

## Scales of Dispersal and the Biogeography of Marine Predator-Prey Interactions

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**ABSTRACT:** Striking differences in the dispersal of coexisting species have fascinated marine ecologists for decades. Despite widespread attention to the impact of dispersal on individual species dynamics, its role in species interactions has received comparatively little attention. Here, we approach the issue by combining analyses of simple heuristic predator-prey models with different dispersal patterns and data from several predator-prey systems from the Pacific coasts of North and South America. In agreement with model predictions, differences in predator dispersal generated characteristic biogeographic patterns. Predators lacking pelagic larvae tracked geographic variation in prey recruitment but not prey abundance. Prey recruitment rate alone explained more than 80% of the biogeographic variation in predator abundance. In contrast, predators with broadcasting larvae were uncorrelated with prey recruitment or adult prey abundance. Our findings reconcile perplexing results from previous studies and suggest that simple models can capture some of the complexity of life-history diversity in marine communities.

*Keywords:* dispersal scale, predator-prey population dynamics, models, biogeography, macroecology, marine.

Species vary enormously in their average dispersal potential. Some never venture far from their natal site; others regularly move on global scales. Large interspecific variation in dispersal distances among coexisting species is common in all ecosystems, both among species within trophic levels as well as between trophic levels (Kinlan and Gaines 2003). Dispersal of individuals determines the scale at which species interact with the physical environment, the nature and consequences of the interaction with other species, the way in which they respond to perturbations, and ultimately the selective forces and rates to evolve, speciate, or become extinct. Consequently, many theoretical models have explored the consequences of varying dispersal rates for individual species as well as species interactions (e.g., Levin 1974; Caswell 1978; Roughgarden and Iwasa 1986; Pulliam 1988; Gaines and Lafferty 1995; Loreau and Mouquet 1999; Chesson 2000; Amarasekare and Nisbet 2001; Lockwood et al. 2002; Amarasekare 2003; Snyder and Chesson 2003). However, because of logistic difficulties, most predictions from models that include differential dispersal of interacting species remain largely untested, except in controlled experimental arenas and involving species with comparatively short dispersal distances (e.g., Gonzalez et al. 1998; Shurin 2001; see Leibold et al. 2004 for review).

Contrasting dispersal capabilities among coexisting species is especially apparent in marine habitats, where variation in the mode of larval development alone imposes average dispersal distances that vary by many orders of magnitude (Kinlan and Gaines 2003; Shanks et al. 2003; Levin 2006). At one end of the spectrum lie many seaweeds, some invertebrates, and a few fish, which produce young that can develop within meters of their parents. These populations are demographically closed on relatively small spatial scales, since the dynamics at a given location are likely to be governed by local processes affecting birth and mortality rates. At the other end of the spectrum are many marine invertebrates and nearly all fish, which pro-

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duce young that develop in the plankton for weeks to months and can be dispersed widely by ocean currents (Scheltema 1986; Caley et al. 1996). The longer the larval development, the larger the scales of dispersal (Kinlan and Gaines 2003; Shanks et al. 2003; Siegel et al. 2003; Levin 2006), and the more a local population becomes demographically open with its growth decoupled from the local production of young (Gaines and Roughgarden 1985; Roughgarden et al. 1985). Existing theoretical explorations (e.g., Iwasa and Roughgarden 1986; Kuris and Lafferty 1992; Gaines and Lafferty 1995; Connolly and Roughgarden 1999b; Velázquez et al. 2005) suggest that this kind of variability in dispersal distances can greatly alter the dynamics and stability of species interactions. Considering that dispersal and connectivity in populations of marine species can occur over scales of tens to hundreds of kilometers, it is not surprising that empirical information to evaluate these model predictions is largely absent. Here, we begin this exploration by examining several intertidal predator-prey interactions where the interacting species have different dispersal scales.

Most studies of predator-prey interactions have examined dynamics at a single location (but see Dethier and Duggins 1988; Menge et al. 1994, 2004; Navarrete et al. 2005; Navarrete and Manzur 2008). Dispersal, however, links populations across sites. Hence, we implemented a unique set of empirical studies that focus on patterns across numerous sites within biogeographically widespread predator-prey systems found along the temperate west coasts of North and South America. Although a wide range of dispersal patterns may be found within marine predator-prey systems, we initially concentrate only on variation in the dispersal scale of predators that prey on invertebrates with pelagically dispersed larvae and sessile adults (e.g., mussels, barnacles), since these commonly dominate space and are by far the most important invertebrate component of the basal trophic level in most benthic marine communities worldwide. We consider the most ubiquitous predator-prey species in each biogeographic region, including two classes of predators: those that produce young locally versus those that broadcast larvae into the plankton. As a first step toward incorporating life history and dispersal in predator-prey models for marine organisms, and since we do not have information on actual dispersal distances of these species, we used simple models of local interactive populations in which species have either completely closed or completely open populations. Evaluation of model predictions was possible thanks to the availability of long-term data on prey recruitment rates over spatial scales exceeding predator individual movement and temporal scales sufficiently long to observe predator population responses.

## Material and Methods

### *Field Data*

Examining the relationship between predators and prey requires information on geographic patterns of population abundances and recruitment rates of young. Moreover, temporal variation in prey recruitment makes it necessary to integrate information over relatively long periods of time with respect to the biological response variable examined (i.e., predator population abundance). We compiled such data sets for several predator-prey combinations from two regions of the world, the Pacific coast in North America and the central coast of Chile in South America. We used essentially the same field methods in both hemispheres, facilitating comparisons across different predator-prey systems. Moreover, comparisons between predators of the same taxa (e.g., muricid whelks) but with contrasting life histories allowed more rigorous examination of the influence of dispersal scale.

All sites in this study were open-coast, wave-exposed rocky shores (fig. B1 in the online edition of the *American Naturalist*). Within a region, among-site variability in physical conditions was minimized by selecting, wherever possible, rocky benches of similar geomorphology, slope, and orientation to prevailing swell. The greatest heterogeneity among sites occurred along the central California coast, where coastline orientation and wave exposure changes sharply about Point Conception.

At 20 rocky intertidal sites spanning 2,100 km from central California to Oregon (fig. B1), we estimated the abundance of predatory whelks and the sea star *Pisaster ochraceus*, the main benthic predators in this system (Navarrete and Menge 1996; Menge et al. 2004). In Oregon, common whelk species included *Nucella canaliculata* and *Nucella ostrina*, whereas *Nucella emarginata* and *Acanthinucella spirata* were prevalent in central California. These whelk species are direct developers that lay benthic egg capsules from which small juveniles crawl away (e.g., Spight 1974). In contrast, sea stars have broadly dispersed pelagic larvae that spend anywhere between 75 and 230 days in the water column (Strathmann 1987). Sea stars and whelks feed on mussels (*Mytilus californianus*, *Mytilus galloprovincialis*, and *Mytilus trossulus*) and barnacles (mostly *Balanus glandula* and *Chthamalus* spp. but also *Semibalanus cariosus* and *Pollicipes polymerus*). Genetically fixed geographic variation in prey preferences has been documented for *N. canaliculata*, which rarely consume large *M. californianus* in Oregon (Sanford et al. 2003). Similarly, *A. spirata* tends to feed on small mussels rather than large, thick-shelled individuals. Although *Pisaster* also feeds on whelks, this intraguild predation does not have significant effects on whelk populations (Navarrete et al. 2000) and is not considered in our model (see below).

Along the central coast of Chile, we selected 22 wave-exposed rocky intertidal sites stretching across approximately 1,000 km of coastline (fig. B1). The main predators here are the sea star *Heliaster helianthus* and the muricid gastropod *Concholepas concholepas*, both of which feed mostly on mussels (*Perumytilus purpuratus* and to a lesser extent *Semimytilus algosus*) and barnacles (*Jehlius cirratus*, *Notochthamalus scabrosus*, and *Notobalanus flosculus*; Navarrete and Castilla 2003; Navarrete and Manzur 2008). These two predator species have planktotrophic larvae that spend from weeks to several months in the water column before settling into the adult habitat (Poulin et al. 2002; Molinet et al. 2005). In central Chile, intertidal predators with direct development (e.g., *Acanthina calcar*) are largely restricted to wave-protected, sand-inundated habitats and were therefore not included in this study.

In both hemispheres, local density of predators and cover of sessile prey at low, mid-, and high intertidal zones were quantified using the standard transect-quadrat method, as explained in detail by Broitman et al. (2001), Menge et al. (2004), and Lagos et al. (2005). A minimum of 10 0.25-m<sup>2</sup> quadrats per transect were sampled. Because of their large size and sparse distribution, densities of sea stars and *Concholepas* were estimated by counting the number of individuals within three to five swaths of large but variable area, depending on local topography. Swath areas were determined by stretching a 6–20-m-long tape parallel to the shoreline along which we counted all individuals found in a strip 1–5 m wide, depending on shore slope. Counts were then divided by the area surveyed. Mussel prey used to estimate relevant local abundance varied among predator species to reflect compositional changes in diet (see above). For *A. spirata*, we considered small individuals (<3 cm) of *M. californianus* + *M. galloprovincialis*; for *N. emarginata*, we considered *M. galloprovincialis* + *M. californianus*; for *N. canaliculata*, we considered *M. trossulus* only; for *N. ostrina*, *M. trossulus* + *M. californianus* were considered. Analyses were also conducted without differentiating between mussel species/size. Because we were interested in population-level responses (as opposed to distributional rearrangement caused by individual behavior), samples were averaged across tidal heights over which predators move and forage. While whelks occupy all intertidal zones, sea stars and *Concholepas* rarely venture into the high shore, and thus this zone was excluded from estimates of density and prey cover for these predators. Between two and three different rocky benches tens of meters apart were sampled at each site, and sites were sampled between two and four times in different seasons. Estimates were averaged to obtain mean values per site.

While large variation in recruitment of mussels and barnacles has been well documented in both hemispheres

(Menge et al. 1994, 2004; Connolly et al. 2001; Navarrete et al. 2002; Lagos et al. 2005), long-term data show that sites along the coast can be consistently ranked as receiving relatively high or low mussel and barnacle recruitment (Connolly and Roughgarden 1999a; Menge et al. 2004; Lagos et al. 2005; Navarrete et al. 2005, 2008). Barnacle recruitment was quantified using 10 × 10-cm Plexiglas plates covered with Safety Walk, (3M, St. Paul, MN), and mussel recruitment was quantified using 10-cm-diameter plastic mesh ovoids (Tuffy, Clorox, Oakland, CA). These collectors have been extensively used in previous recruitment studies and have the advantage of providing a homogeneous surface for larval settlement across sites. Detailed descriptions and discussion of advantages and limitations of this method can be found in studies by Menge et al. (1994, 2004), Martínez and Navarrete (2002), and Navarrete et al. (2002). Replicated recruitment collectors (four to eight per site) were deployed in the mid- (mussels, barnacles) and high (only barnacles) intertidal zones of the same benches where surveys were conducted at each study site and replaced monthly in California–Oregon and Chile for periods of 12–64 months. In other studies (see references above), we have determined that collectors in single zones do not capture the full within-site variability in recruitment but represent well the geographic trends and rankings of sites across each region, since differences among sites are consistent across species and shore/tidal levels (Lagos et al. 2005; Navarrete et al. 2008). Although species-specific recruitment variability has been described for several of these prey (see references above), species of *Mytilus* and *Chthamalus* could not be safely distinguished at a small postmetamorphic size across California–Oregon. Thus, we pooled species of *Mytilus* and *Chthamalus* barnacles in analyses. The large magnitude of variation in prey recruitment and abundance should provide strong tests for the differential responses of sea stars and whelks.

Unfortunately, satisfactory methods for quantifying sea star and *Concholepas* recruitment remain elusive because of apparent differences in habitat utilization by recently settled recruits and that of juveniles and adults (Navarrete and Manzur 2008). However, both the long planktonic larval phases and scarce field data available (Martínez and Navarrete 2002; Menge et al. 2004) suggest that large, substantial variation in recruitment of these predators occurs among sites tens to hundreds of kilometers apart.

Since recruitment of sessile species, as well as prey and predator species composition and behavior, vary greatly between Oregon and California (Connolly et al. 2001; Sanford et al. 2003; Menge et al. 2004), separate analyses were conducted for these regions in the Northern Hemisphere. Because our simple model for locally interacting populations predicts linear relationships between predator-prey

parameters and state variables (see below), we used raw, untransformed data in all analyses. In all cases, the linear trend provided the best fit to the data (see “Results”). In order to compare field results with model predictions and previous studies of predator-prey coupling (e.g., Spight 1974; Connolly and Roughgarden 1999b), we ran separate analyses for mussels and barnacles. However, since these predators choose between and feed on both prey types in nature, we also present analyses of multiple prey. Standard Pearson and partial correlations were used to examine the associations between predator and prey abundances, since both are expected to influence each other over large scales, and thus it is not possible to identify a dependent and independent variable. Linear regression analyses were used to examine the relationship between prey recruitment rate and predator abundance. In this case, it is difficult to visualize any effect of the local predator population (dependent variable) on the arrival of new prey individuals from the plankton to the site (independent variable). For all cases, untransformed data met model assumptions, which were checked by visual inspection of the residuals.

#### *The Model for Locally Interacting Predator-Prey Species*

Since we do not have information on realized dispersal scales and connectivity among local populations, we employ a set of simple models for local populations of interacting species, which capture only the most essential dispersal mechanisms applicable to the empirical studies and deliberately allow for other simplifications, which will be addressed in “Discussion.” We simplify the problem by classifying the prey and predator populations as being dynamically open or closed. Although actual populations have inherent dispersal scales that continuously span several orders of magnitude, the discrepancy in scales for many pairs of interacting species is often so large that this dichotomous view is a reasonable place to start.

We describe the prey ( $V$ ) dynamics with a simple open population model, where larvae recruit from the plankton at a rate that does not depend on local larval production (Roughgarden et al. 1985; Gaines and Lafferty 1995):

$$\frac{dV}{dt} = sA - qVP \quad (1)$$

where  $s$  is the per unit area settlement rate of larval prey from the plankton into shoreline habitat of area  $A$  and  $q$  is the per capita capture rate of the predator ( $P$ ). Predator responses to changes in prey population depend on whether predators produce young through direct development at the natal site ( $P_{\text{dir}}$ ) or through larvae that are broadcast into the plankton ( $P_{\text{pl}}$ ). In the former case, changes in the number of predators depend on the local

production of juvenile predators, which can be described by a simple form of the Lotka-Volterra predator equation:

$$\frac{dP_{\text{dir}}}{dt} = bVP_{\text{dir}} - mP_{\text{dir}}, \quad (2)$$

where  $b$  is the per capita rate at which predators consume prey and assimilate them to produce new predators and  $m$  is the predator mortality rate. By contrast, changes in the abundance of the predator with planktonic larvae will, like those of the prey, be largely independent of the local production of young if recruits to a local population are offspring of adults at other sites:

$$\frac{dP_{\text{pl}}}{dt} = cA - mP_{\text{pl}}. \quad (3)$$

Here  $c$  is the predator settlement rate. If we ignore any interactions among the predators, either directly or through shared food (for relaxation of this assumption, see app. A), we can solve for the equilibrium abundances of predators and prey for the two coupled predator-prey systems.

#### *Open Prey, Closed Predator.*

$$P_{\text{dir}}^* = \frac{sAb}{qm}, \quad (4)$$

$$V^* = \frac{m}{b}. \quad (5)$$

In the open prey, closed predator system, prey abundance is set solely by predator characteristics (as is also true in the classic Lotka-Volterra model; Gurney and Nisbet 1998). By contrast, abundance of the limited dispersing predator scales with a number of predator, prey, and interaction coefficients. Although each of these parameters varies over space and time, one is likely to dominate over biogeographic scales: the settlement rate of the prey. Large-scale studies of larval settlement of both invertebrates and fishes typically show order of magnitude (often multiple orders of magnitude) variation from one site to the next (e.g., see Caffey 1985; Connolly et al. 2001; Navarrete et al. 2002, 2005; Menge et al. 2004). As a result, this simple model predicts that geographic variation in the abundance of marine predators with restricted dispersal relative to their prey should scale with geographic variation in the settlement rates of their prey. Since such predators have locally closed population dynamics, their population size should track geographic variation in the productivity of their prey populations, especially as it is driven by variation

in settlement rates over space. The equilibrium abundance of prey is predicted to negatively correlate with predator abundance through the opposite effects of  $m$  and  $b$  on predator and prey equilibrium populations, although this correlation is likely to be weak or nonexistent if there is large variation in prey settlement rates. Adding natural (predator-independent) mortality to the prey population ( $m_n$ ) does not alter these general conclusions. The prey equilibrium density remains unchanged, while the predator equilibrium should now be reduced by the added mortality of prey, scaled by the predator capture rate ( $m_n/q$ ), which is expected to change considerably less across sites than prey recruitment.

*Open Prey, Open Predator.*

$$P_{pl}^* = \frac{cA}{m}, \quad (6)$$

$$V^* = \frac{ms}{cq}. \quad (7)$$

The open prey, open predator system yields strikingly different predictions. Since the number of larval predators that settle is independent of the reproductive success of local adult predators, the expected population size of predators is independent of prey characteristics, including the prey settlement rate. Geographic variation in the predator population should now be more strongly driven by geographic variation in the predator's own settlement rate. Equilibrium prey and predator numbers should be negatively correlated through the shared influence of the mortality term  $m$ , but as with the case above, this correlation is likely to be weak or nonexistent because of the much more variable prey and predator settlement rates. Negative correlations are also expected through the inverse effects of  $c$  on predator and prey equilibria, depending on whether  $s$  and  $c$  are independent or co-vary across sites. Indeed, one intriguing implication of these model predictions concerns the role of covariation in the prey and predator settlement rates. If geographic variation in average settlement rates between the two species is strongly positively correlated (e.g., because of shared responses to spatial variation in coastal oceanography), predator abundance could scale with prey recruitment (since  $c$  and  $s$  would be correlated) and prey abundance would become independent of prey and predator settlement rates. These predictions converge on those for the open prey, closed predator system. If average settlement rates of predator and prey act independently across the region, no relationship is expected between predator and prey or between prey abundance and settlement rates. However, positive relationships between prey abundance and recruitment are expected if

the magnitude of variation in prey settlement rates is much larger than that of the open predator.

## Results

Results closely followed the general predictions of the simple predator-prey model. Neither sea star nor gastropod densities correlated with local abundance of adult mussels or barnacles in either hemisphere, regardless of the mode of larval development (fig. 1; table C1 in the online edition of the *American Naturalist*). As predicted by model consideration of their life histories, there was no relationship between barnacle or mussel recruitment and the density of the broadcasting predators *Pisaster*, *Heliaster*, and *Concholepas* across sites in Oregon, California, and Chile (fig. 2, long dispersal column; tables C2, C3 in the online edition of the *American Naturalist*). Although *Pisaster* is able to aggregate to areas of high prey recruitment at the scale of patches within a site (Robles et al. 1995), sea star density is independent of prey at larger spatial scales, which capture numerical changes in local population size. In contrast, the number of whelks occupying a site tightly followed prey recruitment rates, generating a striking positive correlation between recruitment rates of mussels and/or barnacles and whelk density (fig. 2, short dispersal column; tables C2, C3). Between 64% and 94% of the large variation in whelk population sizes along the Pacific coast of North America is explained by a simple measure of prey recruitment (tables C2, C3). Given that *Nucella canaliculata* does not seem to readily consume *Mytilus californianus* as prey in Oregon (Sanford et al. 2003), the strong relationship with pooled mussel species is particularly surprising for this whelk and suggests that the large variation in mussel recruitment reflects *Mytilus trossulus* or, more likely, both mussel species. Moreover, in accordance with recent studies showing geographic breaks in barnacle and mussel recruitment between Oregon and California (Connolly et al. 2001), barnacle recruitment tightly correlated with whelk density in California but not in Oregon, while mussel recruitment was the main determinant of whelk numbers in Oregon. This geographic break in prey recruitment thus changes the relative supply of prey and, further, correlates with changes in whelk foraging behavior (Sanford et al. 2003). Adult abundance of these prey species varied extensively along the coast and in general did not track the large variation in recruitment rates among sites (fig. 3; table C1). The exaggerated magnitude of variation in prey recruitment and abundance provided strong tests of differential coupling for predators with long versus short dispersal.

## Prey Abundance - Predator Density

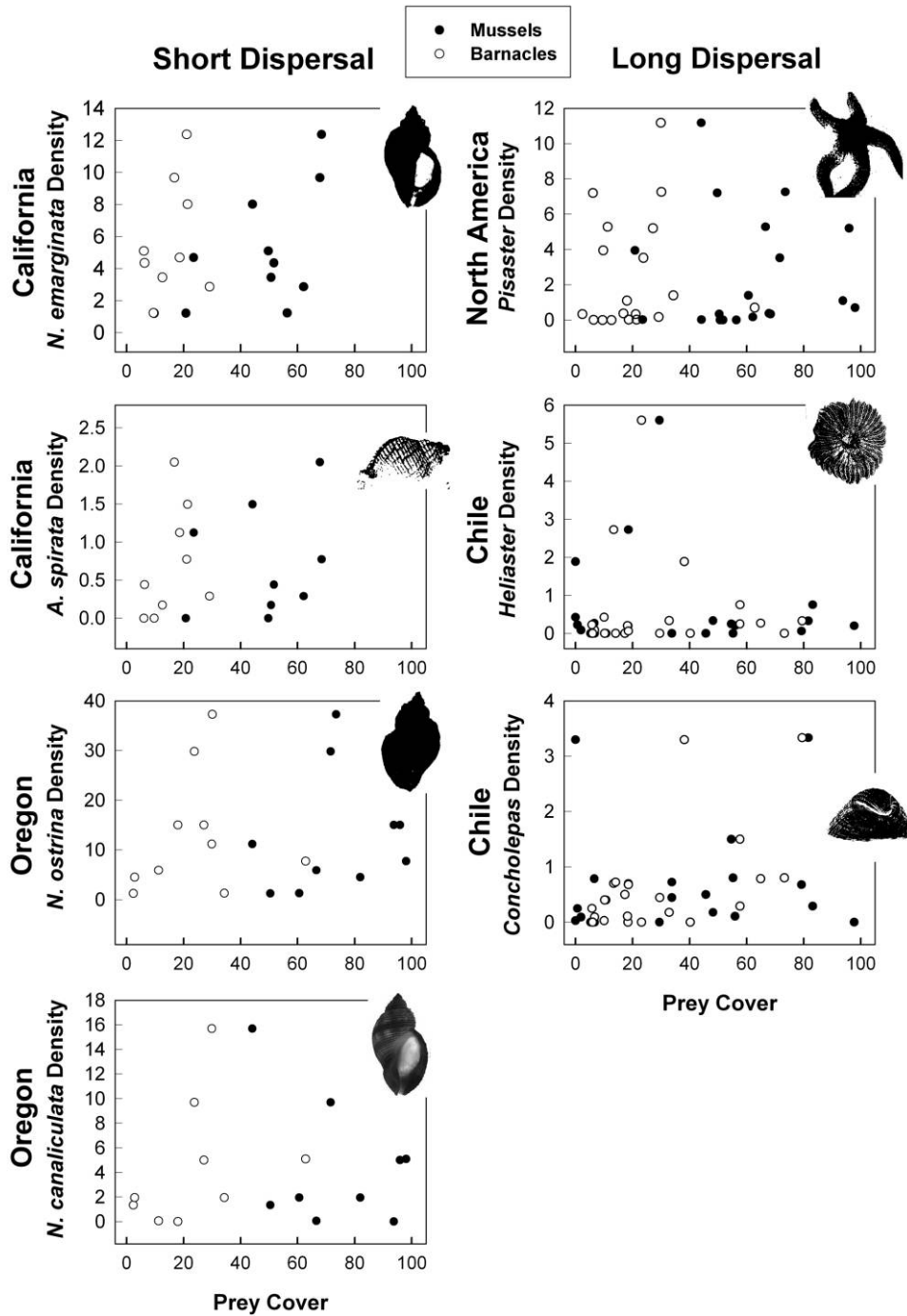
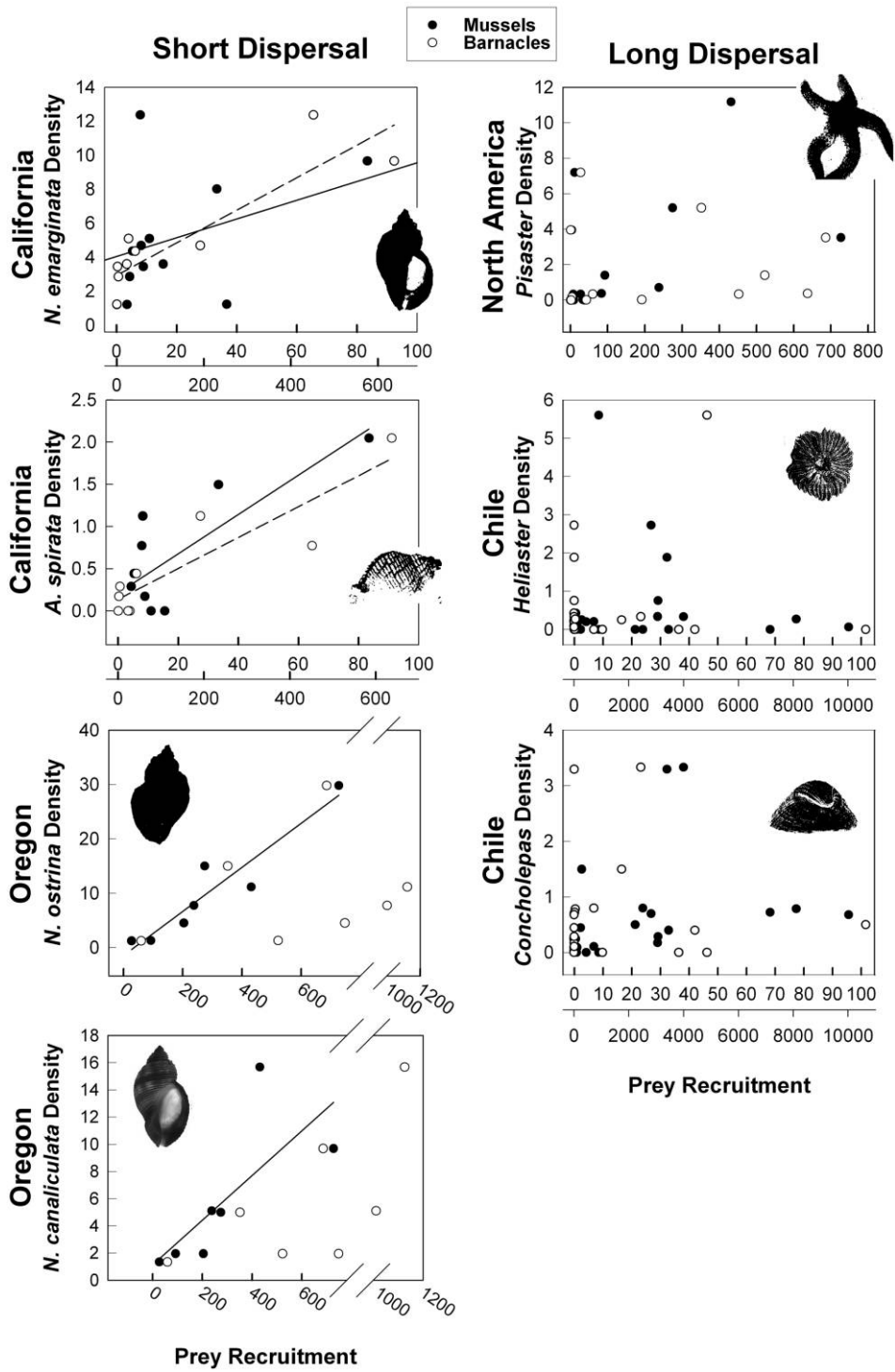


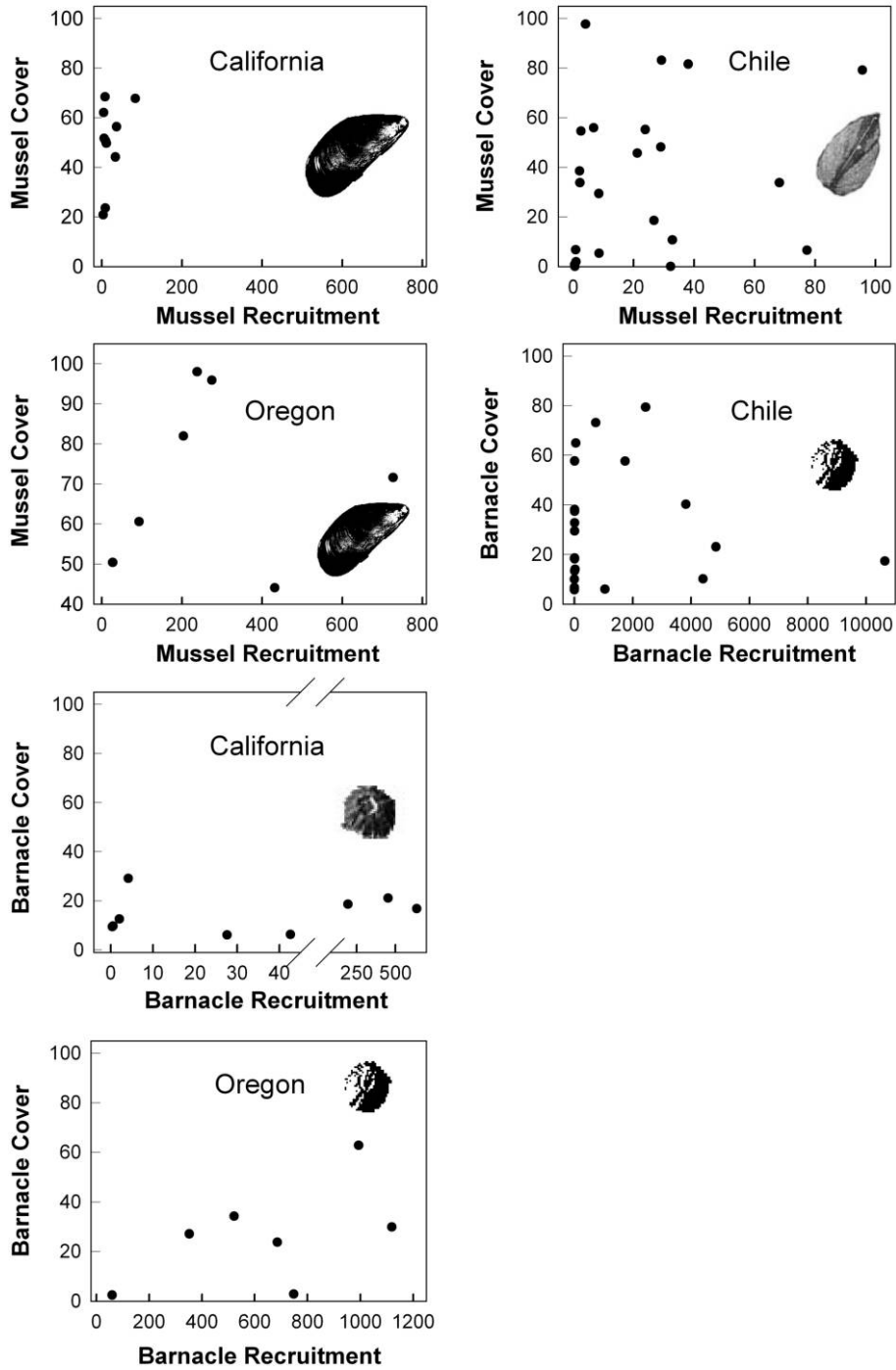
Figure 1: Relationship between mean mussel (solid circles) and barnacle (open circles) adult abundance and mean gastropod and sea star densities. Pearson correlation coefficients for all relationships were not statistically significant at  $\alpha = 0.05$ .

## Prey Recruitment - Predator Density



**Figure 2:** Significant regressions of mean barnacle recruitment (*dashed lines*) and mean mussel recruitment (*solid lines*) versus mean predator density across sites in Oregon, California, and central Chile. Lack of lines indicates linear fit was not statistically significant at  $\alpha = 0.05$ . Note different scales of prey recruitment: barnacles (lower X-axis) and mussels (upper X-axis).

### Prey Recruitment - Prey Abundance



**Figure 3:** Relationship between mean prey recruitment and abundance across sites in Oregon, California, and central Chile. Pearson correlation coefficients for all relationships were not statistically significant at  $\alpha = 0.05$ . Note different scales of prey recruitment (X-axes) as well as that for abundance for Oregon mussels (Y-axes).



## Discussion

Over large spatial scales, essential aspects of the life history of marine organisms could reconcile seemingly opposite results obtained in previous studies and explain the lack of significant predator-prey correlations that has puzzled and generated controversy among marine ecologists in the past (Foster 1990; Paine 1991). Our results strongly suggest that prey production may be a widespread source of variation for “closed” predators. Indeed, other direct developer species, such as whelks along the New England coast (Menge 1976), show positive correlations with prey recruitment and not with local prey abundance. Further, long-term changes of whelk populations in Washington track the recruitment of their barnacle prey over time (Spight 1974). On the other hand, weak predator-prey coupling seems general to other broadcasting predator species, such as crabs along the Chilean coast (Broitman et al. 2001) and sea stars along the northwest Atlantic (Menge 1976). Thus, our results seem general and suggest that simple mathematical models can capture some of the essential aspects of predator-prey dynamics in marine systems and explain the different patterns of spatial association that emerge as a consequence of their life histories.

The usually rapid aggregative responses of mobile predators observed within a site, such as for *Pisaster* and *Concholepas* (Castilla and Durán 1985; Robles et al. 1995; Navarrete and Menge 1996), can lead to erroneous expectations when predator-prey dynamics are observed over larger spatial scales. At the scale of tens to hundreds of meters within a site, most of these predators rapidly rearrange spatially to track changes in prey abundance, but the gains accrued by these behavioral responses would materialize as increased contribution to the total larval pool and not necessarily to new recruits at the same local site. Unfortunately, quantifying sea star and *Concholepas* recruitment remains elusive, limiting rigorous testing of the full suite of model predictions, and thus caution should be employed in interpreting results. However, the few reliable data available suggest that the abundance of sea stars along the Oregon coast appears more closely associated with their recruitment than with prey abundance or settlement rate (Menge et al. 2004), which is consistent with the open model. Unlike sea stars, *Concholepas* is intensely harvested by subsistence and commercial fishers along the coast of Chile, and thus differential mortality among sites could potentially rival recruitment rates and drive variability in population size for this species. Despite this variation in numbers of adults due to harvesting, *Concholepas* recruitment data collected at a subset of six sites within the region between 2004 and 2006 (S. A. Navarrete, unpublished data) and the use of artificial collectors (see Martínez and Navarrete 2002) showed a significant pos-

itive linear relationship between recruitment and adult abundance of this predator species ( $r^2 = 0.6$ ,  $P = .0468$ ,  $df = 1, 5$ ). Although encouraging and supporting model predictions, this relationship should be taken with caution, considering the low number of recruits found per collector at all sites.

While the arrival of new individuals of the open predator does not depend on local prey population size or recruitment, growth and potentially early mortality of the recently settled predators could be a function of prey abundance. If prey recruitment at a site is so low as to become limiting for the survival of the newly settled predators, then positive correlations between prey recruitment and open predator population size might occur. Such an effect of prey on predator mortality rate does not seem to be an important factor influencing population size of the three predator species with pelagic larvae that we examined in this study, either because predators can withstand starvation and/or newly settled recruits consume a wider or different array of prey species (e.g., Feder 1970; Disalvo and Carriker 1994; Navarrete and Manzur 2008). Broad diets of predator recruits will further decouple prey and predator dynamics over geographic scales. Note that even if predator mortality during early stages is inversely related to local prey abundance, large among-site variation in predator recruitment in comparison to mortality could again obscure any correlation between predator and prey abundances.

Earlier, geographically restricted studies comparing two sites in Oregon suggested strong spatial relationships between mussel prey recruitment and mussel adult abundance (e.g., Menge 1992, 2000; Menge et al. 1994). Our long-term, spatially extensive data sets now place these results into a larger context and reveal prey abundance and recruitment to be largely independent of one another over a broader region and across a larger number of sites. However, closer examination of the relationship presented in figure 3 shows that a positive relationship between mussel cover and its recruitment may exist if the two sites with highest recruitment in Oregon are not considered. According to our model, a likely explanation for this result lies in the relative changes in recruitment rates of predators and prey across sites. While mussel settlement varies tremendously among sites tens to hundreds of kilometers apart in Oregon, the limited available data suggest that the magnitude of variation in sea star settlement may be substantially less (relative to mussels) across these scales (Menge et al. 2004). Indeed, if settlement rates of prey are much more variable than that of the open predator, prey abundance should be positively correlated to its own recruitment (eq. [7]). Otherwise, there should be no relationship. Clearly, the interaction between life-history characteristics of mussels and sea stars and how their re-

cruitment varies across sites is key to understanding adult prey structure across mesoscales in this region.

Within each of the regions studied here, patterns of spatial variation in recruitment of prey species are persistent among sites (Navarrete et al. 2002, 2008). Navarrete et al. (2008) analyzed time series of monthly mussel and barnacle recruitment for 16 sites within each region and found that the large recruitment variation among sites, as compared with variation at smaller spatial scales, was also spatially persistent over the 7 years of the study. However, although these results suggest that recruitment data reflect true differences among sites occurring at temporal scales relevant for population abundance, caution must be taken in interpreting lack of relationship. The careful reader may notice that some sites with very low (near zero) average prey recruitment rates had comparatively high adult abundances (e.g., Chile; fig. 3). However, most of these sites were characterized by our longest time series (5+ years), and we thus suspect that populations of long-lived mussels at these generally low-recruitment sites must be able to “store” occasional settlement pulses (Warner and Chesson 1985).

An implicit assumption in our open population model is that the scale of larval dispersal is large relative to the scale of variation in recruitment. Basically, if areas of low or high abundance of predators or prey could cause regional-scale variation in total reproductive output, this could then feed back into recruitment patterns. Indeed, population dynamics of species with pelagic larval stages should become increasingly closed at larger scales (Hughes et al. 2000), and a positive effect of prey on predators should arise as one approaches the dispersal scales of predator species. On global scales, widespread positive relationships are observed between prey recruitment and abundance across diverse systems (e.g., fig. 13 in Menge 2000). A few studies have attempted to examine changes in the intensity of stock-recruitment relationship over increasing spatial scales of aggregation in benthic populations, using hierarchical sampling designs or nonparametric regression approaches (Hughes et al. 2000; Navarrete and Manzur 2008). In a study along the coast of Chile with sites overlapping many of the same sites used in our study, Navarrete and Manzur (2008) examined correlations between abundance and recruitment of a wide variety of prey (mussels, barnacles, limpets, chitons) and the abundance of the sea star *Heliaster helianthus* over scales ranging from few kilometers up to 200 km. Although their results could be considered preliminary because of the sparse spatial sampling, they found no evidence of demographic effects of reproductive output in this open predator-prey system. In our case, sample size and intensity of spatial sampling precluded our ability to perform analyses beyond approximately 200 km or across Califor-

nia and Oregon. Identifying recruitment-abundance feedbacks and the scales at which they occur will require spatially extensive, high-frequency sampling to be able to integrate scales and examine correlations between total production at a given scale and subsequent recruitment. Without knowledge of the shape and intensity of these negative feedbacks that might occur over regional scales, our simplification of completely open, independent local populations seems to provide good approximations for these predator-prey systems.

As a first step, we have concentrated on simple, pairwise interactions: coupled single-predator and single-prey systems. However, local communities are commonly composed of predators with contrasting dispersal scales that share prey, such as whelks and sea stars in California–Oregon. In appendix A, we show that explicit consideration of such interactions theoretically affects only the demographically closed predator and is equivalent to including any other source of mortality caused by something with dynamics unlinked from the prey. Since intraguild predation is weak in our study system (e.g., Navarrete et al. 2000), the pairwise approach appears to capture some aspects of the dynamics of these systems well.

Predators can modify their behavior to better exploit the local offer of prey, which can itself be driven by external factors. In the case of predators lacking a pelagic larva, these plastic responses could lead to local adaptation and changes among populations within the spatial scales examined in this study. This seems to be precisely the case for the variation in feeding preferences of *Nucella canaliculata* along the coast of Oregon–California, as described by Sanford et al. (2003). Although our sites in California were beyond the geographic limit of this species (and were therefore not considered in correlations for this species), some level of variation in feeding preferences along Oregon might occur. Incorporating this type of information into our model, that is, a latitudinally varying capture ( $q$ ) and prey conversion rates ( $b$ ), could further strengthen the correlation between prey recruitment and the abundance of direct developer predators.

The suite of life histories that compose local communities varies greatly among habitats or systems, which poses an intriguing array of questions regarding the scales and context dependency of processes regulating the structure and dynamics of metacommunities (Hanski and Gilpin 1991; Leibold et al. 2004). Our results suggest that differences in life history may determine how far bottom-up effects can penetrate through the food web and explain why bottom-up forcing in marine systems is often observed to be greatest lower in the food web (e.g., Micheli 1999). The propagation of prey supply to higher trophic levels is likely to be restricted to those systems containing demographically closed consumers. Here we focus only on

the consequences of dispersal for local populations across a region. As more information on dispersal and connectivity becomes available, a logical step is the use of meta-community models (Leibold et al. 2004) suited to marine organisms to examine these interactions over space. Considerations of the life history of the species that make up local communities should become a major focus of management and conservation models.

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## APPENDIX A

### Three-Species System

One simple extension of the two-species predator-prey models used as a heuristic guide in this article would be to consider interactions among the predators. Marine communities commonly include predators with different scales of dispersal, and they can share similar prey. We can examine the impact of allowing the open and closed predators to interact through their shared feeding on a common prey. The predator equations remain unchanged,

$$\frac{dP_{\text{dir}}}{dt} = bVP_{\text{dir}} - mP_{\text{dir}}, \quad (\text{A1})$$

$$\frac{dP_{\text{pl}}}{dt} = cA - mP_{\text{pl}}, \quad (\text{A2})$$

but the prey now experience population losses to both predators,

$$\frac{dV}{dt} = sA - V(q_{\text{dir}}P_{\text{dir}} + q_{\text{pl}}P_{\text{pl}}). \quad (\text{A3})$$

For the three-species coupled system, the resulting steady state population sizes are

$$V^* = \frac{m}{b}, \quad (\text{A4})$$

$$P_{\text{pl}}^* = \frac{Ac}{m}, \quad (\text{A5})$$

$$P_{\text{dir}}^* = \frac{A(bs - cq_{\text{pl}})}{mq_{\text{dir}}}. \quad (\text{A6})$$

Two of these steady state values are identical to results from two-species systems. The prey steady state population size is identical to the value for the open prey, closed predator two-species system (eq. [5]). Equilibrium prey population size is set solely by characteristics of the closed predator population (if the closed predator does not become extinct; see below). The open predator steady state is identical to its steady state in the absence of the closed predator (eq. [6]). The open predator's population size should scale largely with geographic variation in its own settlement rate. Only the steady state for the closed predator population takes on a new form that includes characteristics of both the prey and both predators. Essentially, the local population of the closed predator gets the spoils. With a sufficiently high settlement rate of the open predator relative to the settlement rate of the prey, the closed predator population can be driven locally extinct. If the closed predator population persists, it is predicted to share some characteristics with the two-species model developed previously. The steady state number of closed predators should again scale with the settlement rate ( $s$ ) of the prey. The influence of the settlement rate of the open predator ( $c$ ) depends on the covariance in the two settlement rates. If  $s$  and  $c$  are uncorrelated over space, then geographic variation in  $c$  should create statistical noise around the correlation between  $s$  and the abundance of closed predators,  $P_{\text{dir}}$ . If  $s$  and  $c$  are correlated over space, then the correlation between  $s$  and  $P_{\text{dir}}$  should be stronger, similar to the two-species model, albeit with a modified slope.

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