SYMPOSIUM

What Controls Connectivity? An Empirical, Multi-Species Approach

Paola C. López-Duarte,1,* Henry S. Carson,† Geoffrey S. Cook,‡§ F. Joel Fodrie,† Bonnie J. Becker,‖ Claudio DiBacco#, and Lisa A. Levin**

*Marine Field Station, Institute of Marine and Cosatal Sciences, Rutgers University, 800 Great Bay Boulevard, Tuckerton, NJ 08087, USA; †Marine Science Department, University of Hawai‘i at Hilo, 200 W. Kawili St., Hilo, HI 96720, USA; ‡Cooperative Institute for Marine and Atmospheric Studies, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA; §Atlantic Oceanographic and Meteorological Laboratory (AOML), National Oceanographic and Atmospheric Administration (NOAA), 4301 Ruckenbacker Causeway, Miami, FL 33149, USA; †Institute of Marine Sciences & Department of Marine Sciences, University of North Carolina at Chapel Hill, 3431 Arendell Street, Morehead City, NC 28557, USA; ‖Environmental Science/Interdisciplinary Arts and Sciences, University of Washington Tacoma, 1900 Commerce Street, Tacoma, WA 98402, USA; #Bedford Institute of Oceanography, Fisheries and Oceans Canada, Dartmouth, NS, B2Y 4A2, Canada; **Center for Marine Biodiversity and Conservation and Integrative Oceanography Division, Scripps Institution of Oceanography, La Jolla, CA 92093-0218, USA

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1E-mail: lopez-duarte@rutgers.edu

Synopsis The exchange of individuals among habitat patches (connectivity) has broad relevance for the conservation and management of marine metapopulations. Elemental fingerprinting-based research conducted over the past 12 years along the open coastline and bays of San Diego County in southern California evaluated connectivity patterns for seven species: one native and two invasive mussels, an oyster, a brachyuran crab, and two fishes. The studies spanned different years and seasons but overlapped considerably in space, allowing comparisons of dispersal patterns across species, and assessment of the relative importance of location, circulation, and intra-annual and inter-annual variability. We asked whether the species exhibited commonalities in directional transport, transport distances, sources and sinks, self-recruitment, and bay-ocean exchange. Linked connectivity-demographic analyses conducted for two species of mytilid mussels and two fishes allowed evaluation of the contributions of realized connectivity to metapopulation dynamics relative to other life-history attributes. Common trends across species include average along-shore dispersal distances of 15–35 km and seasonal changes in direction of dispersal that mirrored patterns of along-shore circulation. We observed greater isolation of back-bay populations, significant exchange from front bay to ocean, and high self-recruitment in locations on the northern, open coast, and in the southern bays. Connectivity was rarely the most influential driver of growth and persistence of metapopulations, but influenced the importance of other vital rates. Several locations served consistently as sources of larvae or as nurseries for multiple species, but there were few sites in common that were sinks. For the mussels, reproductive timing guided directional transport. These results imply that local management (e.g., habitat protection, opening of the mouths of lagoons, location of aquaculture farms) may be effective along this coastline. Regional, multi-species assessments of exchange of larvae should move us closer to ecosystem-based management.

Introduction to the problem

Early recognition of the vast dispersal potential exhibited by marine larvae and its implications for variability in recruitment gave rise to a fascination with where larvae go—i.e., “larval dispersal” (e.g., Hjort 1914). Today, it is necessary to identify not only where larvae go but where new recruits originate for properly managing exploited stocks, tracking invasions, or designating marine reserves (Levin 2006). Thus, we define the exchange of larvae between
subpopulations as “larval connectivity.” As methodologies for assigning the origins of larvae have emerged, the dynamics of connectivity have been measured more frequently and with greater complexity. Over the past decade, molecular markers (e.g., Burton 1983; Hedgecock 1986; Grosberg and Cuningham 2001; Hellberg et al. 2002), numerical simulation (e.g., Paris and Cohen 2004; Siegel et al. 2003; Witman et al. 2003; Rasmussen et al. 2009; Watson et al. 2010, 2011), and trace elemental fingerprinting (reviewed by Thorrold et al. 2007) have all yielded new insights into connectivity patterns of marine species. In a few instances these methods have been applied in tandem (e.g., Gilg and Hilbish 2003; Jones et al. 2005; Galindo et al. 2006; Planes et al. 2009; Liu et al. 2010). In most cases, studies of connectivity are location-specific and focus on one or two species, usually fish or invertebrates (but not both). However, many of the management decisions that must be made, for example about fishing closures, status of reserves, or restoration of habitats, affect assemblages or communities containing a wide variety of species. Thus, it is useful to know about patterns of regional connectivity of multiple species. To date, studies of empirical connectivity that examine multiple species simultaneously are scarce (e.g., Toonen et al. 2011).

Elemental fingerprinting techniques have been applied previously along the Southern California Bight (SCB) to study patterns of connectivity of kelp rockfish (Sebastes atrovirens) (Standish et al. 2008) and English sole (Pleuronectes vetulus) (Brown 2006) using otolith microchemistry, and the feasibility of using statolith microchemistry to study connectivity has been demonstrated for the market squid (Doryteuthis opalescens) (Warner et al. 2009). Large-scale biophysical circulation models were employed to estimate dispersal of larvae and recruitment patterns in the SCB by Mitarai et al. (2009), White et al. (2010), and Watson et al. (2010, 2011).

The linear coastline of San Diego County in southern California, punctuated by a series of estuaries, bays, and lagoons, has been the location of multiple microchemistry-based studies that generated empirical data on connectivity. These involve seven species: four bivalves, one crustacean, and two fish in studies that span different periods between 1997 and 2009 (Table 1). Here we review and compare the empirical results of these investigations to evaluate dispersal patterns across species and to gain insight into the importance of location, circulation, and temporal variability in driving patterns of connectivity. We ask whether there are similarities across species in directional transport, distances transported, specific sources and sinks, and patterns of self-recruitment or of exchange between bay and ocean. Linked connectivity-demographic analyses conducted for two species of mussels and two fishes allowed us

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Dates</th>
<th>Regions Distinguished</th>
<th>No. sites studied*</th>
<th>Coastline extent (km)</th>
<th>Key elements**</th>
<th>Referenced study</th>
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<tr>
<td>Musculista senhousia (Asian mussel)</td>
<td>May, Nov. 2008</td>
<td>A, D, E</td>
<td>7</td>
<td>50</td>
<td>Mg, Mn, Cu, Ba, Pb, U</td>
<td>P. C. López-Duarte et al. (submitted for publication)</td>
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<tr>
<td>Hypsypops rubicundus (Garibaldi fish)</td>
<td>Spring–Fall 2008, 2009</td>
<td>A, B, C</td>
<td>6</td>
<td>60</td>
<td>Mg, Ca, Mn, Sr, Ba, Pb, U</td>
<td>Cook (2011a, 2011b)</td>
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<td>2004: Mn, Cu, Ba</td>
<td>Fodrie and Herzka (2008)</td>
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*See Appendix for a complete list of study sites.
**Some of the elements (usually the last on the list) were not used for all of the sampling dates within these studies.
to evaluate the contributions of realized connectivity to metapopulation dynamics (i.e., growth and persistence) in southern California. Finally, we assess the implications of cross-species similarities and differences in connectivity for management of habitats and/or species.

**Overview of methods**

The connectivity studies we conducted extended for ~100 km along the southern Californian coast from Dana Point, Orange County to Imperial Beach, San Diego County (Fig. 1), and depending upon the species and the study, included coastal sites, bays, or both. Included were the California mussel (*Mytilus californianus*), the Bay mussel (*M. galloprovincialis*), as well as the Asian mussel (*Musculista senhousia*) which inhabit habitats on the open coast, front of the bay, and back of the bay, respectively. We also studied the Olympia oyster (*Ostrea lurida*), a back-bay species and the striped shore crab (*Pachygrapsus crassipes*) which inhabits open coast and bays. The garibaldi damselfish (*Hypsypops rubicundus*) inhabits shallow subtidal rocky reefs on the open coast; the Californian halibut (*Paralichthys californicus*) uses bays and open coasts as nursery habitats for juveniles that then migrate offshore in the SCB. These species also represent diverse life histories, ranging from brooders (*O. lurida*) or nest builders (*H. rubicundus*) to broadcast spawners (mussels), with durations of the planktonic larval stage lasting ~1–2 weeks (*M. californianus*, *M. senhousia*), 2–3 weeks (*M. galloprovincialis*, *H. rubicundus*), to over a month (*O. lurida*, *P. crassipes*, *P. californicus*). Connectivity of larvae was studied for all species except the halibut, for which connectivity of juveniles between nurseries and the habitat of subadult populations was studied.

Application of elemental fingerprinting to determine natal origins requires knowledge of the chemical signals imparted to larval shells or otoliths at different locations. Local chemical signals imparted to larvae (most species) or juveniles (*P. californicus*) at various reference sites along the coast and within bays (Fig. 1) were assessed in different ways. For mussels, reference signatures were determined by outplanting embryos fertilized in the laboratory and analyzing the amount of larval shell deposited in the field over 1 week (Becker et al. 2007), for crabs and oysters by examining shells of brooded larvae, for garibaldi by sampling otoliths of larvae in benthic nests, and for halibut by studying otoliths of caged and free-living juveniles. The number of sites studied at one time varied from 6 (*H. rubicundus*) to 18 (*Mytilus spp.*) (Appendix 1).

To assign origins and determine patterns of connectivity, elemental analyses were conducted on the calcified shells of newly recruited bivalve larvae, zoea stage I exoskeletons of *P. crassipes*, the otolith core of postdispersal juvenile *H. rubicundus*, and the areas in otoliths of *P. californicus* that correspond to the juvenile stage. Following standard cleaning procedures, elemental ratios were quantified both in shells of bivalve larvae and in fish otoliths using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS). The elemental composition of individual *P. crassipes* larvae was analyzed using inductively coupled plasma-atomic emission spectrometer (ICP-AES). There was significant overlap in the key elements that distinguished among sites (Table 1). Elemental data were analyzed using linear
discriminant function analysis (DFA) to create algorithms that characterize differences in larval/juvenile-shell/otolith microchemistry imparted at various sites. Assignment of origins of recruits was determined both by DFA and maximum likelihood ratio (MLR) analysis. Detailed descriptions of the elemental fingerprinting methods can be found for *P. crassipes* in DiBacco and Levin (2000), for *Mytilus* spp. in Becker et al. (2007) and Carson et al. (2010), for *O. lurida* in Carson (2010), for *P. californicus* in Fodrie and Levin (2008), and for *H. rubicundus* in Cook (2011a).

In most of the studies, success of classification and assignment of origin were conducted at the level of the individual site (i.e., site of recruit collection), and at a regional level (northern coast, southern coast, northern bays, and southern bays). In the case of *P. californicus*, the habitat of juveniles was evaluated (bay, lagoon, estuary, and open coast). The success of classification at the site level was typically 60–70% for most taxa, but closer to 50% for *O. lurida* and *P. californicus*. However, larvae could be classified at the regional level with greater success (typically 64–80%). The success of classification for nursery habitats for *P. californicus* juveniles was 66–92%.

**Connectivity patterns**

**Self-recruitment and local recruitment**

For purposes of this study, self-recruitment is defined as “recruitment to the same site or region as the predicted natal origin”. Across the species studied, there was a trend toward higher self-recruitment in the northern region (Fig. 2). The patterns were not stable over time, however, and other regions, such as San Diego Bay and La Jolla, experienced self-seeding at least intermittently. For example, in May 2003, 87% of northern *M. californianus* juveniles originated in the north region whereas *M. galloprovincialis* exhibited self-recruitment rates of 51%.
of ~40% across all regions (Becker et al. 2007). However, when integrated over a long time period (2003–2008), more self-recruitment was found in *M. galloprovincialis* than in *M. californianus* (Carson et al. 2010). Both species exhibited higher regional self-recruitment in the northern region (*M. californianus* self-recruits 12 and 24% and *M. galloprovincialis* 26 and 36% in November and May, respectively) than in the southern region (*M. californianus* self-recruits 6 and 1% and *M. galloprovincialis* 8 and 4% in November and May, respectively). High self-recruitment by *O. lurida* was also found in lagoons in the northern region and in San Diego Bay during summer 2007 (Carson 2010). For *M. senhousia*, a large amount of self-seeding (73%) was reported in San Diego Bay in May but not in November of 2008 (P. C. López-Duarte et al., submitted for publication). Although DiBacco and Chadwick (2001) did not collect recruits of *P. crassipes*, they found that more larvae originating outside San Diego Bay were collected near the bay’s mouth than in mid-Bay, with possible retention of stage-I zoeae from the inner part of the Bay. *H. rubicundus* was found to self-recruit to the central region (La Jolla) during both years it was studied (61 and 33% in 2008 and 2009, respectively) and at one additional site (Mission Point, 11% in 2008) (Cook 2011a, 2011b). Most *P. californicus* subadults were found close to the region where they developed as juveniles (Fodrie and Levin 2008).

**Directionality of dispersal and relation to prevailing currents**

Across the San Diego region, direction of dispersal varied seasonally, with *M. californianus*, *M. galloprovincialis*, and *O. lurida* exhibiting southward dispersal in the spring or early summer and northward dispersal in the late summer or fall during most years (Fig. 2). The fall of 2004 was an exception, when *M. californianus* was found to travel southward (Carson et al. 2010). Larvae of *M. senhousia* traveled south from Mission Bay to San Diego Bay in November 2008 (P. C. López-Duarte et al., submitted for publication). For *O. lurida*, there was more southward movement in late June 2007 (40.3% southward versus 30.0% northward), and more northward movement in August 2007 (11.1% southward versus 27.8% northward) (Carson 2010). In contrast, the majority of *H. rubicundus* appeared to disperse northward in the summer of 2008 (44% northward and 5% southward) and 2009 (65% northward and 17% southward), although this pattern was more variable on shorter time scales (Cook 2011b).

Concurrent Acoustic Doppler Current Profiler (ADCP) data (measurements of velocity of currents) were collected for the mussel and garibaldi studies, allowing for comparison between the direction of currents and the direction in which larvae disperse. Observed directionality of dispersal by *M. californianus* and *M. galloprovincialis* generally agreed with results from two ADCPs deployed during part of the study period. Average velocity of currents over a 3-year period (2007–2009) were directed northward in the fall and southward in the spring. Of the mussel recruits that were captured when ADCP data were collected, 75% that did not self-recruit moved in the direction of the prevailing currents (Carson et al. 2010). Among *H. rubicundus* there was >90% agreement between larval directionality and ADCP-measured currents in 2008 (Cook 2011b). However, directionality for the back-bay species, *M. senhousia*, in November 2008 (P. C. López-Duarte et al., submitted for publication) and *O. lurida* in summer 2007 (Carson 2010), did not agree with the general seasonal pattern of currents described by Carson et al. (2010). The region exhibits reversals in the direction of currents on a weekly time scale, indicating that larvae are exposed to non-average conditions throughout the duration of this life stage (Carson et al. 2010; Cook 2011b). In addition, larvae nearest to the shore may be more likely to experience higher variability in direction of currents as reversals were recorded at a higher frequency by the ADCP closest to the coastline (Carson et al. 2010).

**Distances dispersed and distance-connectivity relationships**

The majority of species exhibited the potential to disperse over the entire 100-km stretch of coastline studied, but mean distances ranged from 10 to 37 km (Fig. 3). Recruits of *M. californianus* and *M. galloprovincialis* traveled on an average 34.9 km (±25.3; SD) and 37.0 km (±27.6; SD) based on the shortest seagoing distance between generalized regions of origin and destination (Carson et al. 2010). Among the species studied, *M. californianus* has a relatively short larval duration (1–2 weeks), while *M. galloprovincialis* larvae are in the water column an average of 2–4 weeks. Between 2003 and 2009, *M. galloprovincialis* larvae traveling northward dispersed on average 10 km farther in November than in May. There was no seasonal effect on the distances that southward-moving larvae traveled. Distances traveled
from either north or south were not significantly different for *M. californianus* larvae between spring and fall. While most *M. senhousia* were self recruits in May 2008, the majority traveled 15 km from Mission Bay to San Diego Bay in November 2008 (P. C. López-Duarte et al., submitted for publication). Considerable numbers of oyster larvae were exchanged between North County bays, Mission Bay, and San Diego Bay (Carson 2010). Oyster larvae dispersed an average of 21.4 km, while site-specific averages were 27.0, 23.2, and 18.2 km for larvae originating from North County bays, Mission Bay, and San Diego Bay, respectively. These dispersal distances were approximately half of the distances traveled by *M. californianus* and *M. galloprovincialis* larvae (Fig. 3), even though oyster larvae have a longer planktonic stage (over a month). Dispersal of stage-I shore-crab (*P. crassipes*) zoeae was ~20 km for larvae hatched in the inner Bay (DiBacco and Chadwick 2001; DiBacco et al. 2001). Zoeae originating from coastal sites were sampled up to ~15 km into the Bay. Stage-I zoeae are thought to travel additional distances as they undergo development (four more planktonic stages) before settling in habitats occupied by adults. Juvenile halibut emigrating from nurseries in the bay to subadult aggregations in nearby coastal areas generally migrated <10 km (Fodrie and Levin 2008). Overall mean distance dispersed by larvae of *H. rubicundus* in 2008 and 2009 was ~15 km (including self recruits), with a range of 5–59 km. Asymmetric dispersal was observed in *M. galloprovincialis* larvae, which traveled ~15 km further southward than northward in May, but was not observed in *M. californianus* larvae (Carson et al. 2010).

Effect of distance on the similarity of recruit sources

Several of the studies assessed whether adjacent sites were likely to receive recruits from similar sources. This was most clearly the case for juvenile halibut, which migrated very locally to regions where subadults occur, effectively limiting connectivity during this phase of their life history (Fodrie and Levin 2008). In the case of *M. californianus*, site-specific assemblages of recruits differed increasingly with distance between sites (they exhibited a positive relationship) in only 1 (2005) of 6 years sampled; 2 years (2003 and 2004) exhibited a negative relationship, 2 years (2007 and 2008) showed no relationship, and 2006 could not be assessed due to poor success in classification (Carson et al. 2010). Similar analyses for *M. galloprovincialis* in 2005 showed a significant (negative) relationship between distance and sources of recruits (L. A. Levin and L. L. Rasmussen submitted for publication). This is expected given *M. galloprovincialis* larvae originate in bays and have higher self-seeding rates than do those of *M. californianus* (Carson et al. 2010).

Inner versus outer bay, bay-ocean, and bay to bay exchange

The exchange of individuals (invertebrates and fish species) was characterized and quantified between disjunct subpopulations: (1) within and (2) between

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**Fig. 3** Mean dispersal distances for the seven species studied in southern California. *Mytilus californianus* and *Mytilus galloprovincialis* dispersed the greatest distances of the group. *Hypsypsops rubicundus* exhibited inter-annual differences, with almost double the average distance of dispersal in 2009 (light shading) than in 2008 (dark shading). The bay-bay dwellers (*Ostra lurida* and *Musculista senhousia*) were next in line with dispersal distances averaging 15–20 km. Stage-I zoeae of *Pachygrapsus crassipes* fall within that range. However, *P. crassipes* undergoes several planktonic larval stages before settling into habitats characteristic of adults. *Paralichthys californicus* exhibited the shortest distances (~10 km) of dispersal from juvenile habitats to adult habitat.
embryos as well as (3) between embayments and coastal habitats (Fig. 2). The open-coast species *M. californianus* mainly experienced exchange of larvae between different coastal regions, and while larval dispersal from coastal to bay habitats was observed, it is not likely to lead to the establishment of aggregations of either juveniles or adults due to physiological limitations (Becker et al. 2005, 2007). Similarly, *M. galloprovincialis* larvae (24–25%) were exchanged between embayments and open coastal sites (Carson et al. 2010), but the adults are found mainly in front-bay habitats. The persistence of local aggregations of *M. galloprovincialis* in southern Californian embayments, despite limited self-recruitment, supports the hypothesis of larval supply from coastal populations (Becker et al. 2005, 2007; Carson et al. 2010), and also to some extent between large neighboring bays (<2% exchange between San Diego and Mission Bays located <15 km apart) (Carson et al. 2010). In contrast, larval exchange of *O. lurida* between subpopulations within embayments of three southern Californian regions (North County embayments, San Diego Bay, and Mission Bay) revealed significant self-recruitment as well as exchange between bays that are separated by up to 75 km (Carson 2010). Both back-bay species (*O. lurida* and *M. senhousia*) not only exhibited high self-recruitment, but also bay-to-bay exchange of up to 50 km. Stage-I zoeae (*P. crassipes*) collected at the entrance of San Diego Bay were more likely to have originated from outside the Bay than were zoae collected mid-bay (25 versus 5%). These results correspond well with net transport inferred from vertical migratory behavior exhibited by stage-I zoae (DiBacco et al. 2001), while larval origins estimated from elemental fingerprinting suggest considerable bi-directional exchange of larvae between San Diego Bay and nearshore coastal waters (DiBacco and Chadwick 2001). Otolith microchemistry revealed that juvenile halibut nurseries located in bays contributed 65% of the San Diego County recruits in 2003 and 49% in 2004 (Fodrie and Levin 2008). The vast majority of subadult halibut (82–89%) collected from Todos Santos Bay (Baja California, Mexico) during 2002 and 2003 originated from nurseries located in outer regions of a local estuary (Punta Baja Estuary), with no apparent contribution from the innermost region of the estuary (Fodrie and Herzka 2008). Intra-embayment migration was found to be significant for halibut in Baja California, where ~57% of individuals tested migrated between regions of selected embayments.

**Commonality of larval sources and sinks**

Species from the open coast

The studies of *H. rubicundus* and *M. californianus* identified similar subpopulations as sources of larvae along the open coastline of San Diego County. For *H. rubicundus*, the La Jolla area was the leading producer of recruits in both 2008 (82%) and 2009 (52%), followed by the mouth of Mission Bay (13% in 2008; 30% in 2009). Although these two locations had a high abundance of adults, other areas with high abundance in the county were not identified as sources (Cook 2011b). Over the 2003–2008 study period, the La Jolla area was also a source for *M. californianus* (15%), but was not as prominent as were Carlsbad (24%) and Imperial Beach (21%). In both *H. rubicundus* and *M. californianus*, neither the abundance of adult fish nor the cover of adult mussels were accurate predictors of successful production of recruits (Carson et al. 2010; Cook 2011b). A similar disconnect between spawning biomass and the recruitment of larvae was observed for a sculpin (*Clinocottus analis*) in San Diego tidepools (Davis and Levin 2002).

The largest sink subpopulation for *H. rubicundus* was the Carlsbad area, which received 25% of recruits in 2008 and 52% in 2009 but was not a natal site for either year (Cook 2011b). During some years, Cardiff Reef was a common sink for both *M. californianus* (2003, 2007, and 2008) (Becker et al. 2007; Carson et al. 2010) and *H. rubicundus* (2008) (Cook 2011a), although it produced some recruits of both species in other years. Both Oceanside and Dike Rock were prominent sinks for *M. californianus* in some years (2003, 2007, and 2008). Although *M. californianus* recruits that originated elsewhere settled inside San Diego Bay, Mission Bays, and at Cabrillo (Carson et al. 2010), these sites are not considered recruitment sinks as recruits do not survive to adulthood. A comparison of *H. rubicundus* and *M. californianus* at overlapping sites and times (2008–2009) indicated that in 2008 La Jolla was the biggest source of recruits and the Torrey Pines/Dike Rock area was the smallest source, while in 2009 Carlsbad in North Country was the largest source of recruits.

**Species from bays**

The bay-dwelling *O. lurida* and *M. galloprovincialis* had similar source and sink subpopulations. For the oyster, North County lagoons and San Diego Bay produced the majority of recruits (80%), while Mission Bay was identified as a relative sink (Carson 2010). In contrast, Mission Bay produced many more recruits of
*M. galloprovincialis* (*n* = 55) than it received (*n* = 8). The sites of highest production of both *M. galloprovincialis* and *O. lurida* were Oceanside (36%), Carlsbad (25%), and San Diego Bay and its adjacent coastline (22%). There was a positive relationship (Spearman rank correlation = 0.875, *P* < 0.001) in *M. galloprovincialis* between production of recruits and the cover of adults at all sites (likely due to high self-recruitment), while larval sinks were scattered along the open coast where there was low abundance of adults (e.g., Cardiff, La Jolla, and Pacific Beach) (Carson et al. 2010).

**Extent of connectivity**

Four of the species studied (*H. rubicundus, O. lurida, M. californianus, M. galloprovincialis*) dispersed throughout the entire study area in at least 1 year or season. Oyster larvae were readily exchanged between Carlsbad-area lagoons and San Diego Bay in summer 2007 (Carson 2010). In summer 2009, some *H. rubicundus* juveniles (12%) collected in the mouth of San Diego Bay were determined to have originated in Carlsbad, but this extended migration was not observed in 2008 (Cook 2011a). Less than 5% of the recruits of *M. californianus* were determined to have traveled between the northernmost and southernmost study sites during the study period, while <1.5% of *M. galloprovincialis* recruits achieved this maximum dispersal distance (Carson et al. 2010). These results suggest that the ~125 km coastline of San Diego County does not encompass the maximum extent of connectivity for any of these populations, although it most likely captures the majority of dispersal scenarios. Results from a more recent *Mytilus* spp. outplant conducted during the November 2009 El Niño and from additional sites in Baja California, Mexico (70–90 km south of the USA–Mexico border) indicate that up to 13% of the recruits of *M. galloprovincialis* and 33% of *M. californianus* collected in San Diego County could have originated in Baja California (L. A. Levin et al., unpublished data).

**Demographic consequences of connectivity**

Two species of mytilid mussels and two fishes were also the subject of demographic measurements and of modeling efforts aimed at assessing the significance of observed connectivity patterns for metapopulation fitness. For these, data on rates of fecundity, growth, and survival were combined with connectivity data in linked population projection matrices, and sensitivity analyses were used to evaluate the relative contributions of the different parameters to population growth rate λ (i.e., fitness) (Fodrie et al. 2009; Carson et al. 2011; Cook 2011b).

The *Mytilus* spp. were modeled as northern and southern subpopulations, the *H. rubicundus* model had six subpopulations, and *P. californicus* was modeled for type of habitat used by juveniles. In general, between-subpopulation (patch) connectivity terms had smaller effects on metapopulation growth rates (λ) than did within-population (patch) vital rates (survival and fertility) (Carson et al. 2011; see also Figueira 2009). However, the connectivity terms determined “where” and “when” within-patch dynamics mattered most. In the two species of mytilid mussels, directionalities of larval flow were generally synchronized and juvenile growth and mortality were found to be most important in the source subpopulation after the reproductive peak. However, because of differences in the seasons of peak reproduction between the two *Mytilus* species studied, and coincident with reversals in surface currents, the seasons and subpopulations for which juvenile vital rates mattered most were opposite (Carson et al. 2011). Thus, timing of reproduction reversed the demographic outcome. Mytilid mussel demographic models also showed that low levels of “off-season” spawning and recruitment have little effect on adult populations (Carson et al. 2011; Fodrie et al. 2011). The flow of these larvae during various connectivity scenarios, or the fates of resulting juveniles, did not significantly change the rate of population growth for either species (Carson et al. 2011).

The contribution of connectivity to the dynamics of metapopulations of *H. rubicundus* and *Mytilus* spp. appears to be greater when populations are declining (λ < 1) than when they are growing (Cook 2011b). When population numbers are in decline, larval transport away from suitable habitat patches has an inordinately great influence. The transport of larvae to more suitable or less suitable nursery habitats appears to be a particularly important process in sustaining or deterring marine metapopulations. Halibut (*P. californicus*) juveniles that recruited to estuarine and embayment habitats in San Diego contributed positively to overall population growth relative to juveniles within open-coast sites, due to increased mortality of juveniles on the open coast (Fodrie et al. 2009). As noted above, growth and mortality of juvenile mussels were the life-history traits that had the greatest effect on metapopulation growth rates in elasticity analyses (Carson et al. 2011), further highlighting the importance of juvenile habitats.

The influences of connectivity can be greatest in declining populations (λ < 1), as that is when...
transport away from suitable habitat has its largest negative effect and transport to suitable habitat may be most helpful (Carson et al. 2011; Cook 2011b). Dispersal of juveniles or subadults “away” from nursery habitats can also structure adult populations. Reduced dispersal of postjuvenile halibut influenced the abundance of adults, with higher numbers of adults located near the large embayments where they had originated (Fodrie and Levin 2008).

Discussion
What controls connectivity?
Temporal processes
The analysis above reveals several strong time-sensitive processes that emerge as controls on connectivity. Most prominent is the seasonal reversal in the direction of currents which affects the distance and direction of transport of bivalve larvae. This feature implicates reproductive timing as a primary determinant of dispersal (Carson et al. 2010). These results suggest that warming, upwelling, or other aspects of climatic change that affect spawning, the time of larval development, or larval survival may alter connectivity patterns. Seasonal shifts in connectivity have been reported in numerical modeling studies (e.g., Mitarai et al. 2009) as has annual variability in the genetic structure of populations (Toonen 2001). Shorter-term (days to weeks) reversals in directions of currents also affect directional transport and overall patterns of connectivity (Fodrie et al. 2011). As demonstrated in H. rubicundus studies, this can lead to within-season variations such that larvae hatched in 1 week may travel a different direction from those hatched the following week (Cook 2011a, 2011b). We observed only limited inter-annual variation in patterns of connectivity. In the longest study, mytilid mussels exhibited consistent trends in the direction of transport across most years. Both fish species exhibited similar connectivity patterns between years: more northward transport in H. rubicundus (Cook 2011b) and more P. pachygrapsus originating in bays (Fodrie and Levin 2008). El Niño Southern Oscillation (ENSO) events can introduce inter-decadal variation in transport and oceanographic conditions locally (Nam et al. 2011). Increased transport of larvae from Baja CA to the San Diego coastline is likely during these events (e.g., Davis 2001) and is possibly evident in the results of Mytilus spp. outplants from November 2009, an El Niño period (L. A. Levin et al., unpublished data). Genetic evidence of this same phenomenon among intertidal crabs was reported in Northern CA (Toonen 2001). When population declines occur during El Niño, as observed for the sculpin Clinocottus analis, transport and recruitment of larvae (i.e., connectivity) can take on added demographic importance (Davis and Levin 2002).

Development strategies and habitat preference
Body or nest brooding in the study species O. lurida, P. pachygrapsus, and H. rubicundus is usually followed by a lengthy (>3 week) dispersal phase and therefore there was no tendency for brooders per se to exhibit limited dispersal in our analysis. Nor is there any evidence of difference in dispersal distance between Mytilus species that have different average PLDs but overlapping ranges (Fig. 3). The open-coast and front-bay mytilid species exhibited larger average dispersal distances than did the back-bay species M. senhosia and O. lurida (Fig. 3). Given that dispersal out of San Diego Bay is heavily influenced by vertical migrations of larvae (DiBacco et al. 2001), and that bay-to-bay exchange in the region varies temporally (Carson 2010; P. C. López-Duarte et al., submitted for publication), back-bay habitat alone cannot be a primary determinant of connectivity, even in large bays where water masses have long residence times (e.g., San Diego Bay). The distribution of viable habitat patches may also affect apparent differences in the transport of larvae. The smaller average distances traveled by H. rubicundus larvae (Fig. 3), relative to some of the other species, may reflect the limited distribution of suitable rocky reef habitat in the study area (Cook 2011a, 2011b). In general, studies have found a poor correlation between PLD and various estimates of dispersal distances (e.g., Shanks 2009; Selkoe and Toonen 2011).

Implications for management
In this study we have provided a step forward by presenting the first multi-species examination of connectivity based on an empirical tracking approach. Through a retrospective analysis of connectivity patterns over multiple years and species, generalities and commonalities begin to emerge. The ability to identify sources and destinations of successful recruits is critical to many management decisions involving marine protected areas, restoration, coastal development, invasive species, aquaculture, and fisheries. If complete knowledge of the sources and sinks of larvae is known for a multi-species complex, managers would be able to, in theory, protect solely the source populations in common among the species in question. The known sink locations of the various species then could be opened up to extraction, as they would...
be re-supplied by the source populations. In theory this would provide benefits to both consumptive and nonconsumptive users of the marine environment (Cook and Heinen 2005). During the past few years, the southern Californian coastline underwent evaluation and the designation of new marine protected areas (Stokstad 2010) (Fig. 1). The largest of these in San Diego County (La Jolla) is shown by our studies to be a larval source site for mussels and fish. Reciprocal connectivity between the La Jolla Marine Protected Area (MPA) and those in northern and southern San Diego County seems likely for many species, given the seasonally, and sometimes weekly, reversals in currents.

The link between populations serving as a source of adults and successful recruitment remains uncertain. If passive transport during the pelagic larval period and uniform mortality among larvae from different source populations is assumed, probability theory would suggest that the largest populations would produce the greatest number of recruits as they produced a larger proportion of possible recruits. However, the results of Carson et al. (2010) on mytilid connectivity show that for M. californianus, cover of adults was a poor predictor of recruitment success, while for M. galloprovincialis, larger adult populations were the primary source of successful recruits. Use of genetic and fingerprinting methods (e.g., Planes et al. 2009) in concert with demographic methods (Carson et al. 2011) yield the inter-generational demographic consequences of connectivity, and an increasing ability to predict the consequences of various options for managing multiple species.

For all species being examined, the larvae were found to travel shorter distances (tens of km) (Fig. 3) than predicted by earlier work (e.g., hundreds of km) (Caley et al. 1996). These findings are consistent with a general pattern of greater-than-expected retention (Swearer et al. 2002; Levin 2006; Cowen and Sponaugle 2009; Miyake et al. 2011) and indicate that successful plans for the management of multiple species should incorporate some aspect of local management. In addition, the size and site of MPAs must be decided and implemented strategically, ideally targeting regions known to act as sources of larvae or serve as critical nursery habitat (e.g., Fodrie and Levin 2008); such an approach is compatible with traditional management techniques, such as establishing limits for fishing or catching individuals of a certain size to ensure the fecundity of the target species in light of broader scale uncertainty associated with environmental changes related to climatic change (e.g., Bakun 1990; King et al. 2011). Ideally, the distance between reserves would be such that connectivity between the protected areas would be maintained (Christie et al. 2010).

The findings of significant ocean-to-bay and bay-to-bay exchange of larvae in San Diego County can have implications for decisions regarding the eradication of invasive species, the restoration of wetlands, and the establishment of aquaculture farms. Invasive species such as M. senhousia appear capable of reseeding back-bay habitats; thus, local eradication is likely to be ineffective. This is consistent with boom-bust dynamics observed for this species in southern Californian embayments (Crooks 1996). However, such potential for reseeding could be beneficial for species like the native oyster, O. lurida, which is a target for restoration in many Pacific estuaries (Cook et al. 2000). Faunal recovery in restored salt marshes, which are common in southern Californian embayments, should also benefit from significant bay-to-bay exchange of larvae. Rapid recovery is reported for marsh species with planktonic larvae in southern California (e.g., Talley and Levin 1999; Levin and Talley 2000). Even though many of the small lagoons in the center of the study region fill with sand at the mouth and close episodically, active dredging at the mouth to maintain flushing is likely to be an effective restoration tool due to high connectivity with open water and other bays.

Open culture of mussels and oysters in bays and estuaries occurs worldwide and a major source of M. galloprovincialis recruitment throughout San Diego County is the mussel farm in Agua Hedionda Lagoon. M. galloprovincialis is an invasive species on the West Coast of the United States, but is so widespread in front-bay habitats such as rip rap, that it is not managed as an exotic species. Connectivity along the SCB coastline is such that an introduced bivalve, or other invertebrate species, cultured in one of the southern Californian embayments will almost certainly spread to suitable habitat throughout the region (White et al. 2010).

Much uncertainty remains regarding many of the possible influences of climatic change on patterns of connectivity. A general warming of coastal marine waters may affect larval dispersal (O’Connor et al. 2007) and could produce broad-scale shifts in phenotype that result in trophic mismatches, thus altering the structures of food webs (Edwards and Richardson 2004), with possible negative impacts on the success of recruiting larvae. Similarly, there is growing evidence of increased upwelling on the shelf of water with low oxygen and low pH (Feely et al. 2008) leading to deoxygenation (Bograd et al. 2008) and acidification in the SCB. Negative effects
on bivalve larvae, such as morphological abnormalities, are likely, and have been reported (reviewed by Kurihara 2008). Changes in pH, as well as the other sources of variability in the coastal marine environment that influence marine connectivity patterns, will present resource managers with novel challenges for the successful management of natural marine resources. By understanding the variability in the connectivity patterns of present systems and in multiple species, more effective management strategies could be implemented for future climate scenarios.

Conclusions

The interspecific comparisons conducted here illustrate the challenges faced in assessing multi-species connectivity on a regional basis, but also provide general findings that may guide conservation and management of fisheries. The results from this first synthesis of empirical studies support the idea that reproductive timing can affect the direction of dispersal via reversals in direction of currents on seasonal and event scales, and across years. Furthermore, for species with similar habitats, differences in connectivity may result more from timing than from taxonomic affinity or developmental attributes. Thus, species that share reproductive timing, larval lifestyle, and habitat are likely to exhibit similar patterns of connectivity guided by physical processes. Location may be a prime determinant of self-recruitment. Connectivity was more limited for populations in North County and San Diego Bay, which exhibit more self/regional recruitment. However, all species exhibited significant exchange of larvae across the ~100 km study region. Average distances of larval transport were 15–35 km. For the four species studied demographically, between-patch connectivity was important for the persistence of metapopulations and modulated the influence of other vital rates but was rarely the dominant life-history feature driving growth rates of metapopulations. While few of the species studied are harvested commercially, the Californian halibut is fished recreationally and the bivalves are key ecosystem engineers. The observed connectivity patterns are likely to be representative of the many other species in the region that have similar habitats and life-history traits. We note that knowledge of specific multi-species connectivity comes at a cost; trace-elemental fingerprinting is demanding both logistically and fiscally. A further challenge is that estimates of trace elements are exclusively retrospective; they fail to provide managers with real-time data or predictive power. Nevertheless, spatial planning and management in coastal and bay ecosystems can be facilitated by combining fingerprinting-based studies with information about reproductive timing and the patterns of currents.

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## Appendix 1

<table>
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<th>Region</th>
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<th>M. galloprovincialis</th>
<th>M. californianus</th>
<th>H. rubicundus</th>
<th>O. lurida</th>
<th>P. crassipes</th>
<th>M. senhousia</th>
<th>P. californicus</th>
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*Not indicated in Fig. 1 map (sites only in crab, oyster, and/or halibut studies).

**Levin et al. (submitted for publication) for Mytilus spp.