Evaluating the importance of demographic connectivity in a marine metapopulation

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Abstract. Recently researchers have gone to great lengths to measure marine metapopulation connectivity via tagging, genetic, and trace-elemental fingerprinting studies. These empirical estimates of larval dispersal are key to assessing the significance of metapopulation connectivity within a demographic context, but the life-history data required to do this are rarely available. To evaluate the demographic consequences of connectivity we constructed seasonal, size-structured metapopulation matrix models for two species of mytilid mussel in San Diego County, California, USA. The self-recruitment and larval exchange terms were produced from a time series of realized connectivities derived from trace-elemental fingerprinting of larval shells during spring and fall from 2003 to 2008. Both species exhibited a strong seasonal pattern of southward movement of recruits in spring and northward movement in fall. Growth and mortality terms were estimated using mark–recapture data from representative sites for each species and subpopulation, and literature estimates of juvenile mortality. Fecundity terms were estimated using county-wide settlement data from 2006–2008; these data reveal peak reproduction and recruitment in fall for Mytilus californianus, and spring for M. galloprovincialis. Elasticity and life-stage simulation analyses were employed to identify the season- and subpopulation-specific vital rates and connectivity terms to which the metapopulation growth rate \( \lambda \) was most sensitive. For both species, metapopulation growth was most sensitive to proportional changes in adult fecundity, survival and growth of juvenile stages, and population connectivity, in order of importance, but relatively insensitive to adult growth or survival. The metapopulation concept was deemed appropriate for both Mytilus species as exchange between the subpopulations was necessary for subpopulation persistence. However, highest metapopulation growth occurred in years when a greater proportion of recruits was retained within the predominant source subpopulation. Despite differences in habitat and planktonic duration, both species exhibited similar overall metapopulation dynamics with respect to key life stages and processes. However, different peak reproductive periods in an environment of seasonal current reversals led to different regional (subpopulation) contributions to metapopulation maintenance; this result emphasizes the importance of connectivity analysis for spatial management of coastal resources.

Key words: demography; elasticity; larval dispersal; life-stage-simulation analysis; metapopulation; Mytilus californianus; Mytilus galloprovincialis; population connectivity.

INTRODUCTION

The metapopulation conceptual framework has proven useful for the study of many populations, particularly those inhabiting patchy habitats (sensu Levins 1969, 1970). Levins’ seminal work in this field grew from an applied question addressing the spatial components of pests infesting agricultural fields. He found that there are simple equilibria that describe the interplay of colonization via the migration of individuals, the extinction of subpopulations, and population persistence. The extinction of subpopulations has been well studied in a metapopulation context, in part due to the ease with which one can envision a large single population being fragmented into smaller inhabitable patches separated by an uninhabited matrix. This is particularly true in terrestrial systems, where species are lost to habitat fragmentation, invasive species, and over-exploitation (e.g., Loreau 2010). Despite increased attention to the metapopulation concept in recent years, the term itself has been used inconsistently in the literature (Harrison 1991).

In marine metapopulation theory, where numerous species have populations of relatively sedentary adults connected by a widely dispersing larval stage, the extinction and colonization features of metapopulations...
have been de-emphasized in favor of a network of subpopulations which routinely receive new individuals from both local and distant sources (Sale et al. 2006). For the purpose of this work we adopt Sale et al.’s (2006) definition of a metapopulation as “a system in which (1) local populations inhabit discrete habitat patches and (2) interpatch dispersal is neither so low as to negate significant demographic connectivity nor so high as to eliminate any independence of local population dynamics . . . .” While this definition intuitively fits many marine species, the challenge of quantifying the exchange of small, planktonic larvae has made the empirical verification and study of marine metapopulations challenging. These difficulties have also impeded the ability to use informed estimates of connectivity in demographic models. Equally limiting has been the paucity of spatially resolved, quantitative life-history data (fecundity, growth, and survivorship) required to populate those models.

Many researchers have demonstrated the importance of connectivity to metapopulation persistence and management through modeling (e.g., Caswell et al. 2003, Hastings and Botsford 2006) or experimental efforts (e.g., Boudjemadi et al. 1999), and empirical attempts to estimate population connectivity have been escalating in the field of marine ecology. Recent studies have used genetic methods (e.g., Gilg and Hilbish 2003), artificial tagging (e.g., Almany et al. 2007), or trace-elemental fingerprinting of fish otoliths (e.g., Standish et al. 2008, Cook 2011) and invertebrate larval shells (e.g., Becker et al. 2007, Carson 2010). The extension of trace-elemental fingerprinting into a time series has allowed for generalizations about population connectivity instead of relying on extrapolation from relatively brief measurements of larval exchange (Carson et al. 2010). Empirical estimates of dispersal such as these allow, for the first time, realized marine population connectivity to be incorporated into metapopulation models. Such models can evaluate the extent to which actual variation in population connectivity affects metapopulation persistence, compared to variability in other vital rates such as fecundity, growth, and mortality.

Here we combine connectivity time series information derived from trace-elemental fingerprinting with metapopulation matrix models to undertake the first empirical test of the importance of population connectivity to population dynamics in a marine invertebrate with pelagic larvae. Incorporating a time series of mytilid mussel larval connectivity in San Diego County, California, USA (Carson et al. 2010) this study utilizes a simplified two-subpopulation metapopulation matrix model in which fecundity, growth, and mortality rates were estimated using field observations from representative sites within San Diego County and literature estimates of juvenile mortality in Mytilus. We investigate differences in the connectivity and life-history contributions to the demography of two congeneric species of rocky intertidal marine invertebrates coexisting along the same shoreline; a native open-coast inhabitant (Mytilus californianus) and a nonnative bay-dweller (Mytilus galloprovincialis). The key life stages, subpopulations, vital rates, and connectivity processes for persistence are identified for both species. We then use the results to answer fundamental questions about the dynamics of these populations: (1) How much does population connectivity matter? (2) When does connectivity matter? (3) Is connectivity necessary for metapopulation persistence? (4) How does the contribution of connectivity to metapopulation growth compare to that of other vital rates? Does the metapopulation concept apply? (5) Do differences in habitat and life-history between the two species affect the answers to 1–4?

Methods

Model species

Mytilus californianus is the dominant, structure-forming invertebrate in the mid-intertidal throughout much of its range (from Alaska to Baja California; Sooth-Ryen 1955). It is a broadcast spawner; peak spawning in San Diego occurs from October through March (Young 1946, Curiel-Ramirez and Cáceres-Martinez 2004). Between 2003 and 2008, spawning and juvenile settlement were more prevalent in November than May (Carson et al. 2010). In San Diego County, where the majority of intertidal coastal habitat is soft sediment, this species is restricted to pier pilings, rip-rap, and the small amount of natural intertidal bedrock available (Becker 2005).

Mytilus galloprovincialis is native to the Mediterranean but since the early 20th century its distribution has included the Pacific Coast of North America from Baja to Central California (McDonald and Koehn 1988). In San Diego County, M. galloprovincialis inhabits primarily rip-rap in fore-bay habitats, but can be found among M. californianus at open coast locations such as the Scripps Pier (Becker 2005). In contrast to M. californianus, spawning in M. galloprovincialis is more prevalent in May than November in San Diego County and juvenile settlement peaks in the spring (Coe 1932, Young 1946, Curiel-Ramirez and Cáceres-Martinez 2004, Carson et al. 2010).

Estimates of metapopulation connectivity

Empirically derived connectivity estimates were generated to track the exchange of individuals within the study region (Carson et al. 2010). Laboratory-fertilized mussel embryos were outplanted periodically in larval “homes” near the major populations of adults in San Diego County (as per Becker et al. 2007). By analyzing the trace-elemental chemistry of the larval shells using laser-ablation inductively coupled plasma mass spectrometry (LA-ICP-MS), a trace-elemental “map” of larval source populations was created. Newly settled juvenile mussels were collected at those same sites and the trace-elemental chemistry of the portions of their shells formed during early larval dispersal was analyzed.
Using discriminant function analysis and maximum-likelihood estimation methods, juveniles were assigned to a putative region of origin.

In order to evaluate mussel metapopulation dynamics, we summarized the connectivity results to depict the larval exchange between two subpopulations for each species separated by a major habitat break north of La Jolla, California (Fig. 1). This 20-km break contains no appreciable habitat for either species of mussel. This break also corresponds to a difference in seawater chemistry that allowed us to distinguish among northern and southern sites with a high degree of confidence (63–86%; Carson et al. 2010). For *M. californianus*, the northern subpopulation included spawning sites from Cardiff Reef to Oceanside (~7500 m² adult cover), and the southern subpopulation consisted of sites from Dike Rock to Imperial Beach (~8000 m² adult cover). The two *M. galloprovincialis* regions had the same approximate boundaries, with the southern populations residing primarily in San Diego and Mission Bays (~9850 m² adult cover) and the northern populations in Oceanside Harbor and Agua Hedionda Lagoon (~6700 m² adult cover). These cover estimates include an *M. galloprovincialis* aquaculture operation within Agua Hedionda Lagoon (Fig. 1). Suitable habitat and known populations of each species exist in the Southern California Bight outside of the study area, as close as 40 km north of our northernmost study site. Although sampled subpopulations represent the most likely sources of new recruits, larval exchange with distant sites could be a potential source of variability in our fecundity calculations.

**Demographic estimates**

In concert with the collections for trace elemental analysis, mytilid recruits were collected from 17 sites in San Diego County in May and November from 2006 through 2008. Adults, algae, and associated debris were
collected from a 0.25-m$^2$ area of the mid-mussel zone at each site and frozen upon return to the laboratory. The entire sample was inspected under 12× magnification and mytilid recruits <2 mm shell length were collected and returned to the freezer. During cases of abundant recruitment, ~50 recruits were collected from a subset of the material and the total number of recruits in the sample was estimated.

Recruits <2 mm in shell length cannot be reliably identified to species using morphology, therefore a polymerase chain reaction (PCR) method was used to identify the species of each recruit. Genetic material extracted from each recruit’s tissue was compared to primers for each species targeting the 16S ribosomal RNA gene, following the methods of Becker et al. (2005). The shells from any recruits with soft tissue that did not obviously match known marks for either species on stained agarose gel plates were excluded from the results.

Fertilization and larval mortality rates could not be measured accurately in situ; to address this challenge the adult mussel fecundity was estimated for each species, subpopulation, and season (spring or fall) based on the 2006–2008 settlement data at the 17 sites (Fig. 1) and county-wide surveys of adult cover conducted in 2005 (Carson et al. 2010). Fecundity ($F$) was estimated using the methods of Ripley and Caswell (2008) who estimated fecundity for some bivalve species as follows:

$$F_{\text{average}} = \frac{\text{Number of recruits/m}^2}{\text{Number of adults/m}^2}. \quad (1)$$

Based on juvenile growth data (Tables 1 and 2), settlement collections (of individuals <2 mm length) were assumed to represent two weeks of settlement for the purposes of calculating total settlement across the entire reproductive season. Hereafter, the term fecundity is used to represent the sum of the various processes inherent in the delivery of juveniles to settlement habitat (i.e., egg production, fertilization, and larval survival) excluding the directionality (self-recruitment or export) of their dispersal. A discussion of additional fecundity calculations follows in Model construction.

<table>
<thead>
<tr>
<th>Subpopulation</th>
<th>Adults</th>
<th>Mortality (d$^{-1}$)</th>
<th>Growth (mm width/d)</th>
<th>Juvenile</th>
<th>Estimated mortality (d$^{-1}$)</th>
<th>Growth (mm width/d)</th>
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Note: Juveniles have a shell width between 0.5 and 10 mm; adults have shell widths >10 mm. Tuffy juveniles are the number of juveniles found in removed tuffles. Empty cells indicate that no data are available for that time period and metric.
Size-at-first-reproduction was determined for both species from four, 0.25-m$^2$ collections of adults at randomly selected areas along the same transect lines during each sampling. Adult mussels were returned to the laboratory, measured with dial calipers, and opened to note the presence or absence of gonad tissue. Sex ratio at all sites was assumed to be 1:1 (Kiyomoto et al. 1996) after attempts to determine sex using gonad color were inconclusive (see Petes et al. 2008).

To estimate juvenile growth rates, 10 plastic dish scrubbing pads (tuffies) were bolted to rocks at each study site to acquire new recruits during sampling periods. After a one-month period, two tuffies were removed and dissected under magnification to enumerate juvenile mytilids. All juvenile shells were measured under 25× magnification with an ocular scale. At two-week intervals thereafter, the tuffies were removed in sets of two and attached juveniles enumerated and measured. The three largest juveniles found in each set were assumed to represent initial settlement to the tuffies, and the difference in their average size between removal events was assumed to represent the amount of growth that occurred between tuffy removals.

Juvenile mortality was estimated using von der Meden’s (2010) measurement of mean week-one Mytilus juvenile mortality of 60%, and assuming that juvenile mortality decreased over the juvenile stage asymptotically to each subpopulation’s observed stage-one adult mortality.

**Model construction**

We constructed a size-classified, discrete-time-step, seasonal, metapopulation matrix model for each species, using the equation

$$n_{t+1} = A \times n_t$$  \hspace{1cm} (2)

where $n_t$ is the number of individuals at time $t$, $n_{t+1}$ is the number of individuals at time $t+1$, after one time step, and $A$ is an annual metapopulation matrix derived from the product of two seasonal matrices:

$$A = A_{spring} \times A_{fall}.$$  \hspace{1cm} (3)

The annual matrix was divided into two six-month time steps to take advantage of the available biannual measurements of population connectivity and settlement (see Carson et al. 2010). The spring matrix represents the period of 1 January to 30 June, encompassing the spring recruitment period of each species, and the fall represents remaining recruitment events from 1 July through 31 December.

Mussels of each species were divided into three life stages on the basis of reproductive ability and size: juvenile (J), adult stage one (A1), and adult stage two (A2). The estimated size at first reproduction (end of juvenile stage) was 10 mm shell width for *M. californianus* and 15 mm shell width for the lower-aspect-ratio shells of *M. galloprovincialis*. The juvenile stage included all mussels between the size of first detection in settlement collections (between 0.5 and 2 mm shell length) and the size at first reproduction for each species. Adults larger than this size were divided into two stages on the basis of Vandermeer-Moloney calculations (Vandermeer 1978, Moloney 1986) designed to minimize both the range of transition probabilities and the sampling error within a size class. For *M. californianus*, A1 ranged from 10 mm to 28 mm shell width, and all mussels larger than 28 mm width were A2. For *M. galloprovincialis* the adult classes were 15–25 mm (A1) and 25+ mm (A2).

In this model, there are three parameters necessary for the creation of each seasonal matrix: fecundity ($F$), transition probability ($G$), and stasis probability ($P$; see Fig. 2). Fecundities expressed in Eq. 1 were adjusted to account for reproduction that occurred continually over the inter-census interval (“birth flow populations”; Caswell 2001) so that average fecundity was represented by the recruits produced at the midpoint of the time step. This amounted to multiplying the fecundities by

<table>
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<tr>
<th>Subpopulation</th>
<th>Adult Marked</th>
<th>Adult Recovered</th>
<th>Mortality (d$^{-1}$)</th>
<th>Growth (mm width/d)</th>
<th>Juvenile Tuffy juveniles</th>
<th>Juvenile Estimated mortality (d$^{-1}$)</th>
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by the probability of growing into the next stage, while stasis probabilities were the survival probability multiplied by one minus the probability of advancing to the next stage (Caswell 2001).

The overall models for each species had annual metapopulation growth rates ($\lambda$) of close to 1.0 (replacement). Drawing conclusions based on the exact values of $\lambda$ was not the focus of this work; instead we focused on the relative importance of connectivity and vital rates to $\lambda$. The overall model matrices are presented in Appendix A.

**Elasticity analysis**

To evaluate the relative effects of connectivity and vital rate variation on the metapopulation growth rate ($\lambda$), we employed the use of elasticity analysis (Heppell et al. 2000, Caswell 2001). Elasticity is a prospective analysis that determines the proportional contribution of each model parameter to the population growth rate ($\lambda$) by assessing how that rate responds to proportional perturbations to individual elements; it can be thought of as proportional sensitivity (Caswell 2001). We present the results of the elasticity analysis on the overall matrices for each species, which were created using the mean or pooled values for all vital rates and processes.

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**FIG. 2.** Life-cycle diagram and matrix arrangement for the discrete-time, size-classified metapopulation matrix model utilized in this study. Stages are: J, juvenile stages; A, adult stages. $P$ terms are stasis probabilities, $G$ terms are transition probabilities, $F_S$ terms are fecundity retained in the same subpopulation (self-recruitment), and $F_E$ terms are fecundity exported to the other subpopulation. Transition and stasis terms (growth and mortality) are shown in outlined arrows, fecundity (expressed as self-recruits and exports) is shown in solid arrows. The matrix represents the information for one season; two seasonal matrices were multiplied together to create an annual matrix.

the probability of adult stage-specific survival half way through the time step, and survival of the recruits for the remainder of the time step (Morris and Doak 2002). This fecundity was then divided among connectivity pathways of self-recruitment ($F_S$) and export to the other subpopulation ($F_E$) according to observing connectivity percentages so that connectivity terms could be evaluated independently of fecundity (Fig. 3). Finally, fecundity was divided among the A1 and A2 classes according to the body-mass–gonad-mass relationship for *M. californianus* south of Point Conception (southern California) found in Phillips (2007). Larger individuals (A2) had roughly twice the gonad tissue of smaller individuals (A1), therefore the recruits-per-adult value for the A2 stage was set at twice that of the A1 stage.

Probabilities for remaining within a given size class ($P$) and transition to the next size class ($G$; Fig. 2) were calculated as follows. Transition probabilities were the probability of surviving a six-month time step multiplied.
including population connectivity (depicted in Fig. 3). These analyses were done on the full annual matrices, but on the basis of the seasonal parameters that together compose the annual matrix.

Life-stage simulation analysis

To evaluate the potential significance of uncertainty in many of our measured or estimated matrix elements, we also employed life stage simulation analysis (LSA, Wisdom et al. 2000) on the same annual matrices. Adapting a Matlab program used in Sandercock et al. (2008), we used observed and estimated variation in each of our mortality, growth, fecundity, and population connectivity values to bootstrap the above elasticity results over 1000 iterations. Each iteration drew a different random value for each vital rate or connectivity scenario in every stage, subpopulation, and season from the distribution created by the observed or estimated mean (overall) values and standard deviations (Appendix B). We assumed that growth, mortality, fecundity, and connectivity rates were independent and did not include any covariance structures between them. We then conducted a multiple regression on the values chosen for each factor with the overall λ of that matrix as the dependent variable (n = 1000). The resulting partial coefficients of variation were used to evaluate the relationship between the species-specific rate, season, subpopulation, or stage and the population growth rate. In this fashion, we were able to evaluate the robustness of the overall model elasticities in light of reasonable variation or sampling error.

Results

Model parameters

Patterns of metapopulation connectivity inferred from trace-elemental fingerprinting spanning 2003–2008 showed distinct seasonal trends for both *M. californianus* and *M. galloprovincialis* (Fig. 3). Although there was significant interannual variability (see Carson et al. 2010) the majority of larvae of both species moved from north to south in the spring and south to north in the fall. According to settlement collections verified by PCR species identification, *M. californianus* produced more recruits in the fall than the spring by a ratio of over 5:1. This seasonality meant the southern subpopulation produced the majority (61%) of the *M. californianus* metapopulation recruits throughout the year, although adult cover was similar in the northern and southern subpopulations. Conversely, the bay-dwelling *M. galloprovincialis* produced more recruits in spring than fall at a ratio of greater than 6:1, so the northern subpopulation was the primary source of recruits year-round (70%), despite the larger adult population in the south (Table 3).

*M. californianus* adult mortality was invariant, with the rates for both seasons and subpopulations ranging from 0.007 to 0.008 mussels/d (Table 1). Because adult stage one (A1) mortality was used in the calculation for juvenile mortality in each season/subpopulation, juvenile mortality was invariant also (range 0.019–0.020 mussels/d). *M. galloprovincialis* adult mortality was more variable, with high mortality rates for the northern subpopulation in both seasons (0.011 mussels/d in spring, 0.012 mussels/d in fall) compared to the southern area (0.004 mussels/d in spring, 0.005 mussels/d in fall; Table 2). Although the study site for the northern subpopulation was closed to the public, caretakers noted fisherman trespassing on the property to remove mussels for use as bait. When the study site was moved to a more secure location less than 100 m away in fall 2009, the mortality rate decreased and was equal that of the southern subpopulation during the same period (0.007 mussels/d). The fall 2009 rate was assumed to be a more representative measurement, and was therefore used in all calculations.

Mean adult growth rates for the open-coast *M. californianus* were 0.003–0.028 mm/d higher in the southern than northern subpopulation during all three study periods (Table 1). *M. galloprovincialis* did not show consistent subpopulation differences, but had lower mean adult growth in the spring compared to fall (P = 0.012; Table 2). Both species had similar overall mean adult growth (0.029 and 0.027 mm/d for *M. californianus* and *M. galloprovincialis*, respectively). *M. californianus* mean juvenile growth ranged from 0.011 to 0.056 mm/d with no consistent subpopulation or seasonal differences (Table 1). The range of juvenile growth was higher in *M. galloprovincialis* (0.049–0.068 mm/d; Table 2) than *M. californianus*; no *M. galloprovincialis* recruits of this species were available to calculate growth during fall 2008.

Metapopulation model exploration

Individual subpopulations of either species likely could not persist without the input of larvae from the other subpopulation. When exchange between subpop-
ulations was removed from the model there was a resultant reduction in fecundity, and the overall *M. californianus* population growth rate ($\lambda$) dropped to 70% of its original value (1.033 to 0.718). Similarly, *M. galloprovincialis* experienced sharp declines in $\lambda$ when settlers that originated in the other subpopulation were removed from the overall model (again, there was a significant reduction in fecundity). The *M. galloprovincialis* metapopulation growth rate was 1.051, but dropped to 0.865 (82% of original) without exchange.

The population connectivity time series for *M. californianus* included results for four fall seasons and two springs. Switching between the population connectivity observed in either of the two spring "off seasons" changed the metapopulation growth rate only a small amount (0.38%). However, running the model with specific fall population connectivities (and holding all other parameters, including overall fecundity, constant) affected the metapopulation $\lambda$ by as much as 6.3%. Metapopulation $\lambda$ increased in years with high levels of self-recruitment, especially in the southern (i.e., source) subpopulation. The highest $\lambda$ scenario (1.062 in 2006) was observed a year when connectivity was most directionally skewed, with the southern subpopulation retaining a higher proportion of metapopulation recruits (47% of all recruits sampled) than any other year. The slowest-growing scenario ($\lambda = 0.999$ in 2004) had the most balanced exchange between north and south subpopulations, and had the lowest percentage of recruits locally retained in the south (19%).

The time series of *M. galloprovincialis* population connectivity included two fall seasons of low reproduction and four spring seasons of peak reproduction. Switching between the two fall "off seasons" has a small effect on $\lambda$ (1.0% difference), with the strong south-to-north flow of larvae in 2007 (returning recruits to the spring source population) raising metapopulation $\lambda$ slightly compared to 2008. Switching among the four spring scenarios, however, had a much larger impact on $\lambda$ when settlers that originated in the other subpopulation were removed from the overall model (again, there was a significant reduction in fecundity). The *M. galloprovincialis* metapopulation growth rate was 1.051, but dropped to 0.865 (82% of original) without exchange.

**Elasticity Analysis: The Significance of Connectivity and Other Vital Rates**

The population growth rate ($\lambda$) of *M. californianus* in the overall model was proportionately most sensitive to changes in overall fecundity (elasticity = 0.711) in the fall reproductive season (Fig. 4). Connectivity terms during the fall reproductive season had a total elasticity of 0.642, with self-recruitment to the southern subpopulation comprising the majority (0.336). Juvenile survival (0.484) and growth (0.480) during the following spring in the southern subpopulation had the next-highest elasticities. Survival of the first adult stage in both subpopulations and juvenile growth and survival in the northern subpopulation also had elasticities greater than 0.1. Elasticity values for underlying vital rates do not sum to one as they do with matrix-element elasticities. As expected from the south-to-north flow of larvae during the fall reproductive season, changes to the southern subpopulation vital rates and connectivities had greater effects on the overall metapopulation $\lambda$ than did changes to the elements of the northern subpopulation.

*M. galloprovincialis* metapopulation dynamics exhibit similar behavior to the open-coast counterpart, but the importance of seasons and subpopulations was reversed. Proportionately, $\lambda$ was most sensitive to changes to spring fecundity (0.770), northern fall juvenile survival (0.595) and growth (0.588), and northern spring self-recruitment percentage (0.480). Other spring connectivity pathways and stage-one adult survivals had elasticity values >0.10 as well (Fig. 4). Compared with *M. californianus*, there were even greater disparities between the high elasticities of the northern (source) subpopulation terms and low values for the southern (sink) subpopulation due to the increased imbalance in larval flow between regions. As with its congener, parameters which influenced the transport of recruits to the source subpopulation had the highest elasticities. A complete listing of elasticity values for both species is given in Appendix C.

**Life-stage simulation analysis (LSA)**

The results of the LSA suggest that the overall model elasticity results are relevant to a wide range of vital rates and connectivity scenarios for both species. The metapopulation growth rate ($\lambda$) is interpreted to be most sensitive to vital rates with high partial coefficients of variation in the multiple regression, and there was general agreement between the LSA and elasticity analyses despite the range of vital rates represented in the LSA. Over the course of 1000 random draws from the range of observations or estimates, changes to connectivity percentages, juvenile vital rates, and fecundity terms had significant relationships to the metapopulation $\lambda$ of both mussel species (Fig. 5). For *M. californianus*, the LSA results were similar to the elasticity analysis in that fall fecundity (0.357), spring juvenile growth (up to 0.474) and mortality (up to 0.283), and fall connectivity (up to 0.202) had the highest values. Stage-one adult survivorship in the fall was not as relatively important in the LSA (−0.02). Similarly, *M. galloprovincialis* LSA results generally mirrored the elasticities, with north spring self-recruitment (0.379), north fall juvenile survival and growth (0.339, 0.263, respectively), and spring fecundity (0.234) having the highest values (Fig. 5).
The persistence of metapopulations of both mussel species in this study was influenced by the exchange of larvae between the northern and southern subpopulations. Although adult fecundity or juvenile mortality and growth had greater influences on the population growth rate ($\lambda$), the directional transport of larvae controlled where and when those rates were of the greatest importance, i.e., juvenile terms in the source population following the reproductive peak. The two

![Graph](image-url)
Mytilus species had similar metapopulation dynamics despite differences in life history and habitat, with one major caveat; due to a temporal difference in peak reproduction, the season and subpopulation of greatest importance was reversed. The key subpopulation for *M. californianus* metapopulation growth rate was in the south, with reproduction and transport more influential in the fall and juvenile growth and survival having the most impact in the spring. *M. galloprovincialis* had higher elasticities for the northern subpopulation, with reproduction and transport most prominent in the spring and juvenile growth and survival key in the fall.

Although population connectivity was clearly important during each species’ main reproductive season, the
extreme effort needed to measure population connectivity during each species’ off season was largely unnecessary in hindsight, as this connectivity contributed little to metapopulation persistence. The directionality of the “trickle” of *M. californianus* larvae in the spring or *M. galloprovincialis* larvae in the fall did not play a significant role in population growth, nor did the fate of these larvae as juveniles in the subsequent season.

These results generally concur with the metapopulation-simulation findings of Figueira (2009) for coral reef fish. He pointed out that the validity of his results “depends upon the biological relevance of modeled parameters, particularly connectivity values” which were not validated in the field. Figueira (2009) found that population growth was more sensitive to changes in the demographic rates of individual patches, including juvenile survival, than to patch connectivity. The use of empirical connectivity data in this study helps generalize the conclusions of Figueira (2009) to a different system; we found that within-patch vital rates (e.g., adult fecundity, juvenile survival, and growth) had a greater influence on population growth than larval exchange terms.

Managers can benefit from the results of elasticity and LSA approaches because actions can be targeted toward specific life stages, seasons, subpopulations, and processes that may have the greatest effect on metapopulation persistence (Mangel et al. 2006). A complication with marine species has previously been identified by Caswell (2000): “Recruitment in marine invertebrates and fishes, for example, is notoriously variable. I can imagine that it might make an overwhelming contribution to \( \lambda \) in some data set. But it might be an unattractive management target for management, because it is subject to so much environmental variability, due to so many impossible-to-control factors, that any management intervention would be swamped by environmental noise.”

Indeed, many of the key processes identified here, including population connectivity and juvenile vital rates, are the most challenging to accurately estimate as well as to regulate by management activities. The findings of Carson et al. (2010) identified major source populations within this region for each species, and demonstrated their relative stability over a number of years. The present study highlights the roles of those source subpopulations in metapopulation persistence, and other authors have previously documented key roles for source subpopulations (e.g., Wootton and Bell 1992). Marine Protected Areas (MPAs) that preserve the reproductive output and adult survival of *M. californianus* in the southern subpopulation would be likely to help maintain high county-wide recruitment levels. Protection of mussels in the southern subpopulation, however, is unlikely to enhance the other parameters with high elasticities: juvenile survival, growth, or the percentage of larvae retained within the subpopulation.

In the reverse situation, where managers wish to use spatial management techniques to eradicate an invasive “pest” species as in Levins’ (1969) work, the relative importance to the *M. galloprovincialis* metapopulation of juvenile survival in the north county might make a more tractable target. Several years of biocontrol, targeting the northern juveniles after spring recruitment peaks, might contribute to a county-wide collapse of *M. galloprovincialis* populations. However, such an effort is unlikely in this case because of the value of *M. galloprovincialis* to existing aquaculture facilities. Instead, the profitability of future aquaculture operations could benefit from the population connectivity results by locating operations to maximize the natural “set” of recruits on their lines, thus reducing the need to purchase hatchery-reared juveniles.

The time-series approach to connectivity combined with this study’s life-history-based population projection models has confirmed that the concept of marine metapopulations proposed by Sale et al. (2006) is indeed appropriate for these two *Mytilus* species. Self-recruitment to each subpopulation usually contributed more recruits than immigration, but neither subpopulation would likely have a population growth rate \( \lambda \) close to one (replacement) without receiving individuals from the other subpopulation. Although the metapopulation concept is often assumed to apply in marine studies, it is seldom demonstrated with empirical connectivity and demography data. The applicability of the metapopulation concept is, of course, dependent on the scale of study. The two subpopulations here were divided by habitat breaks and the ability to distinguish shell chemistry, but could have been considered a single population with little or no input of recruits from outside the study region (i.e., one large closed population). Conversely, each of the 17 local sites used in the connectivity time series could have been treated as separate subpopulations, which would have resulted in little correlation between local production and local demography (i.e., several smaller open populations).

This system offers a test case for the marine version of the drift paradox (Shanks and Eckert 2005), or the uncertain mechanisms that maintain upstream subpopulations in prevailing current regimes. Possible mechanisms for persistence in this environment of seasonal current reversals include self-recruitment in either season, counterflow recruitment during the main reproductive season, and recruits traveling with the reversed flow in the off season. For the bay-dwelling *M. galloprovincialis*, the upstream subpopulation was in the north, and self-recruitment was the dominant mechanism for persistence. The north received 72% of its recruits due to local retention, 21% from in-season exchange against the flow, and only 7% from off-season exchange. The dominant mechanism was similar for the open-coast *M. californianus*, although the three sources contributing recruits were slightly more balanced. The upstream southern subpopulation received 60% of its...
recruits from local retention, 29% from in-season counter-current exchange, and 11% from off-season imports from the north. The elasticity and LSA results (Figs. 4 and 5) support the relative importance of these mechanisms to overall persistence.

Intuitively, the exchange of larvae among subpopulations appears to be a beneficial process for most metapopulations. However, during the course of model exploration in this study, observed scenarios with increased exchange between the two subpopulations (holding overall fecundity constant) always resulted in lower overall metapopulation growth rates ($\lambda$) compared to scenarios of higher self-recruitment. Essentially, increasing overall exchange always resulted in the advection of recruits away from the most productive subpopulation, and these recruits were not “returned” in subsequent years by the other subpopulation due to asymmetry in larval dispersal. This would also apply to subpopulations with balanced exchange but unequal juvenile mortality rates—with increased flow from a favorable area not being “returned” by the unfavorable area, thus leading to an overall reduction in $\lambda$. Although local retention in the source subpopulation clearly benefits the overall growth rate of the metapopulation, this does not imply that connectivity is a detrimental process. The dispersal of individuals from source populations can allow for persistence of populations in sink habitat via a “rescue effect” (sensu Brown and Kodric-Brown 1977) and sink subpopulations can still contribute to overall metapopulation persistence through network effects (Hastings and Botsford 2006). The decreased $\lambda$ observed during years of high exchange could be considered a “cost” to supporting sink subpopulations, a form of population-level bet-hedging strategy. The cost of this strategy could well be worthwhile over longer time scales, as temperature or current regimes change, or disease, habitat damage, or other disturbances alter the dynamics of the metapopulation.

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