

Using spatial statistics to infer scales of demographic connectivity between populations of the blue mussel, *Mytilus* spp.

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Abstract

We conducted a large-scale survey of blue mussel (*Mytilus* spp.) populations and recruitment along 100 km of the Southern shore of the St. Lawrence Estuary, Québec, Canada. By taking advantage of the residual downstream current of our study system, we used cross-covariance analysis to test the hypothesis that post-recruitment and larval supply processes result in a positive relationship between local adult abundance and recruitment. We found no evidence of within-site correlation between adults and recruits. Alternatively, we hypothesized that demographic connectivity between populations would result in a positive covariance between adult abundance and recruitment at downstream sites separated by the average dispersal distance. We observed significant positive cross-covariance between sites separated by 12–18 km and 24–30 km. These results provide the first direct quantification of demographic connectivity between adult production and larval recruitment of *Mytilus* using simple survey data. The approach developed here measures connectivity over ecological time scales, and thus may be used to monitor temporal fluctuations in dispersal patterns.

Many marine benthic invertebrates which are essentially sessile during the juvenile and adult portions of their lives spend a period of time in the water column as larvae, potentially allowing them to disperse widely from parental populations (Grantham et al. 2003). Such species have historically been modeled as demographically open systems in which local recruitment is decoupled from local production of larvae (Hixon et al. 2002; Johnson 2005). In contrast, fisheries stock-recruitment models are based on such coupling and assume closed populations such that links between adults and recruitment may be detected (Munch et al. 2005). Although estimates of larval dispersal distance (Gilg and Hilbish 2003; Kinlan and Gaines 2003) and the role played by recruitment in structuring benthic invertebrate populations (Hughes 1990; Sutherland 1990) have been investigated, we still know little about the reciprocal link between adult abundance and the recruitment of larvae (Hughes et al. 2000). Quantifying spatial scales of such demographic connectivity is, therefore, a central challenge for the understanding of benthic invertebrate populations.

Demographic connectivity (Kritzer and Sale 2004) is observed when recruitment into a local intertidal population is controlled, at least in part, by adults in other populations through dispersal of larvae at a characteristic spatial scale. In recent years ecologists have begun to embrace spatial statistics to assess correlation among populations. Spatial statistics can be used to characterize spatial aggregation within and among populations, or to detect relationships between species distributions and environmental characteristics. Similar tools can also be

applied to characterization of spatiotemporal variability in the form of spatial synchrony (Engen et al. 2002; Liebhold et al. 2004). However, a strong link between the description of spatial phenomena and the understanding of dynamic spatial processes such as demographic connectivity is still lacking (Engen et al. 2002).

Spatial statistics have been applied to stock-recruitment models to characterize the spatial scale of recruitment while controlling for the effect of adult abundance (Myers et al. 1997). However, with no mechanistic understanding of larval transport, the challenge of quantifying the scale of demographic connectivity per se remains an open problem. Such an understanding can be facilitated by the strong unidirectional flow in many river and estuarine systems that imposes directionality in dispersal, which may have important consequences for population persistence, species interactions, and competition (Speirs and Gurney 2001; Lutscher et al. 2006). Directionality in transport provides a priori knowledge about larval dispersal and predicts that the majority of larvae caught in surface currents of an estuary will be moved downstream. By examining the strength of the statistical relationship between local abundance of adults and downstream recruitment at a variety of spatial scales we can infer the characteristic scale(s) of demographic connectivity between populations that integrates both dispersal distance and the stock-recruitment relationship.

Here we take advantage of spatial statistical techniques and of the net unidirectional transport regime of the St. Lawrence estuary (Québec, Canada) to elucidate the existence and spatial scale of demographic connectivity between the recruitment and adult stages of the mussel *Mytilus* spp. using survey data. More precisely, lack of demographic connectivity predicts that covariance between adult abundance and recruitment is caused by physical conditions and should, thus, decrease with increasing

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spatial scale, reflecting the autocorrelated nature of physical parameters (i.e., sites closer together experience more similar conditions than sites farther apart; Legendre 1993). From this null hypothesis, we build on a simple stock-recruitment model by integrating a dispersal or connectivity function, and quantify the characteristic scale(s) of that function as the spatial scale(s) of significant covariance between upstream adult abundance and downstream recruit density. We predict that this covariance should be strongest along the main flow direction, and reflect the anisotropic nature of larval transport in the St. Lawrence estuary. Our results quantify dispersal distance in *Mytilus* spp. populations over ecological (single generation) temporal scales using spatial survey data. The long-term application of the spatial statistical methods presented here could reveal and quantify spatiotemporal variability in the scale of connectivity among benthic populations, which has mostly been considered as a stationary species trait.

Methods

The St. Lawrence Estuary—Surface currents in the St. Lawrence Estuary are driven largely by the Gaspé Current, a buoyancy-driven coastal jet, which is generated by the freshwater discharge of the St. Lawrence River and its tributaries (Sheng 2001; Fig. 1a). The Gaspé Current typically flows at a speed of about 10 cm s^{-1} , but can reach up to 50 cm s^{-1} along the Gaspé Peninsula, before entering Gulf of St. Lawrence where it weakens (Sheng 2001). Closer to the coast, flow velocities as high as 1 m s^{-1} have been recorded, but are generally $<50 \text{ cm s}^{-1}$ (Archambault and Bourget 1999). This current thus generates a net unidirectional residual transport regime along the Southern shore of the estuary. Because mussel larvae display positive phototaxis and negative geotaxis they are amenable to dispersal models based on surface currents (McQuaid and Phillips 2000; Gilg and Hilbish 2003). Although local shoreline configuration can affect recruitment rates in this region (Archambault and Bourget 1999), this is not always the case (McKindsey and Bourget 2000), and the absence of any major up- or down-welling regimes at the larger scale enable us to focus on the role played by dispersal among sites. The St. Lawrence Estuary was thus selected as an ideal marine system in which to test for demographic connectivity.

Study sites—A stretch of mainly rocky coastline approximately 100 km in length, spanning from Saint-Ulric (67.7559°W , 48.7725°N) to Sainte-Anne-des-Monts (66.5595°W , 49.1286°N), Québec (Fig. 1a), was chosen for study because of its limited topographic heterogeneity and because previous work (McKindsey and Bourget 2000) showed that there was a strong linear trend in mussel recruitment strength in the center of the study area. In order to maximize the number of pairwise comparisons between sites and the distances between them, we adopted a mixed nested-random sampling design. We selected 26 sites along the shore; with distances between sites ranging from 1 km to 100 km. Sites were chosen to represent the spatial scales of interest by examining topographical maps prior to

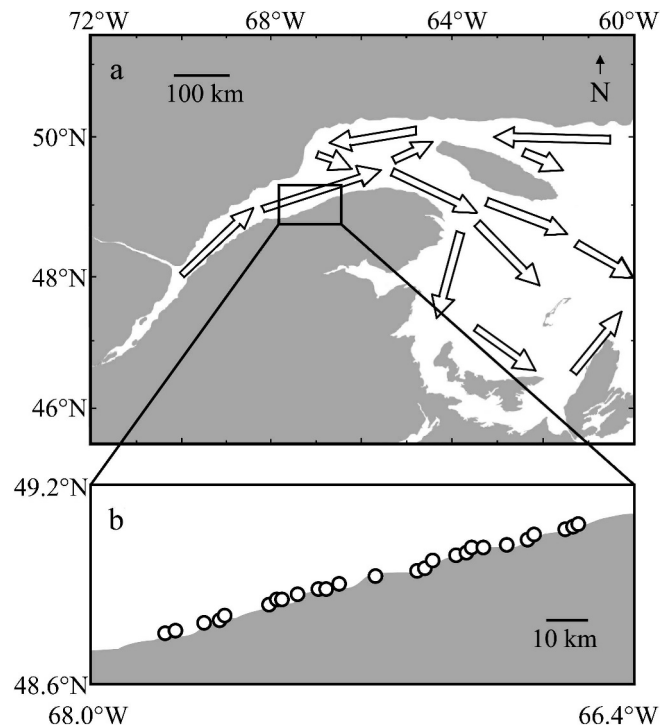


Fig. 1. (a) Map of the St. Lawrence Estuary and the Gulf of St. Lawrence. Major summer surface currents are indicated by arrows (modified from Sheng 2001). (b) Spatial arrangement of study sites along the southern shore of the estuary. Circles represent sampling locations.

visiting the sites, thus eliminating potential researcher bias. The only criteria used to assess the sites once in the field was that they have $>50\%$ of hard substratum and no considerable freshwater run-off in the immediate area. In the field, the sites were located using a hand-held global positioning system device.

Sampling procedures—At each site, eight multifilament nylon net pads (S.O.S. Tuffy Nylon Scouring Pad™; The Clorox Company) were anchored to bedrock or boulders using screws and plastic anchors in the mid-intertidal zone as mussel larvae collectors (Menge et al. 2004) during the third week of July. They were collected in early September and stored in 70% ethanol until processing. The Tuffy deployment and collection dates were selected after a pilot study in 2002 indicated this was the period of maximum mussel recruitment (F. Guichard unpubl.). Adult and juvenile mussel biomass was assessed at each site using transect-quadrat surveys. A $20\text{--}50\text{-m} \times 100\text{-m}$ rectangular area was randomly established in the mid-intertidal zone at each site from which all the mussels from randomly positioned $15 \times 15\text{-cm}$ quadrats (mean $n = 5.3$ per site) were collected. Although large mussel beds have been observed in the shallow subtidal of the northern Gulf of St. Lawrence (Gaymer and Himmelman 2002), these have never been seen along the south shore of the St. Lawrence estuary (F. Guichard unpubl.) where *Mytilus* spp. distribution is largely limited to the mid-intertidal. Mussel samples were then stored in a freezer until processing.

Sample processing—The recruitment pads were removed from the 70% ethanol and placed in a 10% bleach solution for 10 min to degrade the byssal threads of the recruits, thereby detaching them from the pads. A Folsom splitter was used to reduce larval density in the sample and all individuals were counted. Mussels from the quadrats were thawed and rinsed, and their blotted weight (± 0.005 g) was measured. All mussels retained by a sieve with 9.5-mm mesh were classified as adults. Two species of *Mytilus* spp., *M. edulis* and *M. trossulus*, are found along the Gaspé coast (McDonald et al. 1991). Because molecular techniques are required to distinguish both species (Toro et al. 2004), we identified all mussels as *Mytilus* spp.

Analysis—Because our goal is to estimate dispersal distance as the statistical relationship between life stages that are linked through a demographic process, we can define our basic analysis through a stock-recruitment function, linking onshore adult population abundance to recruitment (Ricker 1954; Beverton and Holt 1957). More specifically, if R is the number of recruits, and S is stock size

$$R = f(S) \quad (1)$$

where f defines the functional relationship between R and S , and can, for example, include density dependence and environmental factors. In spatially structured and advective environments, recruitment into a population at location x can be coupled to adult populations upstream at some distance y from x :

$$R_x \propto \int f(S_{x-y})h(x-y)dy \quad (2)$$

where f is more narrowly defined as the functional relationship between adult density and larval production, and h is the dispersal function defining the probability that a larvae released at $x-y$ recruits into the population at x . We can then define the cross-covariance between stock size at y and recruitment at x as

$$\begin{aligned} \text{Cov}(R_x, S_{x-y}) &= \text{Cov}\left[\int f(S_{x-y})h(x-y)dy, S_{x-y}\right] \\ &= \int \text{Cov}[f(S_{x-y}), S_{x-y}]h(x-y)dy \quad (3) \end{aligned}$$

If the stock-production function f is known, the dispersal function can be determined from the spatial recruitment-abundance cross-covariance and from the spatial covariance of adult abundance. Alternatively, the spatial cross-covariance provides an integrated measure of demographic connectivity by comparing adult abundance and larval production.

Simple dispersal functions have been adopted in the literature to develop spatially explicit population models, and transport models have been used to quantify dispersal functions. However, to our knowledge, no attempts have been made to directly estimate dispersal function as demographic coupling between adults and recruitment in natural marine systems. Other approaches have focused on

the spatial autocorrelation contained in the residual error of stock-recruitment functions, with no explicit formulation of dispersal functions (Myers et al. 1997). Here, our goal is to test for and quantify the average and/or the mode(s) of the dispersal function h through the strength of statistical relationships (covariance) between adult biomass at $x-y$ and recruit density at x along a coastline characterized by a residual downstream advective current. This approach allows us to quantify larval dispersal distance as the scale of demographic connectivity over a single generation and could potentially be integrated into time-series analyses of stock-recruitment models in metapopulations, or as a priori in Bayesian approaches to stock-recruitment functions integrating spatial dependence (Su et al. 2004).

Statistical relationships between adult mussel and recruit distribution across sites were analyzed using covariance between abundance at locations X and Y , where

$$\text{Cov}(X, Y)_d = \frac{\sum (x - \bar{x})(y - \bar{y})}{n} \quad (4)$$

where x represents either adult biomass or recruitment at upstream sites, y represents the value downstream, and n is the number of paired sites separated by a distance d . We first examined the spatial distribution of recruits and of adults by calculating the covariance between adult biomass and recruitment values for all pairs that fell within specific distance class d . These covariance values describe the autocorrelation structure of adult and recruit abundance. When covariance is plotted against distance (in what is called a ‘covariogram’) this provides a visual depiction of the spatial scale, or scales, at which adult biomass and recruitment co-vary, either positively or negatively, among sites (Rossi et al. 1992). Covariance analysis is based on a linear, or at least monotonic, relationship and covariograms are easiest to interpret if they possess a single, sharp peak. Nonmonotonic stock-recruitment relationships and multimodal cross-covariograms usually require alternative (nonlinear) statistical models and very large datasets.

The joint spatial dependence between adult abundances and recruitment was assessed using cross-covariograms. Instead of comparing a single variable from two locations, two different variables, namely adult abundance and recruitment, were compared from two locations. This is referred to as ‘cross-covariance’ and is often used to compare distributions of co-occurring species (Rossi et al. 1992). By using directional cross-covariograms we are able to simultaneously account for both direction and distance (Fortin and Dale 2005; Kent et al. 2006), specifically addressing the effects of upstream and downstream adults on recruitment.

Only half the total distance measured across the sampling area may be represented legitimately in a cross-covariogram (50 km in the present study), because at larger distances only edge points are included in each sample (Rossi et al. 1992). Eight spatial lags of 6 km were used for all cross-covariograms and we tested the sensitivity of our results to spatial lag value. We tested the significance of the covariance values using Monte Carlo simulations (Legendre 1993; Manley 1997). Randomizing the geographical position of abundance data provides covariance values that

control for any spatial structure present in the original data. Repeating this procedure generates a distribution of expected values that may be used to assess the significance of the original covariance values used in our covariograms. However, testing for significance of cross-covariance requires that we control for the covariance signatures of both the adult and recruit distributions. We therefore tested significance of cross-covariance values using a restricted randomization procedure (Fortin and Jacquez 2000) that takes into account the spatial covariance found in individual variables (adults and recruits). Specifically, we employed a ‘caterpillar’ restricted randomization test, in which the relative positions of adult and recruit distributions, rather than distributions themselves, are randomized (Purves and Law 2002). Thus, adult and recruit distributions are not affected by the randomization, but the entire set of recruitment values are instead shifted relative to the adult values (like a caterpillar moving along a branch), and thus a new random relationship between variables is generated with each iteration. This method maintains any auto-covariance in adult and recruit distributions and allows testing the unique contribution of the adult-recruit relationship to the total cross-covariance values.

Results

Mussel distribution and within-site demographic connectivity—There was strong spatial variation in mussel abundance and recruitment along the shore. The abundance of adult mussels decreased significantly from west to east (Fig. 2a; $p = 0.0001$, Pearson’s $r = -0.6880$) but no significant trend was observed for juvenile or recruit abundance (Fig. 2b). Furthermore, no significant relationship between adult abundance and recruit density was observed within sites ($p = 0.8563$, Pearson’s $r = 0.0373$).

The spatial analysis of covariance revealed spatial dependence over short to medium distances. Adult mussel abundance covaried significantly between sites separated by distances up to 30 km (Fig. 3a). When we detrended the adult abundance values and compared residuals we observed significant positive cross-covariance only at the shortest spatial lag of <6 km. Recruit abundances were also only significantly correlated at the <6 km lag (Fig. 3b). The pattern of positive covariance at shorter spatial lags, and lack thereafter, indicates the distinct scales of patchiness in the distribution of both adults and recruits (Fortin and Dale 2005).

Spatial statistics and regional demographic connectivity—Covariance between upstream adults and downstream recruits indicated a strong downstream relationship (Fig. 3c). The covariance between upstream adults and downstream recruits is relatively small for sites nearby or very far apart. However, significantly positive covariance was observed at intermediate distances: 12–18 km ($p = 0.0177$), and 24–30 km ($p = 0.0255$). When recruits are considered upstream of adults no significant covariance was observed between sites at any lag distance (Fig. 3d).

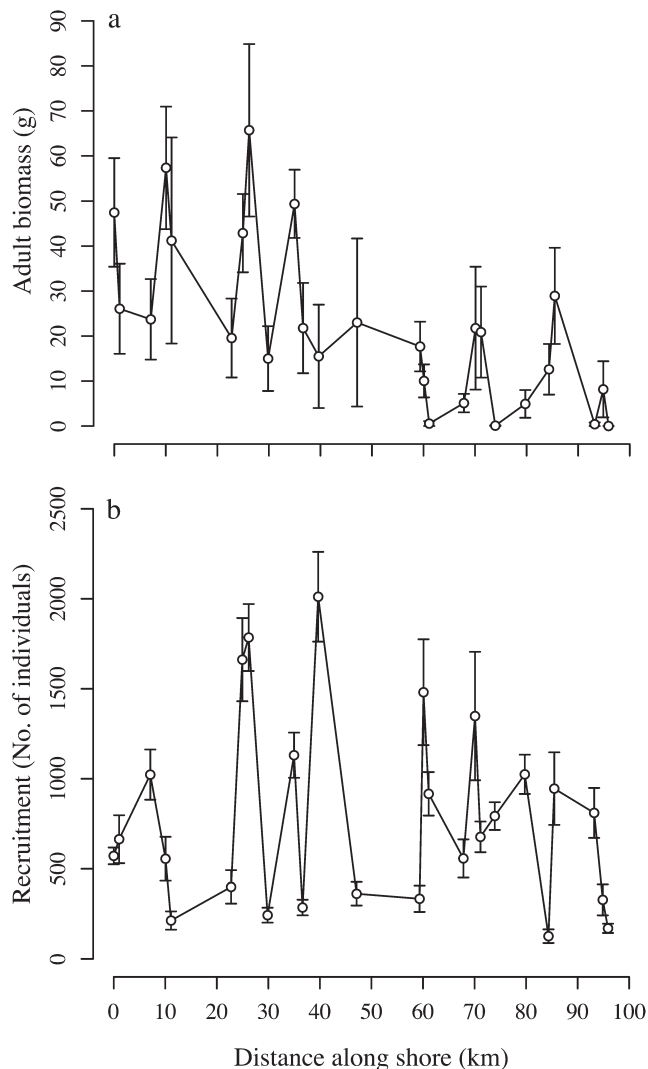


Fig. 2. (a) Distribution of mean *Mytilus* spp. adult biomass across all study sites, \pm standard error (SE; $n_{\text{adults}} = 5.3$ samples collected per site). (b) Distribution of mean *Mytilus* spp. recruitment, \pm SE ($n_{\text{recruits}} = 8.0$ TuffysTM per site).

These results were qualitatively robust to changes in lag distance values. For example, when we increased the lag distance, we observe only one significant peak in our cross-covariograms comparing adults upstream to recruits downstream at 24–32 km ($p = 0.0311$, lag = 8 km). At distance lags shorter than 6 km we lose the power to detect significant departures because of the reduced number of pairs within each bin, and at larger distances we are unable to resolve peaks effectively.

Discussion

We used spatial data to formulate testable hypotheses about the scale of demographic connectivity in a mussel metapopulation with well-characterized larval transport. Covariance between upstream adult mussels and downstream recruitment indicated significant spatial connectiv-

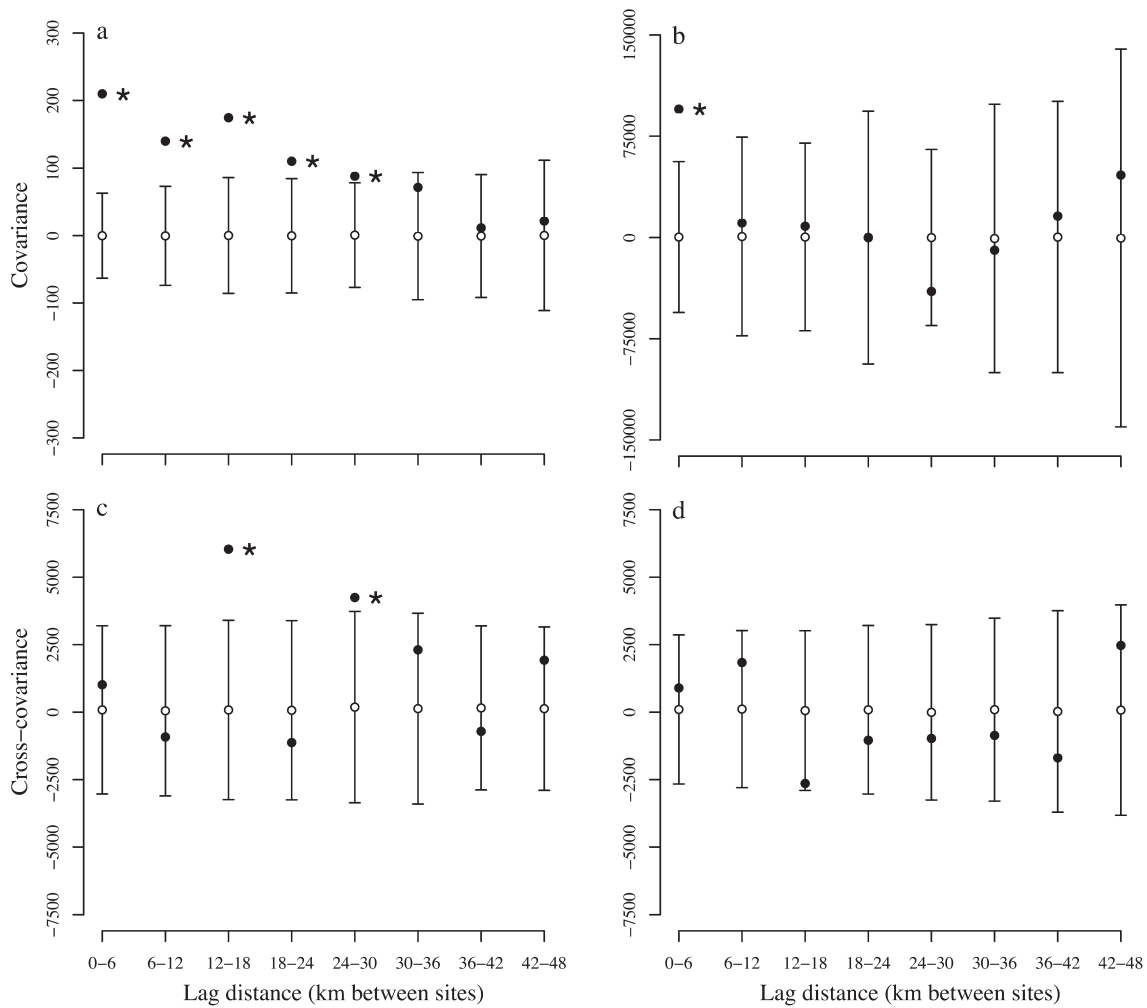


Fig. 3. (a) Covariogram of adult *Mytilus* spp. biomass. (b) Covariogram of *Mytilus* spp. recruitment density. (c) Cross-covariogram comparing adult biomass with downstream recruitment. (d) Cross-covariogram comparing recruitment with downstream adult biomass. Filled circles indicate covariance and cross-covariance values for original data, open circles indicate mean values generated from 10,000 caterpillar randomized permutations, bars represent 95% confidence intervals based on these randomizations, and significant covariance and cross-covariance values are denoted by an asterisk. The sample sizes for each lag-distance class are as follows: 0–6 km, 54 pairwise comparisons; 6–12 km, 37; 12–18 km, 29; 18–24 km, 27; 24–30 km, 32; 30–36 km, 28; 36–42 km, 21; and 42–48 km, 18.

ity between sites 12–18 km and 24–30 km apart from one another. In contrast, no relationship was observed when comparing upstream recruits and downstream adult abundance. This directionality suggests that the significant positive spatial covariance between adults and recruits is evidence of demographic connectivity rather than the effect of along-shore environmental patchiness. The bimodal pattern of covariance observed may be due to regional differences across the study area that cannot be resolved with our data and analysis, or differences in dispersal distance within the genus *Mytilus* (i.e., *M. edulis* vs. *M. trossulus*).

Measuring dispersal on ecological time scales—The mean dispersal scale reported here, between 12 km and 30 km, is within the range of values previously reported for mussel species and is much smaller than the potential scale of

dispersal predicted solely from the advection of passive particles by surface currents. Using a variety of tools, including in situ larval sampling, McQuaid and Phillips (2000) determined that, although some mussel larvae in South Africa were effectively dispersing at scales <100 km, most were traveling <5 km from natal populations. Gilg and Hilbish (2003) reported dispersal distances of 30–50 km based on genetic evidence and circulation mapping. Dispersal distance is known to have important effects on regional population persistence and distribution. However, annual fluctuations in dispersal scale and their effect on regional population dynamics remain unknown. The method reported here provides a way to address this challenge and to complement temporally integrated genetic methods. When dispersal distances are estimated using genetic techniques (for example, employing Wright's F_{ST} to measure neutral genetic differentiation and infer migration

rates), it is in fact the effective dispersal that is being considered, that is, the movement of propagules that successfully establish and reproduce (Kinlan and Gaines 2003). These techniques reveal differentiation of genetic material accumulating over multiple generations and may not be appropriate for detecting trends at ecological time scales.

Open populations and the scale of stock-recruitment relationships—Open-system theories assume a unidirectional link between larval and adult populations. In contrast, recent modeling efforts (Connolly and Roughgarden 1999) explicitly couple local larval pools with interacting onshore populations, thus forming an array of closed communities. Our study supports recent research efforts (Hughes 1990; Kinlan and Gaines 2003) that challenge the assumption of openness in marine benthic systems. At large enough spatial scales, populations become limited by adult stock sizes because all systems are essentially ‘closed’ at some scale (Hixon et al. 2002). Yet averaging production and recruitment at inflated spatial scales is likely to obscure any detectable relationship between the two.

At the metapopulation and metacommunity level, even limited propagule exchange between populations can have large effects on dynamics (Guichard et al. 2004; Gouhier and Guichard 2007). Synchrony, stability, large-scale variability, and population responses to reserve networks all depend, to some degree, on the amount of dispersal within metapopulations (Engen et al. 2002; Hixon et al. 2002). Dispersal limitation may be an important mechanism for creating strong spatial structuring, leading to the maintenance of heterogeneity at scales that may be distinct from those of environmental variables or of ecological processes. Dispersal can also cause synchronized fluctuations, especially in combination with spatially autocorrelated environmental changes (Kendall et al. 2000). Our results reveal a distinct scale of larval transport that leaves no observable signature in the alongshore distribution of recruits or adults. Within the spatial and temporal limits of our study, they thus support the claim that scale of patterns can be distinct from those of underlying processes (Levin 1992). The persistence of a spatial mismatch over longer temporal scales remains to be established.

Lagos et al. (2005) used a similar spatial statistical approach to compare the spatial scale of autocorrelation in barnacle recruitment and sea surface temperatures. Myers et al. (1997) also used correlograms to elucidate the scale at which recruitment in marine fish is patterned. We have built upon these methods by explicitly incorporating the spatial dependence of recruitment on production as the scale of demographic connectivity, tying studies of dispersal to stock-recruitment frameworks.

Directions for future work—Our analysis of mussel distribution and recruitment relies on several assumptions and further application of our method requires their critical evaluation. For example, we used mussel biomass as a proxy for reproductive output. However, previous work in the St. Lawrence has shown that reproductive output of

benthic invertebrates may also depend on seasonal and local conditions such as current velocities, shoreline configuration, and phytoplankton abundance (Archambault and Bourget 1999; McKindsey and Bourget 2000). We have also limited our analysis to *Mytilus* spp., but two species, *M. edulis* and *M. trossulus*, are found along the Gaspé coast (McDonald et al. 1991). Molecular techniques are required to distinguish these cryptic species due to their extreme morphological similarity (Toro et al. 2004). A natural extension of this work would be to evaluate the relative contribution of both species to the larval pool, as well as the differences in both the timing and distribution of recruitment. Additionally, our approach could be applied to other advective systems, including streams, rivers, and coastal areas with strong alongshore currents (Gaylord and Gaines 2000, Lutscher et al. 2006). However, nondirectional transport would prevent the use of directional cross-covariance as a way to infer spatial scale of demographic connectivity and to control for autocorrelation in the environment as an alternative hypothesis.

The results of this study reveal how variability in larval supply may be mediated by onshore productivity, which is itself highly variable (Leslie et al. 2005) and under the control of community-level processes (Forde and Doak 2004). Feedbacks may thus exist between recruitment limitation and community dynamics. Even temporary reproductive isolation can result in consequences for genetic structure of populations and genetic divergence among populations (Palumbi 1994) and changes in dispersal may have important consequences for the synchronization of population fluctuations and metapopulation stability (Paradis et al. 1999; Liebhold et al. 2004). This synchronization may put species at increased risk of extinction (Heino et al. 1997). Better knowledge of actual dispersal patterns, rather than potential dispersal, should thus help inform the design and placement of marine reserve networks (Palumbi 2004).

Our study shows how spatial statistics can be applied to infer the scale of a dynamic process. A complete characterization of spatiotemporal variability in mussel larval dispersal is beyond the scope and aim of the present paper. The broad application of our method over several years and other stretches of coastline is necessary to examine how patterns of connectivity might change from one year to the next or among regions with different current regimes. An important result is the power of our method in detecting the scale of demographic connectivity between populations and its robustness to modest sampling efforts that reflect the constraints imposed on most large-scale ecological studies.

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