study (see description in text, and in Quinn 2014).

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

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925 **Table 2.** Comparison between model-predicted settlement per lobster management area (MA) in  
 926 2005 and 2006 and observed fisheries landings in the same MA six or more years later (see  
 927 Methods for details). Values shown are Pearson's correlation coefficients (R) resulting from  
 928 these comparisons, using a 0 % day<sup>-1</sup> or 20 % day<sup>-1</sup> mortality rate (values separated by a comma)  
 929 in model simulations, considering different settlement-landing year combinations and different  
 930 parts of the model domain: full model domain, Canada only, four geographic regions with  
 931 different oceanographic characteristics (Brickman and Drozdowski 2012a, b; see also Fig. 2)  
 932 (GM: Gulf of Maine (USA); NL: Newfoundland (LFAs 11-14C); GSL: Gulf of St. Lawrence  
 933 (LFAs 15-26B); SS+BF (LFAs 27-41): Scotian Shelf and Bay of Fundy (LFAs 27-41)). The  
 934 number of MAs included in each comparison is listed in parentheses. P-values for each  
 935 correlation are indicated as follows: \*:  $p \leq 0.05$ ; \*\*:  $p \leq 0.01$ ; \*\*\*:  $p \leq 0.001$ ; no label:  $p > 0.05$   
 936 (non-significant). An 'n/a' indicates that settlement in 2006 was not compared to landings in  
 937 2011 because enough time has not elapsed for settlers to have recruited to fisheries within the  
 938 intervening five years.

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

|              |      |                      |                       |
|--------------|------|----------------------|-----------------------|
|              | 2006 | n/a                  | -0.372, -0.363 (11)   |
| <b>NL</b>    | 2005 | -0.260, -0.104 (7)   | -0.252, -0.102 (7)    |
|              | 2006 | n/a                  | -0.231, -0.072 (7)    |
| <b>GSL</b>   | 2005 | 0.719**, 0.592* (13) | 0.772**, 0.612* (13)  |
|              | 2006 | n/a                  | 0.842***, 0.612* (13) |
| <b>SS+BF</b> | 2005 | 0.584*, 0.232 (12)   | 0.581*, 0.242 (12)    |
|              | 2006 | n/a                  | 0.828***, 0.182 (12)  |

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960 **Table 3.** Effect of large-scale modeling on predicted connectivity among lobster MAs within the  
 961 portion of the SGSL (including LFAs 23-26B, but not LFA 22) modeled by Chassé and Miller  
 962 (2010). Values shown are the percentage of larval production lost by each MA to areas outside of  
 963 the SGSL (% export), and the percentage of settlement within each MA that originated from  
 964 areas outside of the SGSL (% import), under model simulations involving larval mortality of 0 %  
 965 day<sup>-1</sup> or 20 % day<sup>-1</sup>.  
 966

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

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971 **Table 4.** Effect of large-scale modeling on predicted connectivity among lobster MAs within the  
 972 portion of the GM (including LFAs 35-38 in the BF and LFAs 34 and 40 on the SS, but not  
 973 offshore areas GB or LFA 41) modeled by Incze et al. (2010). Values shown are the percentage  
 974 of larval production lost by each MA to areas outside of the SGSL (% export), and the  
 975 percentage of settlement within each MA that originated from areas outside of the SGSL (%  
 976 import), under model simulations involving larval mortality of 0 % day<sup>-1</sup> or 20 % day<sup>-1</sup>.  
 977

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

|              |        |        |        |       |
|--------------|--------|--------|--------|-------|
| <b>LMZ G</b> | 24.513 | 0.000  | 74.049 | 0.000 |
| <b>NH</b>    | 15.521 | 0.000  | 52.245 | 0.000 |
| <b>MB</b>    | 20.416 | 7.173  | 51.108 | 0.000 |
| <b>OCC</b>   | 10.061 | 3.928  | 47.994 | 1.919 |
| <b>BIS</b>   | 0.000  | 80.297 | 0.000  | 3.381 |
| <b>GM</b>    | 17.428 | 2.856  | 38.508 | 2.980 |

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**Overall**

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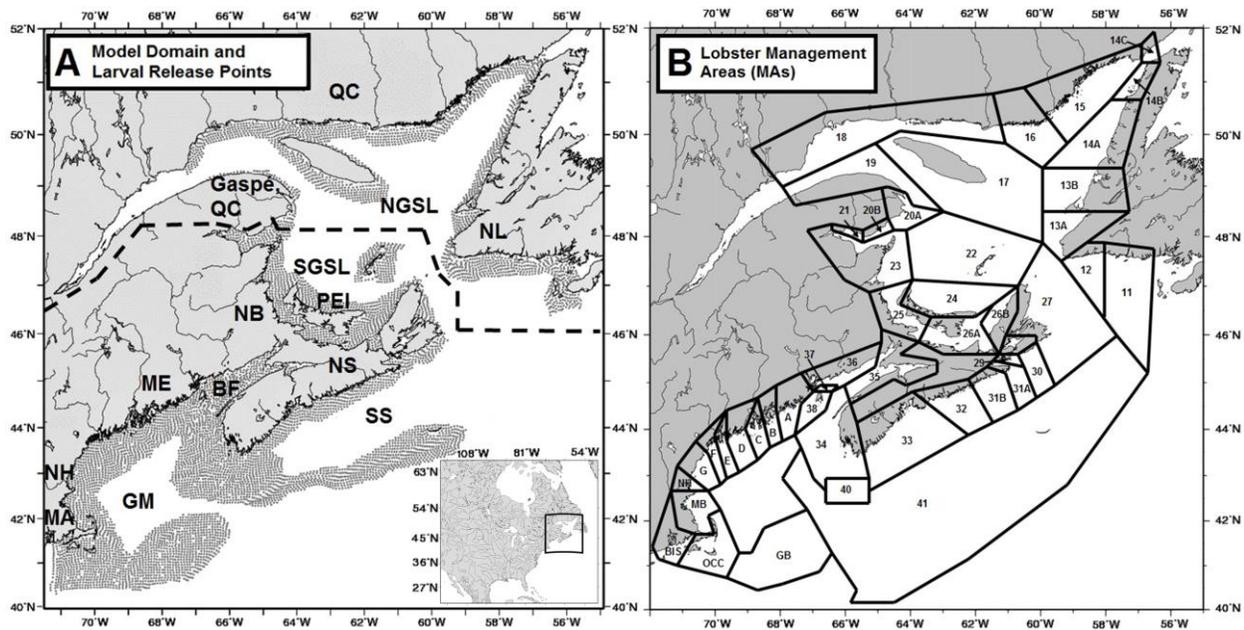
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996 **Fig. 1.** Geographic domain of the large-scale oceanographic model used in this study showing

997 (A) larval release points (dots), the division of the model into ‘northern’ and ‘southern’ domain

998 (black dash line) where different larval development functions were used (see Methods) and

999 regions on land (QC = Quebec, NL = Newfoundland, PEI = Prince Edward Island, NB = New

1000 Brunswick, NS = Nova Scotia, ME = Maine, NH = New Hampshire, MA = Massachusetts) and

1001 in the ocean (NGSL and SGSL = northern and southern Gulf of St. Lawrence, SS = Scotian Shelf,

1002 BF = Bay of Fundy, GM = Gulf of Maine) discussed in the text and (B) fisheries management

1003 areas (MAs) from Canada (LFAs 11-41) and the US (Maine LMZs A-G, NH = New Hampshire,

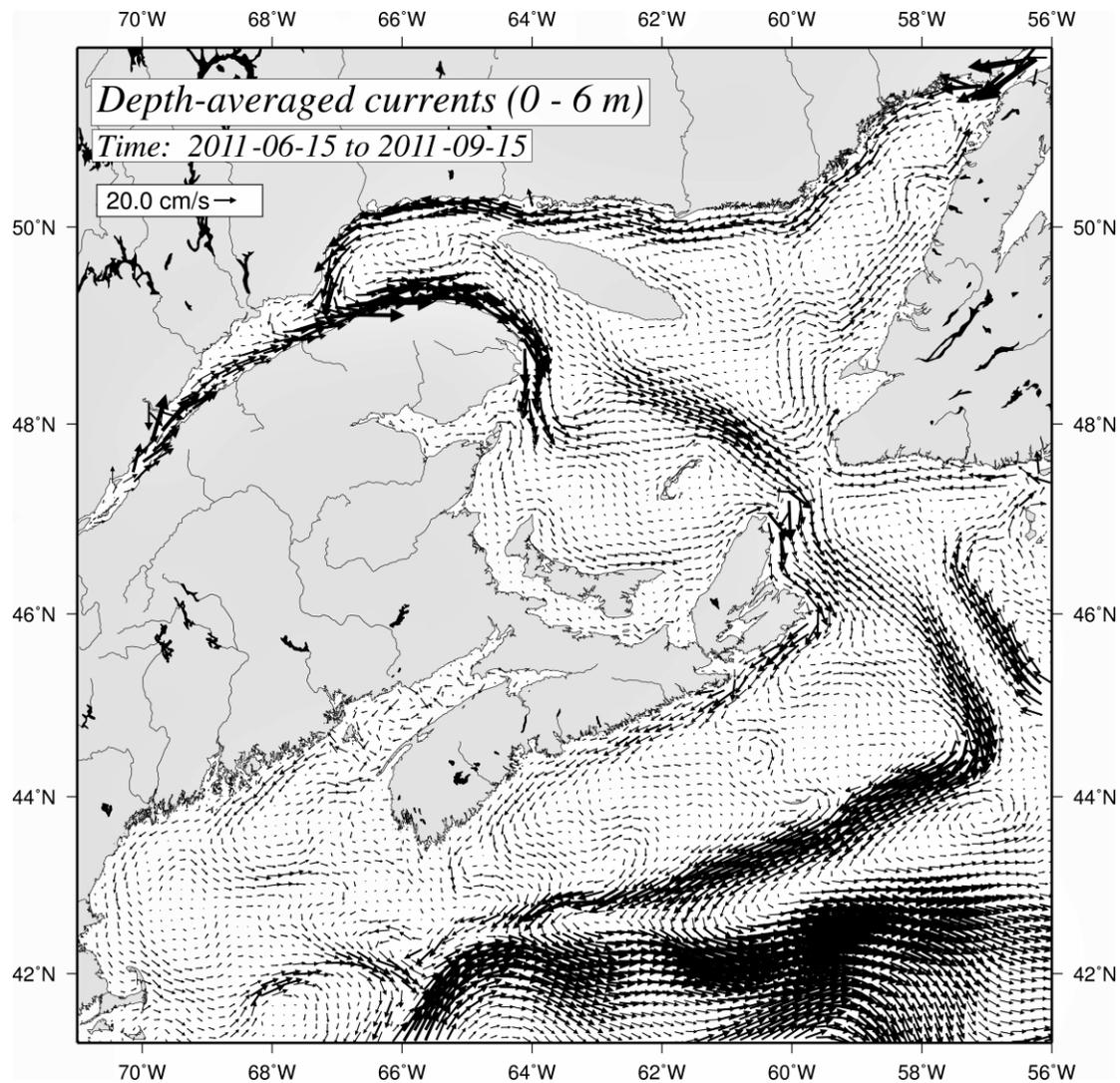
1004 MB = Massachusetts Bay, OCC = Outer Cape Cod, BIS = Block Island Sound, GB = Georges

1005 Bank) that were used as source-sink areas among which connectivity was estimated. The inset in

1006 (A) shows the Atlantic coast of North America, with the model domain outlined in black. Maps

1007 were made using Generic Mapping Tools GMT-5.3.1 (Wessel et al. 2013; available online at:

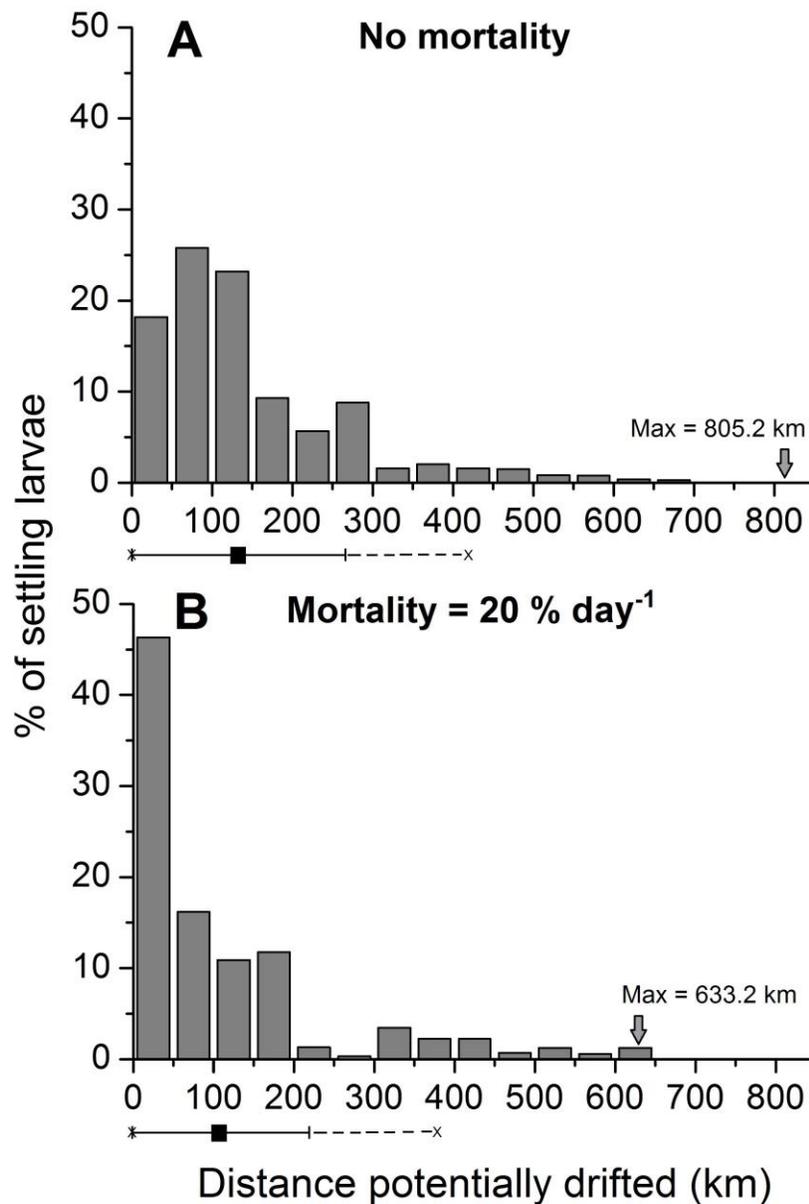
1008 <http://gmt.soest.hawaii.edu/>).



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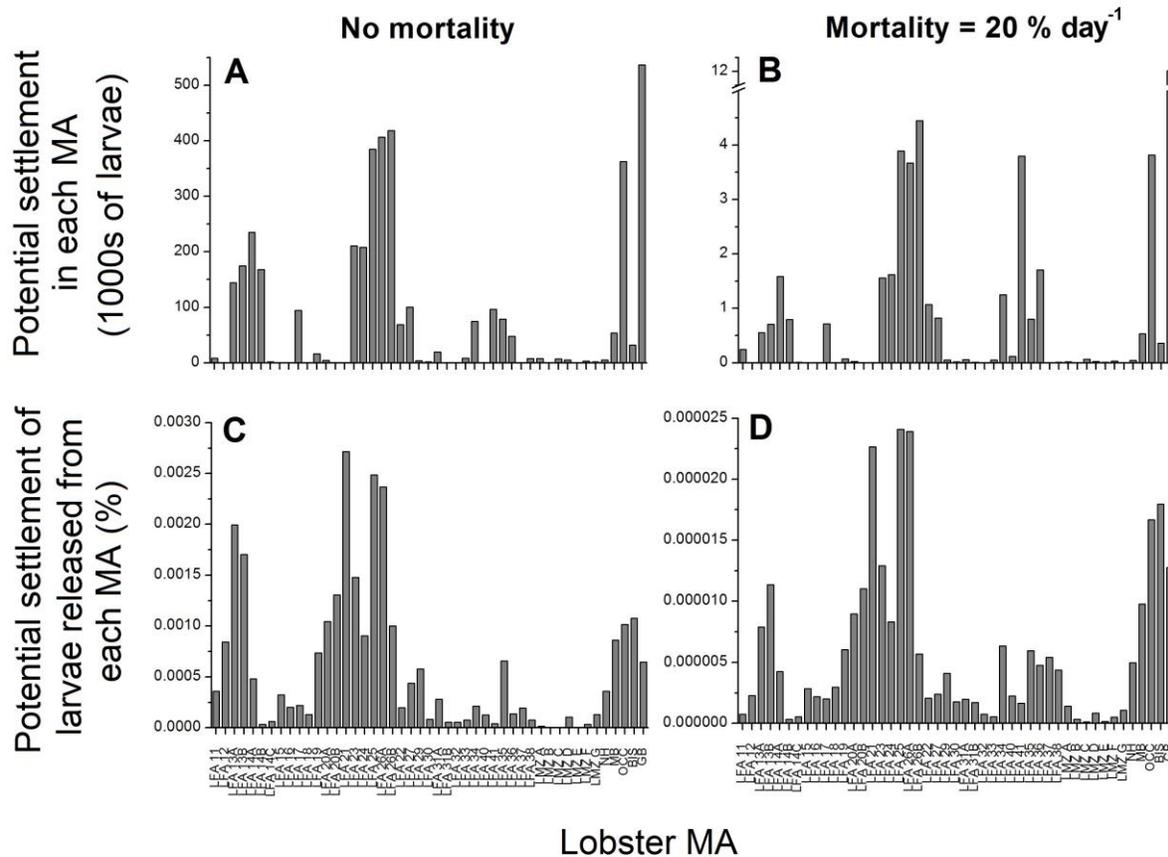
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1011 **Fig. 2.** Representative circulation patterns during the summer across the model domain. Mean  
1012 modeled surface currents (averaged over the top 0-6 m of the water column) derived from the  
1013 physical oceanographic model (Brickman and Drozdowski 2012a, b) used in this study are  
1014 plotted for 15 June to 15 September 2011, which was an ‘average year’ in terms of settlement,  
1015 dispersal, and current data (results not shown). The size of arrows plotted indicates the  
1016 magnitude of mean currents per every fourth 9 km x 6 km model cell. Map made using Generic  
1017 Mapping Tools GMT-5.3.1 (Wessel et al. 2013; available online at: <http://gmt.soest.hawaii.edu/>).



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1019 **Fig. 3.** Frequency distribution of distances drifted by larvae between hatch and settlement in  
 1020 model simulations with larval mortality of (A) 0 % day<sup>-1</sup> or (B) 20 % day<sup>-1</sup>. Values were  
 1021 calculated based on model outputs averaged across 2005-2012 (see Methods). The maximum  
 1022 distance drifted is indicated by an arrow. The black square and solid bars below each x-axis  
 1023 indicate the average distance drifted  $\pm$  SD, and the 'x' symbols with dashed line show the 5<sup>th</sup> and  
 1024 95<sup>th</sup> percentiles of the data.



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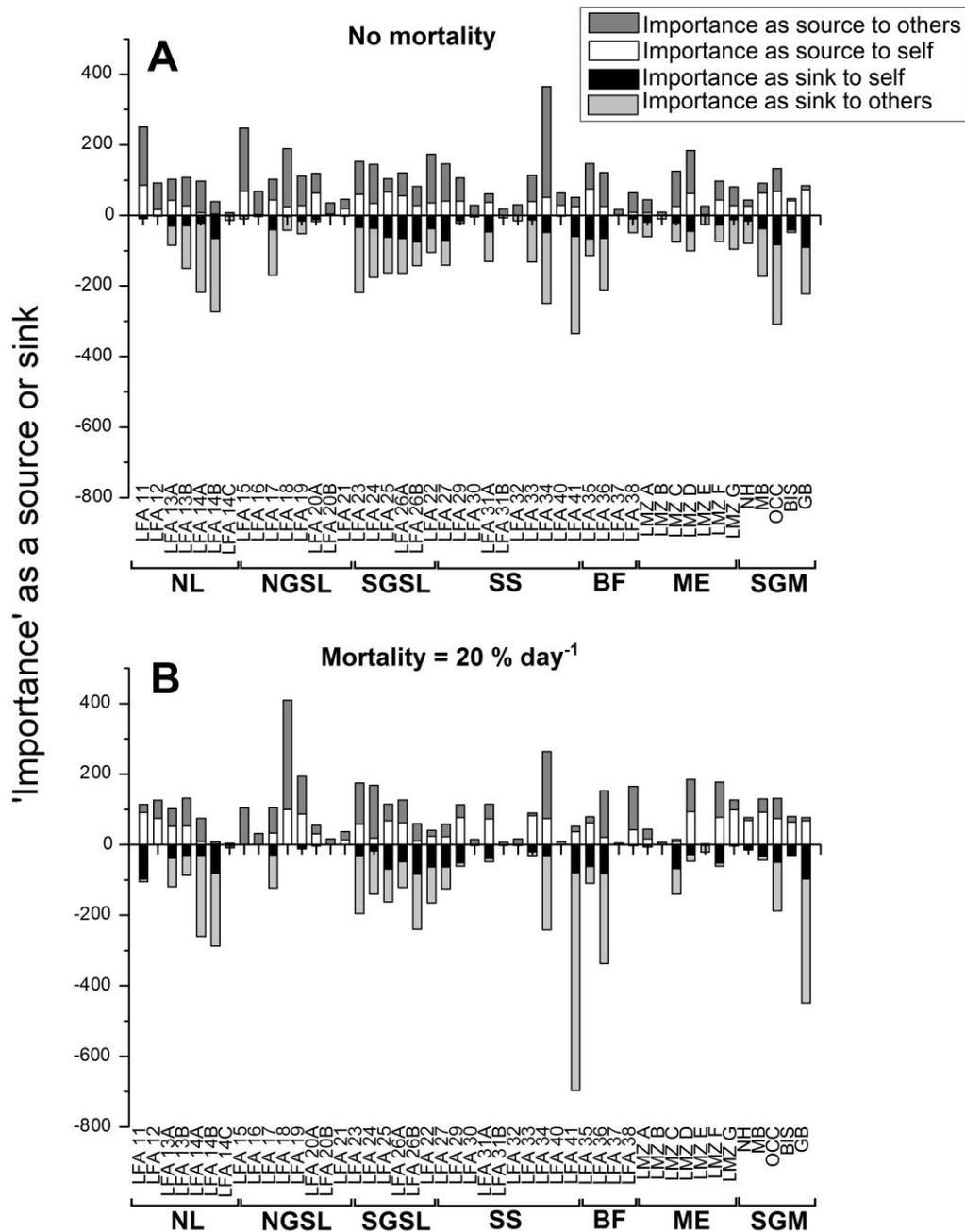
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1027 **Fig. 4.** Average annual potential settlement of larvae in each MA (1000s of larvae) (A, B) and  
 1028 percent settlement of larvae released from each MA (%) (C, D) across all simulated years (2005-  
 1029 2012), assuming larval mortality of (A, C) 0 % day<sup>-1</sup> or (B, D) 20 % day<sup>-1</sup>.

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1038 (rows) or (C, D) predicted to settle in a particular sink area (columns) that were released  
1039 (hatched) from a given source area (rows). Darker shading indicates higher percentages, and the  
1040 values in each column add to 100 %. Areas are labeled with Canadian LFA numbers, Maine  
1041 (USA) LMZ letters, or other abbreviations in the southern GM (SGM, USA) (see Fig. 1B and  
1042 Methods). The larger geographic regions in which MAs are located are also labeled, with  
1043 abbreviations as in Fig 1A.  
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1047 **Fig. 6.** 'Importance' of each lobster management area (MA) as a potential source (positive  
 1048 values) and sink (negative values) of larvae to other MAs (dark and light gray bars) and to itself  
 1049 (white and black bars). Importance indices were calculated based on model simulations assuming  
 1050 (A) larval mortality of 0 % day<sup>-1</sup> and (B) 20 % day<sup>-1</sup>. Importance as a source was assigned a

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1051 positive value and importance as a sink a negative value for clarity of plotting. The magnitude of  
1052 an area's importance is an index of to what extent it is predicted to be connected with other  
1053 areas; for details of the calculation of these values, see Methods. Areas are arranged from left-to-  
1054 right in the approximate order of prevailing currents across the model domain (see Fig. 2).  
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