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Stock structure and connectivity of the American lobster *Homarus americanus* in the southern Gulf of St. Lawrence: do benthic movements matter?

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26 **Key Words**

27 American lobster, *Homarus americanus*, population connectivity, movement, behaviour, larval
28 dispersal, benthic dispersal

Draft

29 **Abstract**

30 The long-range dispersal of pelagic larvae is often assumed to be the dominant force
31 behind connectivity in the marine environment, with little consideration given to benthic
32 movements. We analyzed data from an American lobster tagging study (1980-1996) in the Gulf
33 of St. Lawrence during which 37,579 adults from 14 locations were tagged and 6,296 were
34 recaptured after 1-6 years at large. The 10th percentile greatest distance moved by tagged lobsters
35 after one year at large contributed to demographic connectivity between neighbouring statistical
36 districts, fishing ports, and (in one location) management areas. Considering the incremental
37 dispersal of lobsters after two versus one year at large, we estimate that the 10th percentile
38 greatest benthic dispersal distances after one, two and five years at large represented 7%, 14%
39 and 35% of larval dispersal in the “downstream” direction, respectively, and 75%, 111% and
40 220% of larval dispersal in the “upstream” direction (similar results obtained based on mean
41 dispersal values). We conclude that more attention should be given to benthic movements in
42 estimating connectivity and stock structure in American lobster.

Introduction

Biological dispersal can cause considerable exchange of propagules and individuals over the geographic range of a species, and this “connectivity” can impact the demography and genetics of populations (Clobert et al. 2001; Kinlan and Gaines 2003; Cowen and Sponaugle 2009). Demographic connectivity is broadly defined as the exchange of individuals between spatially separated subpopulations (Lowe and Allendorf 2010; Frisk et al. 2014). Based on results of modeling exercises simulating genetic changes in a “finite island model”, Waples and Gaggiotti (2006) proposed that two subpopulations could be considered transitioning to demographic independence when the fraction of the subpopulation that immigrates from another subpopulation falls below 0.1 (*i.e.*, no more than 10% of individuals in subpopulation A have immigrated from sub-population B). Therefore, demographic connectivity depends on the proportional contribution of migrants in each generation to local subpopulation size. In contrast, genetic connectivity depends on the absolute number of migrants between subpopulations in each generation (Waples and Gaggiotti 2006; Waples et al. 2008), and a small number of migrants every generation is sufficient to result in genetic similarity over time (Slatkin 1993). One of the most important outcomes of these modeling exercises is the demonstration that demographic dependence between two locations requires an exchange of individuals (*i.e.*, >10% *sensu* Waples and Gaggiotti 2006) that is several orders of magnitude greater than that required for the maintenance of genetic dependence between the same two locations.

Connectivity in the marine environment arises from both passive and active means, such as the drift of planktonic stages within ocean currents and directed movements of pelagic larvae in the water column or juveniles and adults on the sea floor. In most marine invertebrate fisheries, the current paradigm is that connectivity is largely a function of physical and biological

processes affecting patterns of larval dispersal and retention, structuring populations at a variety of temporal and spatial scales (Frisk et al. 2014). Based on this paradigm, coupled biological-physical models of larval dispersal have greatly advanced our understanding of population connectivity via larval dispersal in many species (Fogarty and Botsford 2006; Miller 2007; Cowen and Sponaugle 2009). The importance of adult movement to connectivity, including that relative to larval dispersal, has received little consideration, likely due to the difficulties of tracking mobile marine invertebrates over long periods of time. This neglect is probably also partly due to the intuition that the dispersal of larvae by ocean currents must occur over large distances and is likely the process that is most consequential to connectivity. Increasingly, however, studies are showing that larvae display strategies that markedly reduce their dispersal in comparison to the inert particles generally used in larval drift models (e.g., Butler et al. 2011; Lloyd et al. 2011). It has also recently been argued that the movements of adults may result in greater connectivity than those of larvae, due to the comparatively long time period during which movements by adults (years to tens of years) and larvae (minutes to months) are likely to occur (Frisk et al. 2008; 2010). As the focus of marine connectivity research has primarily been on larval drift (Kritzer and Sale 2006), the role of adults in connectivity may have been underappreciated, resulting in an incomplete understanding of the patterns and mechanisms underlying population structuring in marine species (Frisk et al. 2014).

The American lobster (*Homarus americanus*) is distributed along the eastern coast of North America, between North Carolina in the USA and the Strait of Belle Isle in Canada. It supports the most important fishery, in terms of landed value, in Canada (<http://www.dfo-mpo.gc.ca/stats/commercial/land-debarq/sea-maritimes/s2015av-eng.htm>; accessed 1 August, 2017) and in eastern North America overall (Wahle et al. 2004). Lobster fisheries in Canada are

managed using a number of “input control” measures (not quotas) applied to 45 fishing districts, which are referred to as Lobster Fishing Areas (LFAs), including LFA-specific licence limits, trap limits, minimum and/or maximum legal sizes, fishing seasons, and other LFA-specific measures (<http://www.dfo-mpo.gc.ca/decisions/fm-2017-gp/atl-20-eng.htm>; accessed 27 January, 2018). There are two distinct life phases in the American lobster’s life history, a pelagic larval phase and a benthic phase. The pelagic phase comprises three larval stages and one postlarval stage ($\approx 2\text{--}4$ mm carapace length [CL]), and lasts for 11–54 days after hatch, dependent in part on water temperature (reviewed by Cobb and Castro 2008). It is currently unknown whether swimming behaviours by lobster larvae affect their dispersal trajectories and distances in nature, although they are sufficiently mobile (particular the stage IV postlarvae) for this to be likely (Stanley et al. 2016). The benthic phase comprises juvenile, adolescent, and adult individuals that live on the sea floor, and in the absence of heavy commercial exploitation the length of the adult stage may exceed 30 years (Lawton and Lavalli 1995). Both life-history phases are capable of long-distance movements (> 100 km), and these could have large impacts on connectivity in the species.

Larval drift modeling of the American lobster has been done in both the Gulf of Maine (Incze and Naimie 2000; Xue et al. 2008; Incze et al. 2010) and the Southern Gulf of St. Lawrence (sGSL) (Chassé and Miller 2010), and more recently over most of the species’ range (Quinn et al. 2017). These studies suggest that connectivity during the larval phase of the American lobster is highly important to population structure, through the annual movement of larvae over tens to hundreds of kilometers. However, larvae simulated in these models largely behave as inert particles before they are ready to settle (Incze and Naimie 2000; Xue et al. 2008;

Chassé and Miller 2010; Incze et al. 2010), and the drift distances predicted by these models have received very little empirical validation.

Facilitated by an intense commercial fishery, large body size, and ease of handling, mark-recapture tagging studies have been used to quantify exploitation rate, growth, and movement of the American lobster since 1898 (*e.g.*, Bumpus 1901; Krouse 1980; Haakonsen and Anoruo 1994; Comeau and Savoie 2002; Cowan et al. 2007). The long-distance movements (tens to hundreds of kilometers) of mature lobsters observed during some mark-recapture tagging studies (*e.g.*, Uzmann et al. 1977; Campbell and Mohn 1983; Campbell and Stasko 1985; Campbell and Stasko 1986; Campbell 1986) led to suggestions of extensive mixing of adult lobsters in the Bay of Fundy and Gulf of Maine. In contrast, mark-recapture studies in the sGSL (reviewed by Comeau and Savoie 2002) observed only short annual alongshore movements (< 10 km on average) and concluded that these do not contribute to demographic connectivity between neighboring management units (Lobster Fishing Areas) in this region.

The sGSL (Figure 1) is a unique environment within the range of the American lobster. During the harsh winters, the surface waters freeze completely along the coast, but during the summer the wide and shallow (20-40 m) coastal areas of the sGSL warm up to a greater temperature than observed in other parts of the species' range in Canada. Additionally, the sGSL is characterized by the presence of an extensive cold intermediate layer (CIL), which is a large and cold body of water occurring between the surface waters and the deep waters of the Laurentian Channel (Gilbert and Pettigrew 1997). The temperature of the CIL is generally less than 1.5°C. American lobsters can survive in waters between -1.5°C and 30°C, but temperatures below 5°C inhibit molting and other physiological processes while those below 0°C result in a state of hibernation (Waddy et al. 1995). The top of the CIL occurs between 20 and 40 m depth

from June to October and is at the surface from January to April (Gilbert and Pettigrew 1997). Thus, lobsters in the sGSL are only observed within the CIL in the winter, when there is no warm water available, and between the spring and fall they spend their time in the warm shallow coastal waters to facilitate growth and embryonic maturation (Cowan et al. 2007). Most importantly, and contrary to other parts of the species' range (see below), there is no physiological advantage for lobster in the sGSL to make long-distance movements into deep (> 40 m) water (Stasko 1980) in the winter because of the CIL (Comeau and Savoie 2002), even though they are thought to move away from very shallow coastal areas in the fall to avoid ice scouring and temperatures below 0°C (Templeman 1936; Corriveau 1948; Bergeron 1967; Munro and Therriault 1983; Comeau and Savoie 2002). In contrast, in the Gulf of Maine the deep water is warmer than the shallow coastal water during winter months, and lobsters execute extensive shallow-to-deep migrations in late fall that facilitate growth and embryonic development (Campbell and Stasko 1985; Campbell and Stasko 1986; Campbell 1986; Campbell 1989; Cowan et al. 2007).

The purpose of this study was to estimate the relative contribution of benthic and larval dispersal to demographic connectivity in the American lobster within the sGSL. Previous tagging studies in the sGSL concluded that benthic movements by the American lobster are limited and short-ranged (see Comeau and Savoie 2002 for review). These studies are generally based on mean displacement values, and they ignore the potential role of individuals that move longer distances to demographic and genetic connectivity. Furthermore, the directionality of these benthic movements has not been considered, and is likely to be less constrained than that of larvae, which are predicted to drift primarily in the direction of the dominant west to east circulation of the sGSL (Chassé and Miller 2010; Quinn et al. 2017). Finally, there has been no

157 consideration of the fact that benthic movements can accrue over the lifetime of an individual.
158 As a first attempt to compare the scale of connectivity caused by benthic and larval dispersal of
159 American lobster in the sGSL we: (1) used the results of an extensive tagging study conducted in
160 the sGSL between 1980 and 1996 to quantify the magnitude and direction of the movements
161 undertaken by lobsters at large for one and two years; (2) estimated demographic connectivity
162 among Lobster Fishing Areas (LFAs), Statistical Districts, and fishing ports caused by benthic
163 dispersal; and (3) compared estimates of benthic dispersal from 14 tagging-and-release locations
164 to estimates of larval dispersal derived from a bio-physical model for the same release (*i.e.*,
165 hatch) locations. These analyses likely provide a conservative test of the contribution of benthic
166 movements to connectivity in American lobster, because lobsters in other parts of the species'
167 range (*e.g.*, the Bay of Fundy-Gulf of Maine region) are known to execute longer-ranging
168 movements (*e.g.*, Uzmann et al. 1977; Campbell and Mohn 1983; Campbell and Stasko 1985;
169 Campbell and Stasko 1986; Campbell 1986) than those documented in the sGSL (Templeman
170 1935; 1936; Corriveau 1948; Wilder 1963; 1974; Bergeron 1967; Munro and Therriault 1983;
171 Comeau and Savoie 2002).

172

173 **Methods**

174 **Mark – Recapture Dataset**

175 Lobsters were captured using commercial traps, tagged, and then released at 31 sites in
176 the sGSL between 1980 and 1996 by the Department of Fisheries and Oceans (DFO) scientists
177 (Comeau and Savoie 2002). Lobsters were tagged directly after capture onboard either chartered
178 fishing vessels or DFO research vessels between June and November. They were tagged with

orange sphyron anchor tags prior to 1989, and with blue streamer tags after 1992, both of which are designed to remain attached to the lobster during moulting. Between 1989 and 1992 inclusively, both types of tags were used (Comeau et al. 1999). A description of the tags and tagging technique are presented in Moriyasu et al. (1995) and Comeau et al. (1998). Information on the recapture location came from commercial harvesters, as the lobsters were caught during the commercial fishing seasons. Coordinate information was taken by the harvesters, who then passed along the tagged lobsters to DFO representatives and were reimbursed for the market value of the lobster, or in the case of undersized or ovigerous lobsters, released them back where they were caught with their tag still attached. A major awareness and advertising campaign was run to maximize the participation of harvesters reporting recaptured individuals (Comeau et al. 1999).

In this study we used the data from 14 of the 31 sites (Figure 1), which were sites from which at least 20 lobsters were recovered after spending at least one year at large, and for which accurate recapture date and location information was available. A total of 37,579 lobsters were tagged between 1980 and 1996 at these 14 sites; 5,906 tagged lobsters were recaptured after one year at large and 294 lobsters were recaptured after two years at large (Table 1). While a small number ($n = 109$) of lobsters were recaptured 3-6 years after tagging, sample sizes of such individuals at each tagging location were too small to be used in this study. Comeau and Savoie (2002) found no evidence of a relationship between lobster size or gender and distance travelled. Therefore, for simplicity and to increase sample size, we pooled all lobsters by tagging location for the analyses in this study, and did not distinguish them on the basis of size or gender.

200 **Evaluation of Connectivity: Benthic Dispersal**

201 In previous tagging studies in the sGSL (reviewed by Comeau and Savoie 2002), lobsters
202 generally moved alongshore away from where they were tagged because their movements were
203 constrained by the CIL. Therefore, movement distances were estimated in previous studies as the
204 Euclidean distance between tagging and recapture locations. In this study we took a different
205 approach because we were concerned with dispersal that leads to connectivity between fishing
206 ports and management areas along the shore, and not between shallow coastal and deep offshore
207 water. We therefore calculated only the component of individual movements that was parallel to
208 the shore (hereafter longshore movement) was considered, and the component that was
209 perpendicular to the shore was ignored (see Figure 3 for example). Longshore movement of each
210 lobster was classified as “upstream” or “downstream” in relation to the general west to east
211 circulation in the sGSL, as considering directionality of movements could result in important
212 differences in the contribution of adults and larvae to connectivity.

213 The “upstream” and “downstream” lobster movements from each of the 14 tagging
214 locations were summarized in two different ways. First, we estimated the mean Euclidean
215 distance moved between release and recapture, as done in previous studies (*e.g.*, Comeau and
216 Savoie 2002). Second, we also estimated the 10th percentile greatest distance moved by lobsters,
217 as an index of the contribution of these movements to demographic connectivity. The rationale
218 behind these second estimates is that if individuals moving from point A to point B represent <
219 10% of the number of individuals in B, and vice versa, their influence on each other is low, and
220 they can be considered independent demographic populations (*sensu* Waples and Gaggiotti
221 2006). Frequency distributions of both upstream and downstream dispersal distances were
222 generated for each of the 14 tagging locations, based on longshore distances moved by individual

lobsters after one year at large, and from each of these we derived the mean and greatest 10th percentile distance moved. This procedure was then repeated based on longshore dispersal distances of lobsters that were recaptured after being at large for two years, using the six tagging locations from which at least 10 individuals were recaptured after two years at large. The 10th percentile greatest distances moved after one and two years at large were used to estimate demographic connectivity among LFAs, Statistical Districts, and Fishing Ports (Figure 2). Finally, we estimated the dispersal that could occur after 5 years at large based on the observed change in 10th percentile greatest dispersal distance between recaptures after one year (Yr1) and two years at large (Yr2), while assuming that this change is constant across years. Although the rate of change may not be linear between Yr1 and five years (Yr5), we made this assumption because the empirical data collected for Yr1 & Yr2 provides the best estimate for benthic dispersal of adult lobsters over consecutive years in the sGSL.

To make inferences about demographic connectivity based on the 10th percentile greatest distance moved, we assumed that all sub-populations in the sGSL have similar sizes, as demographic connectivity is a function of the relative and not the absolute number of migrants to the subpopulation. For example, 10% of individuals from a small subpopulation moving into a large subpopulation may not be demographically meaningful to the large sub-population, but the same proportion of individuals moving in the opposite direction would be. Unfortunately, we do not know where the “boundaries” of lobster subpopulations are in the sGSL (or elsewhere), nor the number of individuals within each of these subpopulations. It is, in fact, quite likely that there are no hard boundaries to longshore dispersal in the sGSL, although the system is also not completely “mixed” and recent molecular work indicates significant (albeit small) genetic structure at relatively small (≈ 100 – 200 km) spatial scales (Benestan et al. 2015). Importantly,

this assumption of similarly sized sub-populations is of no real consequence to our main objective of estimating the relative contribution of benthic movements and larval dispersal to connectivity.

Fifteen lobsters tagged in the Baie des Chaleurs (Figure 1) were re-captured more than once in subsequent years, providing a small but unique dataset to investigate how individual lobsters move over multiple years. These data were analyzed to determine if the lobsters tended to remain in a general area year after year, gradually moved further away from the tagging location year after year, or behaved differently in different years (*i.e.*, moved away from the tagging location one year, but moved back in the next, or the reverse).

Evaluation of Connectivity: Larval Dispersal

Larval dispersal distances, which reflect the estimated spread of larvae from a spawning site to a settlement site as a result of ocean currents, were derived from simulations with an individual-based bio-physical dispersal model of American lobster larvae (Quinn et al. 2017) coupled to a three-dimensional physical oceanographic model (Canadian Ocean Parallisé (CANOPA)) of the Atlantic Shelf of eastern North America (longitude: 71.5°–54.9°W; latitude: 38.6°–52.0°N; Brickman and Drozdowski 2012). Simulations of the larval drift model were run over 8 years from 2005 to 2012, and while these years do not overlap with those of the tagging studies (1980-1996), modeling results suggest that there is considerable inter-annual consistency in the direction and distance of larval dispersal predictions in the sGSL (Chassé and Miller 2010; Quinn et al. 2017).

During each simulation, clusters of larvae were released every 12 h between June and September, when larval release and drift occur in nature (Aiken and Waddy 1986; Incze et al.

2010). Larvae were released in the same quantity and at the same time in all model cells (≈ 54 km²) of our model domain that fell within the lobster's historical range (Pezzack 1992). Larvae were assumed to drift passively at the surface (*i.e.*, no directional swimming was included in the model), and no mortality was included. Time spent drifting was controlled based on (i) water temperature experienced by larvae, (ii) temperature-dependent development equations derived from laboratory studies on this species (MacKenzie 1988; Quinn et al. 2013), and (iii) settlement beginning halfway through stage IV (Cobb et al. 1989) and occurring where bottom temperature was $\geq 10^{\circ}\text{C}$ (Chiasson et al. 2015). Additional details concerning this model can be found in Quinn et al. (2017).

The circulation model tracks individual simulated larvae, enabling the identification of release and settlement "locations" (*i.e.*, ≈ 54 km² model grid cells) of each larva that was predicted to have successfully settled. For this study we only concerned ourselves with the larvae that were released in each of the 14 model grid cells that were closest to the 14 locations where adult lobsters were tagged. We created "upstream" and "downstream" longshore dispersal-distance frequency distributions of these larvae, as was done for the adults (see Figure 3), and calculated from these 28 distributions (14 release locations x 2 directions) the mean and 10th percentile greatest distances moved. It should be noted that passively drifting larvae obviously cannot move against currents. "Upstream" movement of larvae in this context refers to larvae that dispersed in directions against the *predominant* current directions in their region of the sGSL, during periods of current reversal, eddies, or other transient circulation features.

288 **Evaluation of Connectivity: Benthic versus Pelagic Dispersal**

289 In order to compare the amount of connectivity caused by benthic and larval dispersal of
290 American lobster in the sGSL, we calculated the distance moved by the adults as a percentage of
291 the distance moved by the larvae. For example, 50% would indicate that benthic dispersal was
292 half the distance of larval dispersal, and 4000% would indicate that benthic dispersal was 40
293 times greater than the distance of larval dispersal. These estimates were made separately for
294 upstream and downstream directions at each of the 14 sites, and based on both the mean and top
295 10th percentile dispersal distances.

296 **Results**

297 **Benthic Connectivity - One Year at Large**

298 A total of 5,906 lobsters were recaptured after one year at large over the course of the
299 tagging study in the sGSL. More lobsters were re-caught “upstream” (mean $\pm$ SD of 14 release
300 locations = 262 ± 244 individuals) than “downstream” (160 ± 174) from their release location,
301 and this difference was statistically significant (paired *t*-test, $t=-2.24$, $df=13$, $p=0.04$). The mean
302 longshore distance moved by these lobsters (one direction or the other) at each of the 14 tagging
303 locations was relatively low, varying between 1.1 (Stonehaven, New Brunswick [NB]) and 25.7
304 km (Egmont Bay, Prince Edward Island [PEI]) (mean $\pm$ SD = 7.6 ± 5.9 km), and it caused no
305 movement between neighbouring LFAs, Statistical Districts or fishing ports (Table 2 & 3; Figure
306 4). The 10th percentile greatest distance moved was between two and four times greater than the
307 mean distance, varying between 2.4 km (Stonehaven, NB) and 59.2 km (Egmont Bay, PEI)
308 (mean $\pm$ SD = 16.3 ± 14.5 km), and generally contributed to demographic connectivity between
309 neighbouring Statistical Districts and neighbouring to multiple neighbouring fishing ports, and in

one location between LFAs (Table 2 & 3; Figure 4). Furthermore, while lobsters displayed fairly even benthic dispersal distances in both directions at a number of the tagging locations, in other locations they showed dispersal distances that were approximately two to three times greater in one direction than in the other (Table 2 & 3; Figure 4).

Benthic Connectivity - Two Years at Large

A total of 294 lobsters were recaptured after two years at large, all from six of the 14 tagging locations (Table 2 & 3). A similar (paired t test, $t=0.976$, $df=5$, $p=0.37$) number of lobsters were re-caught in the upstream (mean $\pm$ SD = 26 ± 19 individual lobsters) and downstream (23 ± 14) directions. The mean longshore distance moved over two years by these lobsters (one direction or the other) at each of the six tagging locations was relatively low, varying between 1.0 and 15.7 km (mean $\pm$ SD = 8.1 ± 5.4 km), and it caused no connectivity between LFAs, Statistical Districts or fishing ports (Table 2 & 3; Figure 5 & 6). The 10th percentile greatest distance moved after two years at large was between two and four times greater than the mean distance, varying between 2.3 km (Stonehaven, NB) and 40.1 km (Anse Bleue, NB) (mean $\pm$ SD = 19.8 ± 13.9 km), and generally contributed to demographic connectivity between neighbouring Statistical Districts and neighbouring to multiple neighbouring fishing ports, but not among LFAs (Table 2 & 3; Figure 5). Overall, there was a significant increase in both mean dispersal distances (paired t -test including upstream and downstream distances: $t=-2.87$, $df=11$, $p=0.015$) and 10th percentile greatest dispersal distances ($t=-3.24$, $df=11$, $p=0.0079$) by lobster after two versus one year at large. This increase in dispersal distance after two years at large is important, as it indicates that demographic connectivity based on benthic movements increases over time. While both the mean and 10th

percentile greatest dispersal distances moved by lobsters after two years at large caused no connectivity between LFAs, they increased demographic connectivity between Statistical Districts and fishing ports (Figure 5 & 6). Lobsters from Caraquet, NB, displayed the greatest displacements after two years at large, with 10th percentile greatest distance moved reaching ≈ 70 km and connecting their release location with four Statistical Districts and 11 fishing ports (Figure 5).

Benthic Connectivity - Multiple Recaptures

In the Baie des Chaleurs, where a large proportion (24.5%) of the lobsters included in this study were tagged, 15 lobsters were re-captured in the following year, returned to the water, and then re-captured again one year later. Of these 15 lobsters, 10 moved very little and were recaptured within 2 km of their tagging location for two consecutive years, and five moved considerably more, four moving less than 2 km in the first year but > 40 km in the second year, and one moving 35.9 km in the first year and an additional 33.5 km in the same direction in the second year.

Larval Connectivity

Larval dispersal in the sGSL was significantly (paired t -test: $t=4.07$, $df=13$, $p=0.001$) biased in the “downstream” direction (*i.e.*, in the same direction as the primary west to east circulation), with an average of 76% and 24% of simulated larvae from the 14 study locations dispersing downstream and upstream, respectively. Furthermore, mean predicted dispersal distances of these larvae averaged 71 km in the downstream and 2 km in the upstream direction, across our 14 study locations (Table 2). Dispersal estimates based on 10th percentile greatest

values were greater, averaging 139 km and 57 km in the downstream and upstream directions, respectively, across our 14 study locations (Table 3). The percentage of larvae moving downstream versus upstream varied widely between study locations. For example, in Pleasant Bay, Nova Scotia (NS), 99.99% of simulated larvae moved downstream and only 0.001% moved in the upstream direction, and in Belledune, NB, only 19.91% of simulated larvae moved downstream relative to the general west-to-east circulation in the sGSL and 80.09% moved upstream. As well, larval dispersal distances varied among release locations, with a few locations having similar larval dispersal distances in the upstream and downstream directions, and others showing no larval dispersal in the upstream direction and more than 100 km mean longshore dispersal in the downstream direction (Table 2 & 3).

Comparison between Benthic and Larval Dispersal Distances

Mean Dispersal Values

Comparisons of mean larval and benthic dispersal distances show considerable variability among tagging locations, and even greater differences between dispersal directions (Table 2). After 1 year, benthic dispersal in the downstream direction ranged from 1.2% to 108.7% of larval dispersal distances at the 14 release locations, with a mean $\pm$ SD of $23 \pm 29\%$. After 2 years of benthic dispersal, these values range from 1.1% to 58.2% (mean $\pm$ SD = $16 \pm 21\%$) among the six study locations where some individuals were re-captured after two years at large. When benthic dispersal values were projected over 5 years for the same six study locations, they represented 0.9% to 96.2% (mean $\pm$ SD = $31 \pm 34\%$) of the larval dispersal distances.

The importance of benthic dispersal relative to pelagic dispersal was markedly greater in the upstream than in the downstream direction. After 1 year, benthic dispersal in the upstream

direction ranged from 89.2% to 7,320.5% of larval dispersal distances at the 14 tagging locations, with a mean $\pm$ SD of $1,904 \pm 2,485\%$. After 2 years of benthic dispersal, these values range from 306.5% to 15,510% (mean $\pm$ SD = $4,869 \pm 5,826\%$) among the six study locations where some individuals were re-captured after two years at large, and when these benthic dispersal values were projected over 5 years, they represented 725% to 50,640% (mean $\pm$ SD = $11,096 \pm 19,779\%$) of the larval dispersal distances at these six tagging locations.

10th Percentile Greatest Dispersal Values

The relative importance of larval and benthic dispersal based upon 10th percentile greatest distances moved is similar to the overall trend displayed by the mean dispersal distances (Table 3). After 1 year, upper 10th percentile benthic dispersal values in the downstream direction ranged from 2.5% to 58.3% of larval dispersal distances at the 14 tagging locations, with a mean $\pm$ SD of $16 \pm 17\%$. After 2 years of benthic dispersal, they ranged from 2.4% to 33.4% (mean $\pm$ SD = $14 \pm 11\%$) among the six study locations where some individuals were re-captured after two years at large. When these benthic dispersal values were projected over 5 years for the same six study locations, they represented 2.1% to 92.6% (mean $\pm$ SD = $35 \pm 33\%$) of the larval dispersal distances.

As with the mean dispersal distance comparisons, the importance of benthic relative to pelagic dispersal based on the upper 10th percentile values was markedly greater in the upstream than in the downstream direction. After 1 year, the upper 10th percentile benthic dispersal distance in the upstream direction ranged from 4.7% to 1,479.3% of larval dispersal distances at the 14 tagging locations, with a mean $\pm$ SD of $233 \pm 436\%$. After 2 years of benthic dispersal, these values range from 8.7% to 342.2% (mean $\pm$ SD = $111 \pm 140\%$) among the six study

locations where some individuals were re-captured after two years at large, and when these benthic dispersal values were projected over 5 years, they represented 9.4% to 717.2% (mean $\pm$ SD = $220 \pm 268\%$) of the larval dispersal distances at these six tagging locations.

Discussion

Findings of this study indicate that benthic movements are consequential to demographic connectivity of American lobster in the sGSL. This conclusion is supported by estimates of the contribution of benthic dispersal to connectivity between fishing areas, especially when considering benthic dispersal of adults after multiple years at large, as well as by consideration of the magnitude and directionality of benthic movements relative to those made by larvae in the water column.

Contribution of benthic dispersal to connectivity between ports, Districts, and LFAs

The mean benthic dispersal distances estimated were somewhat lower than those previously reported for the same data and 14 tagging locations in the sGSL (reviewed by Comeau and Savoie 2002), because they only reflected the longshore component of movements rather than Euclidian distances. These mean longshore dispersal estimates did not connect fishing ports, Statistical Districts, or LFAs. However, the 10th percentile greatest dispersal distances did lead to benthic connectivity between fishing ports and Statistical Districts, and at one site between neighbouring LFAs (Figure 4). Also, it should be noted that the 14 tagging sites used in this study are an arbitrary subset of the 100+ fishing ports in the sGSL, and if these 14 spatial landmarks had been located closer to LFA boundaries we would have concluded that benthic movements contribute more strongly to connectivity between LFAs. The latter point also

serves to highlight more generally one important limitation to these analyses, which is that they are based on arbitrary spatial units (e.g., release locations, fishing ports, Statistical Districts, LFAs) that are not reflective of lobster meta-population structure.

Our study is the first to explicitly investigate connectivity in American lobster on the basis of the greater movements displayed by a small fraction of the population, or more specifically the 10th percentile greatest distances moved, rather than only the mean distances moved by a group of individuals. Importantly, these 10th percentile values allowed us to more directly speak to the potential demographic connectivity (*sensu* Waples and Gaggiotti 2006) of lobsters in the sGSL, and estimates like these are becoming more widely recognized as useful to the management of populations, including those exploited by fisheries. For example, Palsbøll et al. (2007) proposed that the identification of management units (stocks in fisheries science) from population genetic data should be based on the amount of genetic divergence at which populations become demographically independent, rather than genetic divergence at which the null hypothesis of panmixia is rejected. They suggest that populations should be assigned to different management units if the rate of dispersal of individuals among populations is < 10% (*sensu* Waples and Gaggiotti 2006), and that if the assessment is to be based on genetic data, the threshold should not be rejecting panmixia but rather reaching the level of genetic differentiation that corresponds to a dispersal rate of 10% for the sub-populations being studied (Palsbøll et al. 2007).

Contribution of benthic versus pelagic dispersal to connectivity in the sGSL: magnitude

This study is also the first to compare the magnitude of dispersal by adults and larvae of American lobster from the same area, and results suggest that these are loosely comparable and

likely both need to be considered to obtain an accurate picture of demographic connectivity. Furthermore, benthic movements may be particularly important in areas where larval modeling predicts almost no larval retention and/or minimal settlement (Quinn et al. 2017). Our findings suggest the need for an expansion of research focus, as connectivity in American lobster has mainly been studied on the basis of larval dispersal, both in the sGSL (Comeau and Savoie 2002; Chassé and Miller 2010; Quinn et al. 2017) and elsewhere over the species' range (Incze and Naimie 2000; Xue et al. 2008; Incze et al. 2010; Quinn et al. 2017). There are probably several explanations for this research bias (see Introduction), but our findings suggest that impact on connectivity should probably not be one of these. For example, at Beach Point, PEI, Egmont Bay, PEI and Ballantyne Cove, NS, the 10th percentile greatest benthic dispersal in the “downstream” direction after one year was 31%, 44%, and 58% of the larval dispersal distance at each of the sites, respectively, and in the “upstream” direction it was 919%, 1,479%, and 17%. Furthermore, when considering the six sites where lobsters were recaptured after two years at large, we estimate that the 10th percentile greatest benthic dispersal distances after one, two and five years at large represented 7%, 14% and 35% of larval dispersal in the “downstream” direction, respectively, and 75%, 111% and 220% of larval dispersal in the “upstream” direction. These multi-year estimates are justified by the fact that both mean and 10th percentile greatest distances were found to increase significantly between lobsters collected after one and two years at large, indicating that adults were not consistently/strongly homing to a same location year after year, but were rather continuing to drift (at least to some extent) from the initial release location. Therefore, the magnitude of benthic connectivity becomes increasingly comparable to that of pelagic connectivity as we consider that adults live and move multiple years, whereas larvae disperse over a single season. Additionally, the conclusion concerning the relative

465 contribution of benthic and pelagic movements to connectivity is unchanged when analyses are
466 based on mean rather than 10th percentile greatest dispersal distances.

467 One challenge to our multi-year estimates of adult dispersal is that the American lobster
468 is among the most heavily exploited marine species in the world, and in many parts of its range
469 between 70% and 90% of legal-size lobsters are estimated to be taken each year (Cobb 1995). In
470 the sGSL, the average exploitation rate between 1999-2011 (estimates during our study period,
471 1980-1996, are not available) was estimated to be 63% (DFO 2013), ranging from 47% to 81%
472 in different LFAs. This high fishery mortality rate will obviously reduce the contribution of
473 multi-year benthic movements to demographic connectivity. It is important to note, however,
474 that females have enhanced protection from the fishery compared to males, and may thus
475 contribute more to demographic connectivity than them; increased protection to females is
476 afforded through a complete ban on landing of ovigerous individuals, as well as a maximum
477 legal size of non-ovigerous females in LFA 25 (114 mm CL) and protection of “window-size”
478 non-ovigerous females (115-129 mm CL) in LFAs 23, 24 and 26A (MacMillan et al. 2009;
479 Rondeau et al. 2015). Adult lobsters also experience natural mortality, which varies with habitat,
480 predator abundance, and lobster size, but is estimated at $\approx$ 10%-15% in Atlantic Canada (Gendron
481 and Gagnon 2001; Comeau and LeBreton 2012; Tremblay et al. 2013). It must be noted that in
482 this regard, connectivity will also be affected by larval mortality, which has been estimated to be
483 as high as 90% between hatch and settlement (Ennis 1995). Once larvae successfully recruit to
484 the bottom, post-settlement mortality will occur for 5-7 years before individuals recruit to the
485 fishery, but is expected to be markedly less than mortality during the larval stage (Wahle et al.
486 2004).

Contribution of benthic versus pelagic dispersal to connectivity in the sGSL: directionality

Another reason why benthic movements should not be ignored in demographic connectivity studies is that their directionality is not constrained by ocean currents like those of larvae. This means that even if the magnitude of benthic and pelagic movements were the same, their impact on connectivity and stock structure could still differ based on directionality. If benthic movements and larval drift move lobsters in the same direction, their combined effects could favour greater demographic interdependence over the area investigated, which would offer less resilience to overfishing (Hastings and Harrison 1994; Botsford et al. 2001). In contrast, benthic movements and larval drift may work together to enhance the resilience of specific areas to harvesting if benthic movements occur in opposite direction (e.g., “up-current”) to larval drift (“down current”) in the area, creating a cyclical “re-seeding loop” (Dadswell 1979). In this study we found some evidence of re-seeding loops for lobsters in the sGSL, as (i) larval dispersal was markedly skewed towards the “downstream” direction, both in terms of number of larvae and the distance they travelled, (ii) a greater number of adult lobsters were re-captured “upstream” versus “downstream” from their original tagging locations after one year at large, and (iii) upstream dispersal distances were much greater for benthic adults than for pelagic larvae. Interestingly, a similar scenario has been hypothesized for lobster in two other parts of the species’ range. First, in the Gulf of Maine, a re-seeding loop has been proposed based on adults displaying directed benthic movements from inshore to offshore banks with larvae released on these offshore banks drifting with currents to seed inshore areas (Fogarty 1998). Secondly, it has been proposed that larvae hatching in the northeast portion of the Scotian shelf seed southwest areas, and then adults return to northeast areas (Dadswell, 1979). Similar cyclical life history has also been hypothesized in other lobster species (*i.e.*, *Jasus edwardsii*, Kelly 2001; *Panulirus*

510 *argus*, Cruz and Bertelsen 2008), with directed benthic movements thought to move egg-bearing
511 lobsters to areas offshore or alongshore away from productive nursery areas before eggs are
512 released into the currents, with the larvae passively and/or actively moving back to shallower and
513 warmer coastal habitats that are more favourable to settlement and survival of early benthic
514 stages.

515 **Influence of benthic movements on connectivity outside the sGSL**

516 The sGSL is a unique environment within the range of the American lobster, and was an
517 ideal region to estimate the relative influence of benthic and larval movements to connectivity
518 for the first time. As the sGSL is characterized by the presence of an extensive CIL (Gilbert and
519 Pettigrew 1997) where the water is $< 1.5^{\circ}\text{C}$ year round, it is assumed that there would be no
520 physiological advantage for lobster to make seasonal movements into deep (> 40 m) water in the
521 sGSL. Therefore, the study of benthic movements in the sGSL can be largely thought of as a
522 two-dimensional problem, with lobsters moving along the shore away from the tagging locations.
523 In most other areas south of the sGSL (*i.e.*, Scotian shelf and southwards) water temperatures
524 and topography allow lobsters to be found over a much greater depth range (Richaud et al. 2016)
525 and to be markedly less restricted to movements along the coastlines. Many tagging studies have
526 been conducted in and around the Gulf of Maine over the past 120 years (*e.g.*, Bumpus 1901;
527 Uzmann et al. 1977; Campbell and Mohn 1983; Campbell and Stasko 1985; Campbell and
528 Stasko 1986; Campbell 1986; Campbell 1989), and these have revealed that most adult lobsters
529 make relatively short yearly or multi-yearly movements (10s of km over 1-6 years at large).
530 However, these studies have also consistently shown that some individuals undertake markedly
531 longer-range movements (hundreds of kms over 1-6 years at large, with a maximum distance

ever recorded of 798 km [undertaken by a male lobster in 3.5 years; Campbell and Stasko 1986]], which radiate out from the tagging locations in all directions. In the sGSL, the maximum individual distance moved at each tagging location after one year at large ranged from 16 km to 93 km, with an average of 52 km ($n = 14$ tagging locations), and this sub-100 km maximum movement continued even for individuals at large for 2 years after tagging. In contrast, movements over 100s of km in length after 1 to 6 years at large are relatively common in and around the Gulf of Maine (Campbell and Stasko 1985; 1986) suggesting that benthic movements in that region are much more important to population connectivity than they are in the sGSL. However, since these benthic movements have not been directly compared against larval drift estimates for the same areas, their overall contribution to population connectivity are unknown.

Implications

The findings of this study indicate that benthic movements are likely consequential to demographic connectivity of American lobster in the sGSL, or more specifically that the importance of benthic movements is significant relative to that of pelagic dispersal. Our findings therefore contrast with the current paradigm in the marine literature, where connectivity is generally assumed to be mainly a function of physical and biological processes that affect patterns of larval dispersal and retention. Our findings do, however, agree with a growing body of work suggesting that benthic movements are of importance to demographic connectivity in marine species, which led Frisk et al. (2014) to argue that only management and research pursuits that integrate the full life cycle of these species will generate a complete understanding of the patterns and mechanisms underlying structuring of their populations. As we continue to increase our understanding of population structure in the American lobster (*e.g.*, genetics:

554 Benestan et al. 2015; 2016; larval dispersal: Quinn et al. 2017; juvenile and adult movements;
555 Morse and Rochette 2016, this study), we are hopefully getting closer to being able to consider
556 the distance(s) over which larval and benthic movements are consequential to demographic
557 connectivity and management of the fishery.

Draft

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MANUSCRIPT TABLES

Table 1 - Details of the mark-recapture dataset used in this study. Tagging was conducted in the southern Gulf of St. Lawrence between 1980 and 1996 at 14 locations. For each tagging location the Lobster Fishing Area (LFA), total number of lobsters tagged, number of lobsters recaptured after one year and number of lobsters recaptured after two years are reported. A dash indicates that no lobsters were recaptured from that site.

Tagging Location	LFA	Total Number of Lobsters Tagged	Number of Recaptures after 1 year-at-large	Number of Recaptures after 2 years-at-large
Belledune, NB	LFA 23	2,638	496	72
Stonehaven, NB	LFA 23	1,135	502	38
Anse Bleue, NB	LFA 23	510	234	47
Caraquet, NB	LFA 23	3,931	1,190	99
Miscou, NB	LFA 23	1,005	130	25
Val Comeau, NB	LFA 23	1,995	374	-
Malpeque, PEI	LFA 24	2,813	492	-
Tracadie, PEI	LFA 24	462	27	-
Egmont Bay, PEI	LFA 25	6,489	20	-
Beach Point, PEI	LFA 26 A	4,879	188	-
Ballantynes Cove, NS	LFA 26 A	1,968	226	-
Port Hood, NS	LFA 26 B	1,986	339	-
Margaree, NS	LFA 26 B	4,868	1,317	13
Pleasant Bay, NS	LFA 26 B	2,900	371	-
Total		37,579	5,906	294

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Table 2 - Mean dispersal distances of American lobster larvae (in water column) and adults (on sea floor) in “upstream” and “downstream” directions from 14 locations within the southern Gulf of Saint Lawrence (sGSL). The larval dispersal distances and percentage of larvae from each site that moved “upstream” and “downstream” are based on simulations by a bio-physical model (Quinn et al. 2017). The adult benthic distances are based on a large tagging study in the sGSL between 1980–1996 (Comeau et al. 1999). Benthic values for one and two years are based on lobsters that were re-captured after one and two years at large, whereas values for 5 years are projected based on the increase in mean dispersal distance between animals at large for two and one year. Benthic dispersal after one, two, and five years is also calculated as a percentage of yearly larval dispersal, to illustrate the relative importance of benthic and pelagic dispersal distances to demographic connectivity. (LFA = Lobster Fishing Area; NB = New Brunswick; NS = Nova Scotia; PEI= Prince Edward Island).

Source	LFA	Direction	1 yr Dispersal		1 yr Dispersal		2 yr Dispersal		Extrapolated		Benthic Dispersal as Percentage of Yearly Larval Dispersal		
			(km) Larvae	Percentage of Larvae	(km) Benthic	n	(km) Benthic	n	5 yr Benthic		1 year	2 years	5 years
Belledune, NB	LFA 23	Downstream	12	19.91	5.5	185	7.0	34	11.5		45.5	58.2	96.2
Belledune, NB	LFA 23	Upstream	0.1	80.09	6.2	311	7.4	38	11.1		6180.0	7420.0	11140.0
Stonehaven, NB	LFA 23	Downstream	88	93.35	1.1	234	1.0	16	0.8		1.2	1.1	0.9
Stonehaven, NB	LFA 23	Upstream	0.1	6.65	1.8	268	1.7	22	1.6		1750.0	1700.0	1550.0
Anse Bleue, NB	LFA 23	Downstream	80	85.61	1.8	144	2.5	28	4.6		2.3	3.1	5.7
Anse Bleue, NB	LFA 23	Upstream	0.1	14.39	3.8	90	15.5	19	50.6		3800.0	15510.0	50640.0
Caraquet, NB	LFA 23	Downstream	87	85.23	10.1	652	12.5	59	19.9		11.6	14.4	22.8
Caraquet, NB	LFA 23	Upstream	2	14.77	7.8	538	13.7	40	31.4		390.0	685.5	1572.0
Miscou, NB	LFA 23	Downstream	167	99.20	4.6	70	15.7	13	49.3		2.7	9.4	29.5
Miscou, NB	LFA 23	Upstream	0.1	0.80	4.5	60	3.6	12	1.0		4470.0	3590.0	950.0
Val Comeau, NB	LFA 23	Downstream	97	93.18	9.5	107					9.8		
Val Comeau, NB	LFA 23	Upstream	3	6.82	8.1	267					271.0		
Malpeque, PEI	LFA 24	Downstream	79	78.31	10.4	218					13.2		
Malpeque, PEI	LFA 24	Upstream	11	21.69	9.8	274					89.2		
Tracadie, PEI	LFA 24	Downstream	101	91.74	13.8	13					13.7		
Tracadie, PEI	LFA 24	Upstream	0.1	8.26	7.3	14					7320.0		
Egmont Bay, PEI	LFA 25	Downstream	13	38.13	14.1	16					108.7		
Egmont Bay, PEI	LFA 25	Upstream	3	61.87	25.7	4					856.7		
Beach Point, PEI	LFA 26 A	Downstream	20	54.64	8.2	65					41.0		
Beach Point, PEI	LFA 26 A	Upstream	1	45.36	8.4	123					840.0		
Ballantyne Cove, NS	LFA 26 A	Downstream	57	77.89	23.2	38					40.6		
Ballantyne Cove, NS	LFA 26 A	Upstream	4	22.11	6.5	188					162.0		
Port Hood, NS	LFA 26 B	Downstream	12	61.07	3.7	56					30.4		
Port Hood, NS	LFA 26 B	Upstream	4	38.93	4.6	283					116.0		
Margaree, NS	LFA 26 B	Downstream	99	90.90	3.0	370	10.2	8	31.7		3.0	10.3	32.0
Margaree, NS	LFA 26 B	Upstream	2	9.10	3.3	947	6.1	5	14.5		167.0	306.5	725.0
Pleasant Bay, NS	LFA 26 B	Downstream	85	99.97	3.2	67					3.8		
Pleasant Bay, NS	LFA 26 B	Upstream	1	0.03	2.4	304					244.0		
Mean of Locations		Downstream	71	76	8		8		20		23	16	31
Mean of Locations		Upstream	2	24	7		8		18		1904	4869	11096

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Table 3 - 10th percentile greatest dispersal distances of American lobster larvae (in water column) and adults (on sea floor) in “upstream” and “downstream” directions from 14 locations within the southern Gulf of Saint Lawrence (sGSL). The larval dispersal distances and percentage of larvae from each site that move “upstream” and “downstream” are based on simulations by a bio-physical model (Quinn et al. 2017). The adult benthic distances are based on a large tagging study in the sGSL from 1980 – 1996 (Comeau et al. 1999). Benthic values for one and two years are based on lobsters that were re-captured after one and two years at large, whereas values for 5 years are projected based on the increase in 10th percentile dispersal distance between animals at large for two and one year. Benthic dispersal after one, two, and five years is also calculated as a percentage of yearly larval dispersal, to illustrate the relative importance of benthic and pelagic dispersal distances to demographic connectivity. (LFA = Lobster Fishing Area; NB = New Brunswick; NS = Nova Scotia; PEI= Prince Edward Island).

Source	LFA	Direction	1 yr Dispersal		1 yr Dispersal		2 yr Dispersal		Extrapolated		Benthic Dispersal as Percentage of Yearly Larval Dispersal		
			(km)	Percentage of	(km)	n	(km)	n	5 yr	1 year	2 years	5 years	
			Larvae	Larvae	Benthic		Benthic		Benthic				
Belledune, NB	LFA 23	Downstream	63	19.91	8.6	185	21.0	34	58.4	13.6	33.4	92.6	
Belledune, NB	LFA 23	Upstream	5	80.09	10.9	311	17.1	38	35.9	217.2	342.2	717.2	
Stonehaven, NB	LFA 23	Downstream	96	93.35	2.4	234	2.3	16	2.0	2.5	2.4	2.1	
Stonehaven, NB	LFA 23	Upstream	2	6.65	3.9	268	4.6	22	6.5	195.0	227.5	325.0	
Anse Bleue, NB	LFA 23	Downstream	94	85.61	4.8	144	6.2	28	10.3	5.1	6.6	11.0	
Anse Bleue, NB	LFA 23	Upstream	96	14.39	7.5	90	40.1	19	138.2	7.8	41.8	143.9	
Caraquet, NB	LFA 23	Downstream	272	85.23	38.1	652	40.8	59	49.0	14.0	15.0	18.0	
Caraquet, NB	LFA 23	Upstream	91	14.77	14.0	538	29.9	40	77.7	15.4	32.9	85.4	
Miscou, NB	LFA 23	Downstream	246	99.20	8.9	70	33.7	13	108.1	3.6	13.7	43.9	
Miscou, NB	LFA 23	Upstream	64	0.80	5.4	60	5.6	12	6.0	8.5	8.7	9.4	
Val Comeau, NB	LFA 23	Downstream	124	93.18	18.2	107				14.7			
Val Comeau, NB	LFA 23	Upstream	60	6.82	13.3	267				22.1			
Malpeque, PEI	LFA 24	Downstream	182	78.31	19.9	218				10.9			
Malpeque, PEI	LFA 24	Upstream	92	21.69	17.9	274				19.4			
Tracadie, PEI	LFA 24	Downstream	185	91.74	31.8	13				17.2			
Tracadie, PEI	LFA 24	Upstream	5	8.26	16.9	14				337.2			
Egmont Bay, PEI	LFA 25	Downstream	65	38.13	28.5	16				43.9			
Egmont Bay, PEI	LFA 25	Upstream	4	61.87	59.2	4				1479.3			
Beach Point, PEI	LFA 26 A	Downstream	64	54.64	19.9	65				31.1			
Beach Point, PEI	LFA 26 A	Upstream	2	45.36	18.4	123				919.0			
Ballantyne Cove, NS	LFA 26 A	Downstream	94	77.89	54.8	38				58.3			
Ballantyne Cove, NS	LFA 26 A	Upstream	91	22.11	15.1	188				16.6			
Port Hood, NS	LFA 26 B	Downstream	90	61.07	3.8	56				4.2			
Port Hood, NS	LFA 26 B	Upstream	90	38.93	8.6	283				9.5			
Margaree, NS	LFA 26 B	Downstream	185	90.90	7.2	370	23.4	8	72.3	3.9	12.7	39.1	
Margaree, NS	LFA 26 B	Upstream	95	9.10	7.4	947	14.1	5	34.3	7.8	14.9	36.1	
Pleasant Bay, NS	LFA 26 B	Downstream	188	99.97	6.6	67				3.5			
Pleasant Bay, NS	LFA 26 B	Upstream	98	0.03	4.6	304				4.7			
Mean of Locations		Downstream	139	76	18		21		50	16	14	35	
Mean of Locations		Upstream	57	24	14		19		50	233	111	220	

MANUSCRIPT FIGURES

Figure 1 - The 14 tagging locations in the southern Gulf of St. Lawrence (NB: New Brunswick; PEI: Prince Edward Island; NS: Nova Scotia) that were used in this study to evaluate adult-mediated connectivity of American lobsters (*Homarus americanus*). The boundaries of the Lobster Fishing Areas (LFAs) in the sGSL are indicated.

Figure 2- Overview of the recapture locations of all 6,200 lobsters used in this study (white circles) in relation to the Lobster Fishing Areas (large numbers), Statistical Districts (small numbers), tagging locations (large black circles with white crosses) and fishing ports (small black circles) in the southern Gulf of St. Lawrence. Note that there are a large number of lobsters that were recaptured along the coastline, near the tagging sites, and thus many recaptures overlap in this figure.

Figure 3- Illustration of two ways to estimate lobster movements between their tagging and recapture location. The animal in this example was tagged close to the coast (light grey area at bottom of figure), and it moved at an angle relative to the coast and towards the Cold Intermediate Layer (hatched line at top of figure). Line “A” displays the Euclidean distance between the two points, which is what has been reported in previous tagging studies of lobster in the southern Gulf of St. Lawrence (*e.g.*, Comeau and Savoie 2002). Line “B” captures only the component of the movement away from the tagging location that is parallel to the shore (*i.e.*, measurements made in this study). The larval dispersal estimates were obtained the same way.

Figure 4- Visual representation of the mean (black line) and 10th percentile greatest (white line) longshore dispersal distance of adult American lobsters released at each of the 14 tagging locations in the southern Gulf of St. Lawrence (sGSL), and recaptured after one year at large. The six tagging locations in and near the Baie des Chaleurs are in the top panel, and the eight tagging locations in the remainder of the sGSL are in the bottom panel. The dispersal lines were drawn to generally follow the coast, keeping within the Cold Intermediate Layer (CIL) and the shore. For the one tagging location where different options exist for movement route (*i.e.*, Caraquet, New Brunswick) given the distances measured and individual recapture locations, the three route options are presented. The actual distance values can be found in Table 2 & 3, and site names can be found in Figure 1. Fishing ports are identified by asterisks, Statistical Districts by thin solid lines, LobsterFishing Areas by single dotted lines, and the CIL is indicated by the thin crossed line.

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Figure 5- Visual representation of the 10th percentile greatest longshore dispersal distances of adult American lobsters re-captured after one (white line) and two (black double dotted line) years at large after being tagged at six locations (stacked black circles) in and near the Baie des Chaleurs. The dispersal lines were drawn to generally follow the coast, keeping within the Cold Intermediate Layer (CIL) and the shore. At one of the tagging locations there were no lobsters that were re-captured after two years at large. Note that the Caraquet, New Brunswick, tagging location has three possible dispersal routes, based on the 90th percentile movement distance in the easterly direction. The actual distance values can be found in Table 2 & 3, and site names can be found in Figure 1. Fishing ports are identified by asterisks, Statistical Districts by thin solid lines, Lobster Fishing Areas by single dotted lines, and the CIL is indicated by the thin crossed line.

Figure 6- Visual representation of the 10th percentile greatest longshore dispersal distances of adult American lobsters re-captured after one (white line) and two (black double dotted line) years at large after being tagged at six locations (stacked black circles) in Nova Scotia. The dispersal lines were drawn to generally follow the coast, keeping within the Cold Intermediate Layer (CIL) and the shore. The actual distance values can be found in Table 2 & 3, and site names can be found in Figure 1. Fishing ports are identified by asterisks, Statistical Districts by thin solid lines, Lobster Fishing Areas by single dotted lines, and the CIL is indicated by the thin crossed line.