

CHAPTER NINE

DISPERSAL AND GEOGRAPHIC RANGES IN THE SEA

STEVEN D. GAINES, SARAH E. LESTER,
GINNY ECKERT, BRIAN P. KINLAN,
RAFE SAGARIN, AND BRIAN GAYLORD

One of the most fundamental characteristics of any species is its geographic range—the collection of all locations where the species occurs. Although the study of geographic ranges has been a historically important component of the field of biogeography, it has emerged in recent decades as its own discipline—areography (Rapoport 1982). Geographic ranges vary dramatically in size, shape, and location. This variation has been obvious for centuries and has yielded important insight into a wide range of fundamental issues in ecology and evolution (Gaston 2003). There is no shortage of hypothesized explanations for areographic variation.

One factor that has garnered considerable attention as a potential driver of species' ranges is dispersal. Darwin (1859) wrote extensively on the potential influences of dispersal and barriers to dispersal on the extent of species' distributions. He even performed experiments on the potential for seeds and dried materials from scores of species to disperse by floating in the sea. Moreover, his observations that the fauna of a given location cannot be entirely explained by environmental conditions and that striking faunistic differences exist between the New and Old World suggest an important role for dispersal shaping species' distributions.

In considering the distribution of organic beings over the face of the globe, the first great fact which strikes us is, that neither the similarity nor the dissimilar-

ity of the inhabitants of various regions can be wholly accounted for by climatal and other physical conditions. Of late, almost every author who has studied the subject has come to this conclusion. The case of America alone would almost suffice to prove its truth; for if we exclude the arctic and northern temperate parts, all authors agree that one of the most fundamental divisions in geographical distribution is that between the New and Old Worlds; yet if we travel over the vast American continent, from the central parts of the United States to its extreme southern point, we meet with the most diversified conditions; humid districts, arid deserts, lofty mountains, grassy plains, forests, marshes, lakes, and great rivers, under almost every temperature. There is hardly a climate or condition in the Old World which cannot be paralleled in the New—at least as closely as the same species generally require. No doubt small areas can be pointed out in the Old World hotter than any in the New World; but these are not inhabited by a fauna different from that of the surrounding districts; for it is rare to find a group of organisms confined to a small area, of which the conditions are peculiar in only a slight degree. Notwithstanding this general parallelism in the conditions of the Old and New Worlds, how widely different are their living productions!

Similarly, by the early twentieth century, Grinnell (1922) clearly recognized the role of rare dispersal events on species' distributions.

These *pioneers* are of exceeding importance to the species in that they are continually being centrifuged off on scouting expeditions (to mix the metaphor), to seek new country which may prove fit for occupancy. The vast majority of such individuals, 99 out of every hundred perhaps, are foredoomed to early destruction without any opportunity of breeding. Some few individuals may get back to the metropolis of the species. In the relatively rare case two birds comprising a pair, of greater hardihood, possibly, than the average, will find themselves a little beyond the confines of the metropolis of the species, where they will rear a brood successfully and thus establish a new outpost. Or, having gone farther yet, such a pair may even stumble upon a combination of conditions in a new locality the same as in its parent metropolis, and there start a new detached colony of the species.

Despite centuries of interest, definitive connections between dispersal scale and many biogeographical patterns have remained speculative. One of the key problems has been the difficulty of studying dispersal. Unbiased quantitative estimates of dispersal distances are rare across the range of variation within and among species in most natural ecosystems. The ultimate goal is

to characterize the probability that individuals will disperse any given distance and see how this dispersal kernel varies among species, locations, and times. In practice, techniques for measuring dispersal distances generally offer a very narrow window on the full kernel. For example, mark recapture studies can definitively show that an individual moved between two locations, but they frequently underestimate the long-distance tails of dispersal distributions, since the likelihood of recapture declines with distance. Moreover, many species have dispersing life stages that are difficult to tag at all. This is especially true in the sea, where most species have a microscopic planktonic life stage that can disperse on ocean currents for days to months, depending on the species.

However, while measuring dispersal in the ocean may be difficult, dispersal data are particularly valuable for marine systems, where species show remarkable variation in both dispersal capability (Kinlan and Gaines 2003; Shanks, Grantham, and Carr 2003; Siegel et al. 2003; Kinlan, Gaines, and Lester 2005) and biogeographic patterns (Lester and Ruttenberg 2005; Lester et al. 2007).

Fortunately, in the last few years, the window on dispersal in the sea has begun to open with advances in archival and broadcasting tags (Block et al. 1998; Block et al. 2001; Boustany et al. 2002; Block et al. 2005), syntheses of rates of spread of exotic species (Kinlan and Gaines 2003; Shanks, Grantham, and Carr 2003; Kinlan and Hastings 2005), syntheses of genetic estimates of average dispersal distance (Wares, Gaines, and Cunningham 2001; Kinlan and Gaines 2003; Palumbi 2003; Kinlan, Gaines, and Lester 2005), new tagging techniques to identify sites of natal origin (Levin et al. 1993; Swearer et al. 1999; Thorrold et al. 2001; Thorrold et al. 2002; Palumbi et al. 2003; Zacherl et al. 2003; Jones, Planes, and Thorrold 2005), and new models of particle transport (Siegel et al. 2003; Cowen, Paris, and Srinivasan 2006; Gaylord et al. 2006).

As a result of progress in quantifying dispersal in the sea, there has been a resurgence of interest in exploring the consequences of variation in dispersal distance on characteristics of marine species' ranges. Here we examine recent advances in these connections for three characteristics of species ranges in the sea: (a) the size of geographic ranges, (b) the location of species borders, and (c) the distribution of individuals within a species' range. We chose these three characteristics because they each highlight notable findings. For the first two, the emerging results differ greatly from prior expectations. For the third, we are at the incipient stages of developing a strong mechanistic link between the marine biogeographic patterns and dispersal.

The issues we explore are not restricted in any way to marine systems.

Indeed, the connections between dispersal and these three macroecological characteristics of species' distributions are of broad ecological importance in all habitats (see general discussions in Gaston 2003). Marine species, however, offer several advantages for characterizing both the patterns and the potential underlying mechanisms. First, a broad diversity of marine animals and plants have relatively sedentary adults and disperse only as larval propagules. The isolation of dispersal within this early life stage helps separate the roles of dispersal from migration and other more directed forms of adult movement. Second, the range of variation in propagule dispersal is enormous. Average dispersal distance varies by more than seven orders of magnitude among species (Kinlan and Gaines 2003; Shanks, Grantham, and Carr 2003; Kinlan, Gaines, and Lester 2005). Third, this broad range of dispersal distances occurs within many distantly related taxonomic groups, which affords better opportunities to separate the effects of dispersal from other phylogenetically confounded factors (Kinlan and Gaines 2003; Kinlan, Gaines, and Lester 2005). Finally, for shallow-water coastal species, ranges have a simplified geometry. Since the depth component of the range is typically miniscule for such species relative to their latitudinal or longitudinal extent, coastal species essentially have a one-dimensional range with only two boundaries. Compared to the two-dimensional boundary that circumscribes most terrestrial species' ranges, this geometrical simplification greatly facilitates the exploration of a wide range of macroecological issues (Sagarin, Gaines, and Gaylord 2006).

The Influence of Dispersal on Range Size

Geographic ranges vary dramatically in size. They can be as small as a single reef or bay and as large as all of the world's oceans. The underlying causes of this variation are surely myriad and include both ecological and evolutionary factors. An organism's ability to disperse is one of the more commonly cited causes of variation in range size (Hanski et al. 1993; Kunin and Gaston 1993; Brown, Stevens, and Kaufman 1996; Gaston 1996). Examples of this claim abound for both marine (Shuto 1974; Hansen 1978; Hansen 1980; Jablonski 1982; Perron and Kohn 1985; Jablonski 1986; Scheltema 1989; Emler 1995; Bonhomme and Planes 2000; Victor and Wellington 2000; Bradbury and Snelgrove 2001) and terrestrial species (insects—Juliano 1983; Gutierrez and Menendez 1997; Dennis et al. 2000; birds—Duncan, Blackburn, and Veltman 1999; and plants—Edwards and Westoby 1996; Thompson, Gaston, and Band 1999; Clarke, Kerrigan, and Westphal 2001; Kessler 2002).

Although the specific rationale for a connection between dispersal scale

and range size is rarely stated explicitly, there are three broad classes of mechanistic hypotheses proposed to account for such a relationship (Lester et al. 2007):

- Site colonization hypotheses
- Speciation-rate hypotheses
- Selection hypotheses

Site Colonization: If you cannot get there, it will not be part of your range. This is the simple logic behind a set of hypotheses coupling range size to dispersal scale. For one, species with limited dispersal ability may have more geographically restricted ranges, simply because they fail to reach as many sites (Juliano 1983; Wellington and Victor 1989; Gutierrez and Menendez 1997; Thompson, Hodgson, and Gaston 1998). This logic is at the heart of the earlier comments by Darwin and Grinnell. A second formulation of the site colonization hypothesis originates from the theory of metapopulation dynamics (Levins 1969; Hanski et al. 1993). If local populations at the periphery of the range occasionally go extinct, the species' range diminishes in size until sites are recolonized. In such a dynamic setting, time to recolonization plays a critical role, and species with limited dispersal may therefore occupy smaller geographic ranges, since sites will remain unoccupied for longer periods of time. A special case of the site colonization hypothesis follows from the concept of the "rescue effect" (Edwards and Westoby 1996; Duncan, Blackburn, and Veltman 1999), where fringe populations at the edge of the range are demographic sinks that would otherwise go extinct without regular immigration from populations elsewhere in the range (Brown and Kodrick-Brown 1977; Gotelli 1991). If such a rescue effect is operating, the degree of range expansion should scale with dispersal distance; short distance dispersers can only "rescue" nearby sink populations.

Speciation Rate: Species with limited dispersal may experience greater isolation and lower gene flow, and thus a greater potential for local adaptation. Hence, restricted dispersal may enhance rates of speciation (Jackson 1974; Shuto 1974; Scheltema 1977; Hansen 1980; Hansen 1982; Jablonski 1986; Palumbi 1992). A higher rate of speciation at the margin of a species' range can decrease average range size by two mechanisms: (a) speciation cleaves off a piece of the historical range, and the new species may restrict expansion of the parental species, and (b) new species may have had insufficient time to expand their ranges (Hansen 1980; Oakwood et al. 1993). Thus, higher speciation rates could yield a distribution of range sizes that is skewed to smaller sizes.

Selection: In addition to the potential for dispersal influencing range size, range size could determine dispersal distance. If there is a cost, or at least no benefit, to long-distance dispersal when range size is small, species with small geographic ranges might experience selection for restricted dispersal (Gutierrez and Menendez 1997; Thompson, Gaston, and Band 1999). The hypothesis relies on an assumption that more geographically restricted species have a narrower range of tolerances, are more ecologically specialized, or occupy a restricted, isolated or infrequently disturbed habitat type, so that the costs of broad dispersal exceed any potential benefits. This may be true when the range size of a species is close to its average dispersal distance, as for small-island endemics; in this case, the costs of broad dispersal are extreme (Baskett, Weitz, and Levin 2007).

Many studies claim or assume a correlation between dispersal distance and range size based on these types of arguments. One would think that the presumed association between dispersal and range size would have been well tested and that these hypotheses would have been critically evaluated. However, this has not been the case, in part because the relationship has been difficult to test in any quantitative way. Since estimates of average dispersal distances are rarely available, dispersal ability has generally been classified by a proxy: for example, reproductive strategy (Kessler 2002) or seed size (Aizen and Patterson 1990; Oakwood et al. 1993; Edwards and Westoby 1996) in plants, developmental mode (planktonic versus nonplanktonic larvae) in marine gastropods (Hansen 1980; Perron and Kohn 1985; Scheltema 1989), and flight ability (flightless versus flight-capable) in insects (Juliano 1983; Gutierrez and Menendez 1997). Proxies, however, have inherent problems if they mistakenly characterize dispersal potential (e.g., because other independent traits also affect dispersal distances—Kinlan and Gaines 2003; Kinlan, Gaines, and Lester 2005). In addition, since they typically include a very small number of classes of species, it is impossible to characterize the functional relationship between dispersal and range size, even when the qualitative groups differ significantly (Lester and Ruttenberg 2005).

Recent advances in techniques for estimating dispersal in the sea have provided rapidly expanding quantitative data sets of the distribution of dispersal distances of marine species, which can be used to explore how range size scales with dispersal distance. To illustrate the new insight garnered by having more direct estimates of dispersal distances, consider a comparison among a taxonomically and geographically diverse group of more than thirty species of marine invertebrates, using a common proxy for dispersal distance—mode of larval development (Hansen 1980; Perron and Kohn 1985; Scheltema 1989). As has been found in other studies examining various marine invertebrate taxonomic groups, range size (here defined as the

maximum linear distance within the range, in km; see Lester et al. 2007 for a description of data set and more detailed methods) is larger for species with planktotrophic (feeding planktonic larvae) larval development (fig. 9.1). Given that species with this mode of development spend longer periods, on average, drifting in the plankton compared to nonfeeding larvae or to species with direct development (no planktonic phase), they presumably also have larger average dispersal distances (but see Shanks and Eckert 2005 for a range of ways that larval behavior might diminish these differences). As a result, dispersal is commonly cited as an important component of the variation in range size found across taxa with different modes of development.

These thirty-five species, however, provide an opportunity to probe this issue further, since we have estimates of their average dispersal distance from genetic isolation by distance slopes (fig. 9.2, Kinlan and Gaines 2003; Palumbi 2003). When the same range size data are plotted against quantitative rather than categorical estimates of dispersal scale, we see a very different pattern (fig. 9.3). Although the mean range size for species with feeding planktonic larvae is larger than for species with the other two development modes, dispersal distance seems to play little role in generating this pattern. All three groups have substantial variation in dispersal distance, but

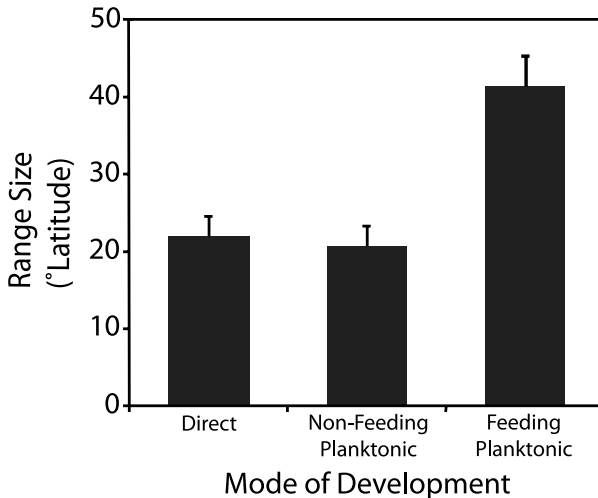


FIGURE 9.1 Average range size (measured here as maximum linear distance within the range, in km) for marine invertebrate taxa classified by a commonly used proxy for dispersal—mode of larval development. Direct developers have no planktonic dispersal, since young develop at their natal site. Time in the plankton is on average much larger for species with feeding larvae than for species with nonfeeding larvae. This data set includes a diverse set of invertebrate species, representing five phyla from around the world. See Lester et al. (2007) for more details on this data set and a complete description of how range size was calculated.

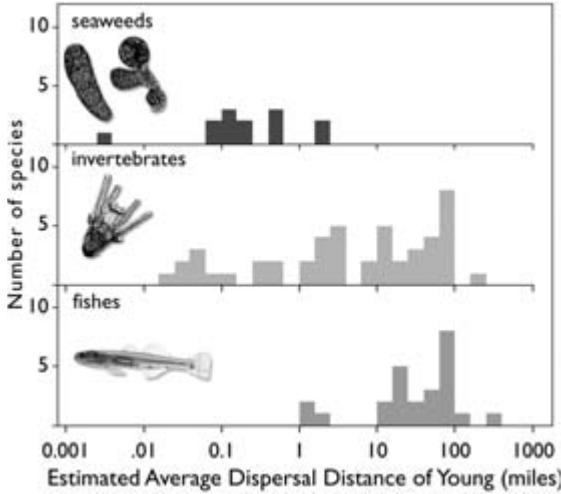


FIGURE 9.2 Frequency distribution of dispersal distances estimated from genetic measures of isolation by distance. (redrawn from Kinlan and Gaines 2003)

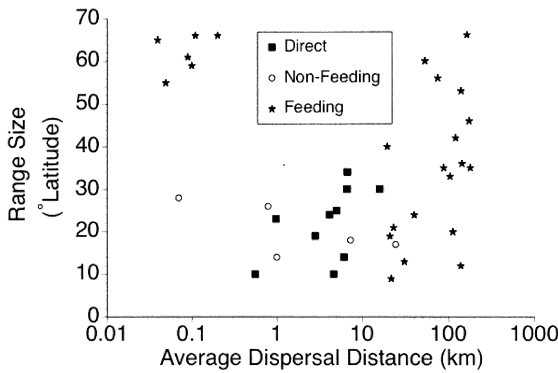


FIGURE 9.3 Average range size (measured here as maximum linear distance within the range, in km) for the same marine invertebrate taxa in fig. 9.1, as a function of average dispersal distance estimated by slopes of genetic isolation by distance.

there is no correlation for any group between this variation and range size. Range size is entirely uncorrelated with four orders of magnitude variation in dispersal.

Much broader evaluations of this connection have reached similar conclusions. There is strikingly little correspondence between range size and dispersal distance. Lester and Ruttenberg (2005) examined tropical reef fish from a wide diversity of families and geographical settings and found that dispersal scale (inferred from pelagic larval duration) only appears to influence range size in settings where there are enormous gaps between suitable habitat (e.g., in the tropical Pacific). When reef habitats are arrayed in more closely spaced stepping stones, range size is independent of dispersal scale for all fish families examined. Similarly, Lester et al. (2007) expand this comparison to include seaweeds, invertebrates, and marine fish from higher lati-

tudes. They similarly find that dispersal scale correlates with range size only in selective situations. Given that there are several intuitively appealing hypotheses drawing a connection between dispersal and geographic range size, these findings suggest we need to reconsider the logic behind these hypotheses (Lester et al. 2007) and refocus on identifying the actual mechanisms underlying the enormous variation in species' range size.

The Influence of Dispersal on the Location of Range Boundaries

A second critical feature of a species' range is where it ends. If the causes of range boundaries were idiosyncratic to the unique tolerances, traits, and interactions of different species, we might expect that species' range boundaries would be distributed somewhat randomly along coastlines. However, known marine species distributions strongly suggest this is not the case in the sea. Striking clusters of species boundaries occur within some relatively short stretches of coastlines on most continental margins (Briggs 1974; Lüning 1990). These relatively abrupt latitudinal shifts in species composition make it possible to define some boundaries of marine biogeographic provinces with general consensus (Dana 1853; Ekman 1953; Valentine 1966; Briggs 1974; Pielou 1979).

Does the common location of range boundaries imply common causality? It has long been noted that clusters of range boundaries of marine species are typically associated with major coastal headlands or points that are characterized by distinctive oceanographic features (e.g., the convergence of two current systems, mesoscale eddies, or gyres; Dana 1853). Two classes of hypotheses have been proposed to account for the clustering of range boundaries at these prominent points:

The evidence seems overwhelming that the boundaries of [marine] biotic provinces are determined by modern abiotic factors. . . . One of two possible [explanations] is that each offers unique environmental conditions, to which species from other provinces are unadapted; intruders therefore cannot establish themselves in a "wrong" province although nothing prevents their entering it. The other possibility is that actual barriers to dispersal exist that are difficult to cross. . . . Where such barriers to dispersal coincide with boundaries between differing environments, it is difficult to judge the relative importance of the two factors in maintaining the distinctness of biotic provinces (Pielou 1979).

Pielou's last sentence poses the fundamental problem. There are two classes of causes—one based on mortality outside the species' range, either due to

physical or biological causes (hereafter the *mortality hypothesis*), the other based on barriers to larval dispersal (hereafter the *dispersal barrier hypothesis*). Unfortunately, the underlying climatic mechanisms potentially responsible for these two causes of range limits—steep physical gradients versus hydrographic barriers to dispersal—are typically confounded in space. Steep gradients in ocean temperature or other physical parameters cannot be generated without anomalous circulation patterns (e.g., convergent currents pushing water offshore), which tend to restrict along-coast larval dispersal.

Although the possible roles of both physical gradients and circulation have been noted in most marine biogeographic studies of the past century, the emphasis has been placed disproportionately on the physical gradients per se (generally temperature) as the ultimate cause (Clarke, chapter 10, this volume). This stems in part from the influence of the Hutchinsonian niche concept (Hutchinson 1957) on thinking in biogeography, whereby the geographic range is viewed as a “spatial reflection” of a species’ niche (Brown and Lomolino 1998), emphasizing the role of environmental conditions in setting species’ distributions. However, the evidence to support such a bias is not particularly compelling. As noted previously, correlations between the position of species boundaries and thermal parameters (e.g., maximum temperature, minimum temperature, temperature range) are necessarily confounded, because the isotherms themselves are correlated with changes in the pattern of circulation. In addition, correlations of the number of species range limits with thermal parameters rarely show strong statistical relationships (Valentine 1966; Doyle 1985; Lüning and Freshwater 1988). Furthermore, experiments that transplant marine species beyond their normal range, although extremely rare, do not commonly support the mortality hypothesis (Crisp 1950; Yamada 1977; Doyle 1985; Gilman 2006). Despite the lack of a clear causal connection between coastal marine provincial boundaries and corresponding gradients in physical conditions, only a few field studies of single species have advocated the dispersal hypothesis as the primary determinant of range limits (Crisp 1950; Yamada 1977; Cowen 1985; Doyle 1985).

One way to gain insight into the relative roles of mortality and dispersal barrier hypotheses is to use the life history variation within marine species as an exploratory tool. As noted earlier, marine invertebrates are a diverse group with considerable variation in their mode of reproduction and scales of dispersal. With respect to the clustering of range boundaries at particular locations, we can gain insight into the roles of mortality- versus dispersal-based hypotheses by considering two dispersal classes. The majority of marine invertebrate larvae develop for weeks or months in the plankton and

currents may transport them far from their parents (hereafter *broad dispersers*). The direction and distance they disperse depend on patterns of circulation, potentially modified by the swimming behavior of the larvae (e.g., Botsford et al. 1994; Pineda 1991; Shanks and McCulloch 2003; Cowen, Paris, and Srinivasan 2006). The remaining species, however, spend little (minutes to hours) or no time developing in the plankton and do not disperse far from their parents (hereafter *limited dispersers*). Thus, they are affected less directly by patterns of coastal circulation.

Unlike the previous section, where we explored range size relative to quantitative estimates of dispersal distance, this simple dispersal dichotomy may provide considerable insight for this particular macroecological pattern. The reason is that only one of these two groups (broad dispersers) will be *directly* influenced by the pattern of circulation at biogeographic breaks, while both groups will be *indirectly* affected by the physical and biological gradients the circulation patterns create. Therefore, if we focus on invertebrates with relatively sessile adults, one test of the role of dispersal barriers is to ask if species that reproduce via broadly dispersing larvae are more likely to have a range boundary at a biogeographic boundary than species with limited-dispersing larvae. If hydrographic barriers to dispersal play an important role in clustering species range limits at major points and headlands, we would predict that species with broadly dispersing larvae should be more likely to have a range limit at these headlands than species with nondispersing larvae. By contrast, if steep physical gradients (e.g., in temperature) are the primary cause of the clustering of range limits, we would predict that both groups of invertebrates are equally likely to have range limits at these points.

To test such contrasting predictions, we assembled data on the range limits of intertidal invertebrates from the Pacific coast of North America (Morris, Abbott, and Haderlie 1980; Eckert 1999). Figure 9.4 plots the percentage of range limits (northern and southern limits plotted separately) for species with broadly dispersing versus limited-dispersing larvae in 0.5° increments of latitude. Sharp peaks indicate that the ranges of a large percentage of species end within a short stretch of coastline. Note that there is little correspondence between the latitudinal distribution of range limits for the two groups ($r^2 < 0.05$ between species with dispersing versus limited dispersing larvae for both northern and southern range limits). The differences are especially noteworthy for some prominent biogeographic breaks. For example, Point Conception, California (34.5°) is a clear northern boundary for species with broadly dispersing larvae but not for species with limited dispersing larvae (fig. 9.4). Similarly, two prominent headlands in Baja California

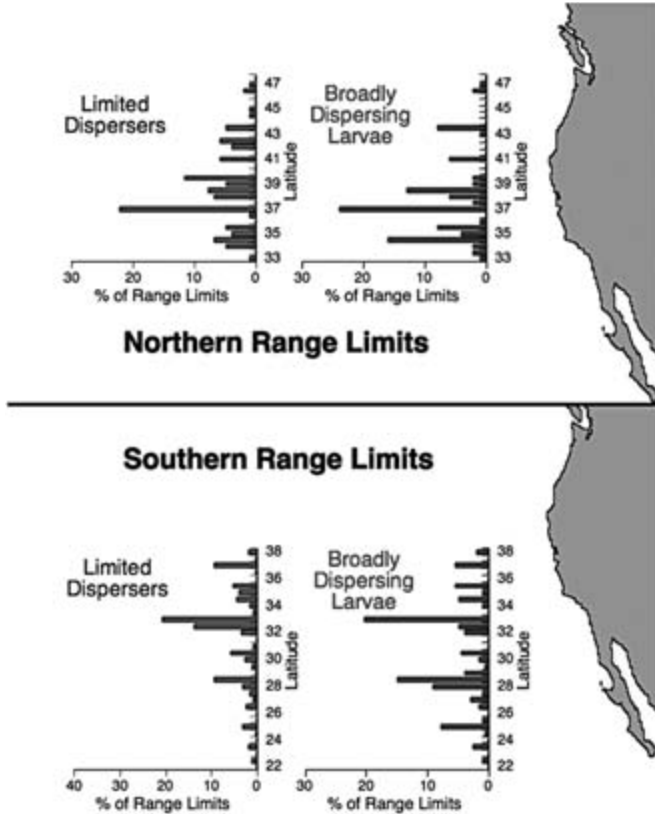


FIGURE 9.4 Distribution of species' borders for marine intertidal invertebrates with relatively sessile adults. Species are placed in two groups, based on their larval development. Those species whose larvae spend either no time in the plankton (direct developers) or only minutes to hours are classed as limited dispersals. Species whose larvae develop for many days to months in plankton are classed as broad dispersers. Range boundaries are from Morris, Abbott, and Haderlie (1980) with extensive updates from the literature (see Eckert 1999 for details).

are clear southern boundaries for species with dispersing larvae, but not for species with nondispersing larvae (fig. 9.4). Along this stretch of coastline, only the Monterey Bay region (36.5°) seems to be a common boundary for species with both larval types (fig. 9.4).

Further evidence for a connection between dispersal and the location of range boundaries comes from comparing northern versus southern range limits rather than comparing across species with different life histories. Figure 9.4 shows that some headlands represent “one-way” boundaries. Most noteworthy, Point Conception is a prominent northern boundary for species

with broadly dispersing larvae, but it is not a southern boundary. This pattern is difficult to reconcile with hypotheses based upon physical or biological gradients that affect mortality, which would predict clustering of both northern and southern range limits. By contrast, the unidirectional nature of this boundary for broad dispersers follows directly from the general patterns of circulation and their likely effects on dispersal (Gaylord and Gaines 2000). Point Conception represents a point of convergence between a large coastal current (the California Current) and a large, seasonal mesoscale eddy (Lasker, Pelaez, and Laurs 1981; Husby and Nelson 1982; Doyle 1985). The pattern of flow is such that larval dispersal may be much more difficult from south to north around the point than the reverse. In support of this hypothesis, genetic analyses within populations of intertidal barnacles that span Point Conception show differential rates of gene flow (north to south > south to north; Wares, Gaines, and Cunningham 2001). In addition, recent range expansions of species that previously had northern range limits at Point Conception are consistent with a breakdown in dispersal barriers under altered flow conditions (e.g., during El Niño—Zacherl et al. 2003).

Simple models of larval dispersal under commonly observed flow conditions can create range boundaries surprisingly easily with convergent flows (Gaylord and Gaines 2000; Byers and Pringle 2006) even when there is no spatial variation in mortality in the adult habitat. The irony is that species with longer potential for dispersal are more susceptible to such flow-induced barriers than species with restricted propagule movement. Historically, dispersal barriers have been viewed more as a problem for species with quite limited dispersal who were unable to cross the barrier (see summary in Gaston 2003). For such hypothetical flow-induced boundaries, however, the absence of sufficient larvae that do not disperse is fundamental to the establishment of the species border (Gaylord and Gaines 2000). Even when the barrier to dispersal is quite leaky, a range boundary can be maintained, because larvae that settle and survive to adulthood beyond the boundary produce larvae that disperse disproportionately back toward the region of convergence (Gaylord and Gaines 2000). The observation that species of invertebrates with longer-lived planktonic larvae are the primary species with range boundaries at two sites along the west coast of North America with convergent flows (Point Conception and Punta Eugenia) suggests that the role of dispersal barriers in setting range boundaries in the sea warrants considerably more attention. Although alternative explanations to the dispersal barrier hypothesis (e.g., enhanced gene flow in species with long-distance dispersal may swamp local adaptation to changes in physical or biological conditions or differential larval mortality during development on opposite

sides of the boundary) can account for some of the pattern data observed along the west coast of North America, they all include a fundamentally important role for larval dispersal. These issues are ripe for exploration of both the generality of the macroecological patterns at other biogeographic boundaries and for detailed experimental studies at the edges of species' ranges (e.g., see Gilman 2006 for an excellent example).

The Influence of Dispersal on Abundance across a Species' Range

So far, we have focused on the impact of dispersal on issues related to range edges. Such boundary definitions simplify the evaluation of population size to a problem of presence/absence. As a result, we have been able to ignore population size during all of this discussion. However, patterns of abundance across a species' range can have important consequences for a wide range of issues such as gene flow, species interactions, and responses to harvesting. Thus, it is critical to document geographic patterns of population abundance and understand the factors determining these patterns. Although a wide range of ecological theory and empirical studies have examined connections between dispersal and population size (e.g., Pulliam 1988; Boyce 1992; Lande, Engen, and Saether 1999), two emerging bodies of research suggest this connection may be strong across broad geographical scales in marine populations.

First, the modeling studies of the link between dispersal and range boundaries discussed briefly previously also consider the consequences of dispersal under different flow conditions to patterns of population size across species' ranges (Gaylord and Gaines 2000; Byers and Pringle 2006; see also Siegel et al. 2003 for new modeling approaches to dispersal in turbulent flows). Such models generate a diverse set of abundance patterns across geographic scales in the presence of different oceanographic flow fields (e.g., see fig. 9.5 and multiple figures in Gaylord and Gaines 2000 for simple examples).

In parallel with these modeling efforts, the last decade has seen a great expansion of studies of actual population sizes across entire species ranges (see Sagarin and Gaines 2002a; Sagarin and Gaines 2002b; Gaston 2003 for recent reviews). Contrary to the simple and ubiquitous biogeographic presumption that species are typically most abundant at sites near the center of their geographic range, these large-scale ecological studies have found a rich diversity of distributions of abundance with a surprisingly large number of cases where peaks in species' abundance occur relatively close to range boundaries rather than near range centers (see fig. 9.6 for a few examples

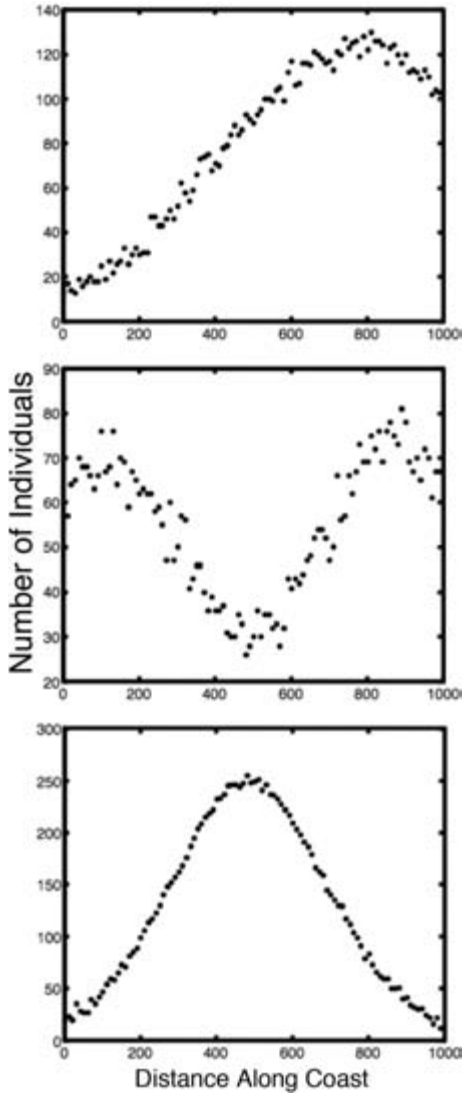


FIGURE 9.5 Population abundance across a species' geographic range with different patterns of coastal circulation and larval dispersal (sensu Siegel et al. 2003). Top panel: Unidirectional flow to right, mean flow = 5 cm/s, std. dev. = 15 cm/s, PLD = fourteen days, gaussian dispersal kernel. Middle panel: Diverging flow at midpoint, mean flow = ± 5 cm/s, std. dev. = 15 cm/s, PLD = fourteen days, gaussian dispersal kernel. Bottom panel: Converging flow toward midpoint, mean flow = $-/+5$ cm/s, std. dev. = 15 cm/s, PLD = fourteen days, gaussian dispersal kernel.

from the larger range of patterns summarized in Sagarin and Gaines 2002a; Sagarin and Gaines 2002b; Defeo and Cardoso 2004; Sagarin, Gaines, and Gaylord 2006).

Since the presumption of an abundant center is at the core of a number of ecological, evolutionary, biogeographic, and conservation theories and frameworks (see review in Sagarin, Gaines, and Gaylord 2006), these empirical findings and syntheses call into question a number of results and

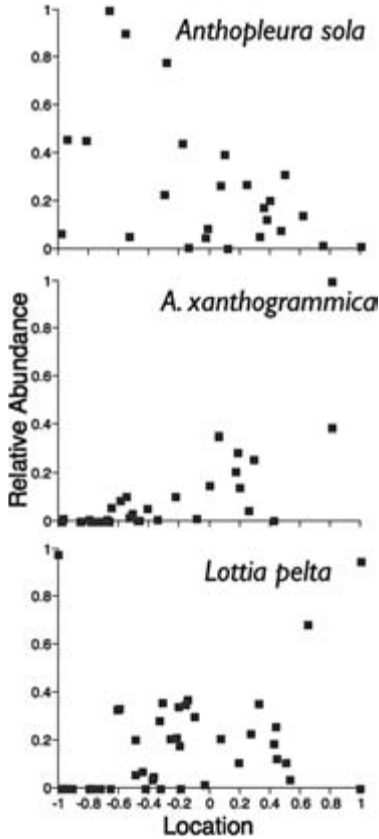


FIGURE 9.6 Selected examples of abundance distributions for marine species that show peaks of abundance near the range boundary (redrafted from Sagarin and Gaines 2002).

approaches. As a consequence, recent studies have begun to examine how such issues as genetic population structure (Vucetich and Waite 2003), habitat conservation (Hampe and Petit 2005), and species responses to climate change (Helmuth, Kingsolver, and Carrington 2005) might be altered by different patterns of abundance across species' ranges.

Further modeling work connects these empirical patterns of abundance to the theoretical findings demonstrating the geographic influence of dispersal and oceanography on population sizes. This work shows that a number of circulation scenarios lead to theoretical predictions of abundance patterns with peak abundances near the edge of species' ranges (e.g., see the middle panel of fig. 9.5 and numerous examples in Gaylord and Gaines 2000). Although other hypotheses could undoubtedly account for skewed abundance distributions (e.g., nonlinear physical gradients—Helmuth and Hofmann 2001; Helmuth et al. 2002), the connections with patterns of dispersal war-

rant more focused attention. This conclusion is supported by the observation that many of the species observed to have peaks of abundance at the edge of the range have these abundant edges at prominent biogeographic boundaries with convergent flows (e.g., Punta Eugenia in Baja California, Mexico—see Sagarin and Gaines 2002b, Sagarin, Gaines, and Gaylord 2006).

Although the number of species with detailed data on abundance across their geographical range does not currently permit the kinds of larger macroecological comparisons across species with different life-history traits or patterns of dispersal that were possible as discussed earlier, the fact that abundant edge distributions for some species coincide with locations that have disproportionate numbers of range boundaries for species with broadly dispersing planktonic development (fig. 9.4) suggests a significant role of dispersal. Whether this is just coincidence or an important new finding awaits more detailed studies at other locations and field experiments that test among competing hypotheses more rigorously. Furthermore, the question of whether abundance patterns tell us anything about the mechanisms setting range boundaries (Caughley et al. 1988; Sagarin and Gaines 2002a; Sagarin, Gaines, and Gaylord 2006) remains currently unresolved, but there are hints that they may be an important source of insight for some larger-scale dynamics in marine populations.

Conclusions

Dispersal redistributes individuals in space. Thus, it is not surprising that it is functionally linked to a wide range of large-scale issues in biogeography and macroecology. Here we have explored recent advances in our understanding of how dispersal might structure marine populations at large biogeographic scales. We considered three issues (size of ranges, location of range boundaries, and distribution of individuals across entire ranges) that illustrate both differences in approach and differences in conclusion.

In the first case (range size), dispersal was long suspected to play a disproportionately large role in determining the size of species' geographic distributions. New syntheses, however, that include more detailed and/or quantitative estimates of dispersal distances are tempering that conclusion. Dispersal may play a smaller role in setting the range size of marine species than previously suspected. By contrast, the role of dispersal barriers in setting the location of range boundaries in the sea has received comparatively little attention. Although dispersal barriers are usually listed as one of several hypothetical causes for the location of range boundaries, it is commonly assumed that gradients in environmental conditions are the primary deter-

minant of species' range boundaries, particularly when species' boundaries cluster at a given location. Comparisons across taxa with different life histories, and thus different dispersal characteristics, suggest that the role of dispersal barriers in establishing species' range limits may be far more important than previously suspected, particularly in certain oceanographic settings (e.g., convergent flows).

Finally, explorations of range edges have been historically somewhat divorced from studies of geographical variation in population size. The emerging data on patterns of abundance across entire species' ranges and modeling work predicting patterns of abundance under different dispersal and oceanographic scenarios both suggest that it could be fruitful to further study the potential for dispersal to influence geographic patterns of population size. In examining these three issues, we stress the value of a multifaceted approach to macroecological studies. These insights were gained by a combination of empirical documentation of large-scale patterns for different life history groups, modeling efforts, and critical examinations of mechanistic hypotheses.

REFERENCES

- Aizen, M. A., and W. A. Patterson, III. 1990. Acorn size and geographical range in the North American oaks (*Quercus L.*). *Journal of Biogeography* 17:327–32.
- Baskett, M. L., J. S. Weitz, and S. A. Levin. 2007. The evolution of dispersal in reserve networks. *American Naturalist* 170:59–78.
- Block, B. A., S. L. H. Teo, A. Walli, A. Boustany, M. J. W. Stokesbury, C. J. Farwell, K. C. Weng, H. Dewar, and T. D. Williams. 2005. Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* 434:1121–27.
- Block, B. A., H. Dewar, S. B. Blackwell, T. D. Williams, E. D. Prince, C. J. Farwell, A. Boustany, et al. 2001. Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science* 293:1310–14.
- Block, B. A., H. Dewar, C. Farwell, and E. D. Prince. 1998. A new satellite technology for tracking the movements of Atlantic bluefin tuna. *PNAS* 95:9384–89.
- Bonhomme, F., and S. Planes. 2000. Some evolutionary arguments about what maintains the pelagic interval in reef fishes. *Environmental Biology of Fishes* 59:365–83.
- Botsford, L. W., C. L. Moloney, A. Hastings, J. L. Largier, T. M. Powell, K. Higgins, and J. F. Quinn. 1994. The influence of spatially and temporally varying oceanographic conditions on meroplanktonic metapopulations. *Deep Sea Research* 41:107–145.
- Boustany, A. M., S. F. Davis, P. Pyle, S. D. Anderson, B. J. Le Boeuf, and B. A. Block. 2002. Satellite tagging: Expanded niche for white sharks. *Nature* 415:35–36.
- Boyce, M. S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* 23:481–97.
- Bradbury, I. R., and P. V. R. Snelgrove. 2001. Contrasting larval transport in demersal fish and benthic invertebrates: The roles of behaviour and advective processes in determining spatial pattern. *Canadian Journal of Fisheries and Aquatic Sciences* 58:811–23.

- Briggs, J. C. 1974. *Marine Zoogeography*. New York: McGraw-Hill.
- Brown, J. H., and A. Kodrick-Brown. 1977. Turnover rates in insular biogeography: Effect of immigration on extinction. *Ecology* 58:445–49.
- Brown, J. H., and M. V. Lomolino. 1998. *Biogeography*, 2nd ed. Sunderland, MA: Sinauer Associates.
- Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: Size, shape, boundaries and internal structure. *Annual Review of Ecology and Systematics* 27:597–623.
- Byers, J. E., and J. M. Pringle. 2006. Going against the flow: Retention, range limits and invasions in advective environments. *Marine Ecology Progress Series* 313:27–41.
- Caughley, G., D. Grice, R. Barker, and B. Brown. 1988. The edge of the range. *Journal of Animal Ecology* 57:771–85.
- Clarke, P., R. A. Kerrigan, and C. J. Westphal. 2001. Dispersal potential and early growth in 14 tropical mangroves: Do early life history traits correlate with patterns of adult distribution? *Journal of Ecology* 89:648–59.
- Cowen, R. K. 1985. Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: Causes and implications. *Journal of Marine Research* 43:719–42.
- Cowen, R. K., C. B. Paris, and A. Srinivasan. 2006. Scaling of connectivity in marine populations. *Science* 311:522–27.
- Crisp, D. J. 1950. Breeding and distribution of *Chthamalus stellatus*. *Nature* 166:311–12.
- Dana, J. D. 1853. On an isothermal oceanic chart, illustrating the geographical distribution of marine animals. *American Journal of Science and Art, Second Series* 16:153–67.
- Darwin, C. 1859. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.
- Defeo, O., and R. S. Cardoso. 2004. Latitudinal patterns in abundance and life-history traits in the mole crab *Emerita brasiliensis* on South American sandy beaches. *Diversity and Distributions* 10:89–98.
- Dennis, R. L., H. B. Donato, T. H. Sparks, and E. Pollard. 2000. Ecological correlates of island incidence and geographic range among British butterflies. *Biodiversity and Conservation* 9:343–59.
- Doyle, R. F. 1985. Biogeographical studies of rocky shores near Point Conception, California. PhD diss., University of California, Santa Barbara.
- Duncan, R. P., T. M. Blackburn, and C. J. Veltman. 1999. Determinants of geographical range sizes: A test using introduced New Zealand birds. *Journal of Animal Ecology* 68:963–75.
- Eckert, G. L. 1999. Consequences of diverse reproductive strategies in marine invertebrates. PhD diss., Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara.
- Ekman, S. 1953. *Zoogeography of the Sea*. London: Sidgwick and Jackson.
- Edwards, W., and M. Westoby. 1996. Reserve mass and dispersal investment in relation to geographic range of plant species: Phylogenetically independent contrasts. *Journal of Biogeography* 23:329–38.
- Emlet, R. B. 1995. Developmental mode and species geographic range in regular sea urchins (Echinodermata: Echinoidea). *Evolution* 49:476–89.
- Gaston, K. J. 1996. Species-range-size distributions: Patterns, mechanisms and implications. *Trends in Ecology & Evolution* 11:197–201.
- . 2003. *The structure and dynamics of geographic ranges*. Oxford: Oxford University Press.
- Gaylord, B., and S. D. Gaines. 2000. Temperature or transport? Range limits in marine species mediated solely by flow. *American Naturalist* 155:769–89.

- Gaylord, B., D. C. Reed, P. T. Raimondi, and L. Washburn. 2006. Macroalgal spore dispersal in coastal environments: Mechanistic insights revealed by theory and experiment. *Ecological Monographs* 76:481–502.
- Gilman, S. E. 2006. Life at the edge: An experimental study of a poleward range boundary. *Oecologia* 148:270–79.
- Gotelli, N. J. 1991. Metapopulation models: The rescue effect, the propagule rain, and the core-satellite hypothesis. *American Naturalist* 138:768–76.
- Grinnell, J. 1922. On the role of the accidental. *Auk* 39:373–80.
- Gutierrez, D., and R. Menendez. 1997. Patterns in the distribution, abundance and body size of carabid beetles (Coleoptera: Caraboidea) in relation to dispersal ability. *Journal of Biogeography* 24:903–14.
- Hampe, A., and R. J. Petit. 2005. Conserving biodiversity under climate change: The rear edge matters. *Ecology Letters* 8:461–67.
- Hansen, T. A. 1978. Larval dispersal and species longevity in lower tertiary gastropods. *Science* 199:885–87.
- . 1980. Influence of larval dispersal and geographic distribution on species longevity in neogastropods. *Paleobiology* 6:193–207.
- . 1982. Modes of larval development in early Tertiary neogastropods. *Paleobiology* 8:367–77.
- Hanski, I., J. Kouki, and A. Halkka. 1993. Three explanations for the positive relationship between distribution and abundance of species. In *Species diversity in ecological communities: historical and geographical perspectives*, ed. R. E. Ricklefs and D. Schluter, 108–16. Chicago: University of Chicago Press.
- Hanski, I., P. Turchin, E. Korpimäki, and H. Henttonen. 1993. Population oscillations of boreal rodents: Regulation of mustelid predators leads to chaos. *Nature* 364:232–35.
- Helmuth, B., C. D. G. Harley, P. M. Halpin, M. O'Donnell, G. E. Hofmann, and C. A. Blanchette. 2002. Climate change and latitudinal patterns of intertidal thermal stress. *Science* 298:1015–17.
- Helmuth, B., J. G. Kingsolver, and E. Carrington. 2005. Biophysics, physiological ecology and climate change: Does mechanism matter? *Annual Review of Physiology* 67:177–201.
- Helmuth, B. S. T., and G. E. Hofmann. 2001. Microhabitats, thermal heterogeneity, and patterns of physiological stress in the Rocky Intertidal Zone. *Biological Bulletin* 201:374–84.
- Husby, D. M., and C. S. Nelson. 1982. Turbulence and vertical stability in the California Current. *CalCOFI Reports* 23:113–29.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Symposia on Quantitative Biology* 22:415–27.
- Jablonski, D. 1982. Evolutionary rates and models in late Cretaceous gastropods: Role of larval ecology. *Proceedings of the Third North American Paleontological Convention* 1:257–62.
- . 1986. Larval ecology and macroevolution in marine invertebrates. *Bulletin of Marine Science* 39:565–87.
- Jackson, J. B. C. 1974. Biogeographic consequences of eurytopy and stenotopy among marine bivalves and their evolution significance. *American Naturalist* 108:541–60.
- Jones, G. P., S. Planes, and S. R. Thorrold. 2005. Coral reef fish larvae settle close to home. *Curr. Biol.* 15:1314–18.
- Juliano, S. A. 1983. Body size, dispersal ability, and range size in North American species of *Brachinus* (Coleoptera: Carabidae). *Coleopterists Bulletin* 37:232–38.
- Kessler, M. 2002. Range size and its ecological correlates among the pteridophytes of Carrasco National Park, Bolivia. *Global Ecology and Biogeography* 11:89–102.

- Kinlan, B., and S. D. Gaines. 2003. Propagule dispersal in marine and terrestrial environments: A community perspective. *Ecology* 84:2007–20.
- Kinlan, B., and A. Hastings. 2005. Rates of population spread and geographic range expansion: what exotic species tell us. In *Rates of population spread and geographic range expansion: What exotic species tell us*, ed. D. F. Sax, J. J. Stachowicz, and S. D. Gaines, 381–19. Sunderland, MA: Sinauer.
- Kinlan, B. P., S. D. Gaines, and S. E. Lester. 2005. Propagule dispersal and the scales of marine community process. *Diversity and Distributions* 11:139–48.
- Kunin, W. E., and K. J. Gaston. 1993. The biology of rarity: Patterns, causes and consequences. *Trends in Ecology & Evolution* 8:298–301.
- Lande, R., S. Engen, and B.-E. Sæther. 1999. Spatial scale of population synchrony: Environmental correlation versus dispersal and density regulation. *American Naturalist* 154:271–81.
- Lasker, R., J. Pelaez, and R. M. Laurs. 1981. The use of satellite infrared imagery for describing ocean processes in relation to spawning of the northern anchovy (*Engraulis mordax*). *Remote Sensing of the Environment* 11:439–53.
- Lester, S., and B. I. Ruttenberg. 2005. The relationship between pelagic larval duration and range size in tropical reef fishes: A synthetic analysis. *Proceedings of the Royal Society of London B* 272:585–91.
- Lester, S., B. I. Ruttenberg, S. D. Gaines, and B. Kinlan. 2007. The relationship between dispersal ability and geographic range size. *Ecology Letters* 10:745–58.
- Levin, L., D. Huggett, P. Myers, T. Bridges, and J. Weaver. 1993. Rare-earth tagging methods for the study of larval dispersal by marine invertebrates. *Limnology and Oceanography* 38:346–60.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237–40.
- Lüning, K. 1990. *Seaweeds: Their environment, biogeography and ecophysiology*. New York: Wiley.
- Lüning, K., and W. Freshwater. 1988. Temperature tolerance of Northeast Pacific marine algae. *Journal of Phycology* 24:310–15.
- Morris, R. H., D. P. Abbott, and E. C. Haderlie. 1980. *Intertidal invertebrates of California*. Stanford, CA: Stanford University Press.
- Oakwood, M., E. Jurado, M. Leishman, and M. Westoby. 1993. Geographic ranges of plant species in relation to dispersal morphology, growth form and diaspore weight. *Journal of Biogeography* 20:563–72.
- Palumbi, S. R. 2003. Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications* 13:S146–S158.
- . 1992. Marine speciation on a small planet. *Trends in Ecology and Evolution* 7:114–17.
- Palumbi, S. R., S. D. Gaines, H. Leslie, and R. R. Warner. 2003. New wave: High-tech tools to help marine reserve research. *Frontiers in Ecology and the Environment* 1:73–79.
- Perron, F. E., and A. J. Kohn. 1985. Larval dispersal and geographic distribution in coral reef gastropods of the genus *Conus*. *Proceedings of the 5th International Coral Reef Congress, Tahiti* 4:95–100.
- Pielou, E. C. 1979. *Biogeography*. New York: Wiley.
- Pineda, J. 1991. Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Science* 253:548–51.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–61.
- Rapoport, E. H. 1982. *Areography: geographical strategies of species*. Oxford: Pergamon.

- Sagarin, R. D., and S. D. Gaines. 2002a. The “abundant centre” distribution: To what extent is it a biogeographic rule? *Ecology Letters* 5:137–47.
- . 2002b. Geographical abundance distributions of coastal invertebrates using 1-dimensional ranges to test biogeographic hypotheses. *Journal of Biogeography* 29:985–98.
- Sagarin, R. D., S. D. Gaines, and B. Gaylord. 2006. Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology & Evolution* 21:524–29.
- Scheltema, R. S. 1989. Planktonic and non-planktonic development among prosobranch gastropods and its relationship to the geographic range of species. Reproduction, genetics and distributions of marine organisms. *23rd European Marine Biology Symposium* 183–88.
- . 1977. Dispersal of marine invertebrate organisms: Paleobiogeographic and biostratigraphic implications. In *Dispersal of marine invertebrate organisms: Paleobiogeographic and biostratigraphic implications*, ed. E. G. Kauffman and J. E. Hazel, 73–108. Stroudsburg, PA: Dowden, Hutchinson, and Ross.
- Shanks, A. L., and G. L. Eckert. 2005. Population persistence of California current fishes and benthic crustaceans: a marine drift paradox. *Ecological Monographs* 75:505–24.
- Shanks, A. L., B. A. Grantham, and M. H. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications* 13:S159–S169.
- Shanks, A. L., and A. McCulloch. 2003. Topographically generated fronts, very nearshore oceanography, and the distribution of chlorophyll, detritus, and selected diatom and dinoflagellate taxa. *Marine Biology* 143:969–80.
- Shuto, T. 1974. Larval ecology of prosobranch gastropods and its bearing on biogeography and paleontology. *Letha* 7:239–57.
- Siegel, D., B. P. Kinlan, B. Gaylord, and S. D. Gaines. 2003. Lagrangian descriptions of marine larval dispersion. *Marine Ecology Progress Series* 260:83–96.
- Swearer, S. E., J. E. Caselle, D. W. Lea, and R. R. Warner. 1999. Larval retention and recruitment in an island population of a coral-reef fish. *Nature* 402:799.
- Thompson, K., K. J. Gaston, and S. R. Band. 1999. Range size, dispersal and niche breadth in the herbaceous flora of central England. *Journal of Ecology* 87:150–55.
- Thompson, K., J. G. Hodgson, and K. J. Gaston. 1998. Abundance-range size relationships in the herbaceous flora of central England. *Journal of Ecology* 86:439–48.
- Thorrold, S. R., G. P. Jones, M. E. Hellberg, R. S. Burton, S. E. Swearer, J. E. Neigel, S. G. Morgan, and R. R. Warner. 2002. Quantifying larval retention and connectivity in marine populations with artificial and natural markers. *Bull. Mar. Sci.* 70:291–308.
- Thorrold, S. R., C. Latkoczy, P. K. Swart, and C. M. Jones. 2001. Natal homing in a marine fish metapopulation. *Science* 291:297–99.
- Valentine, J. W. 1966. Numerical analysis of marine molluscan ranges on the extratropical northeastern Pacific shelf. *Limnology and Oceanography* 11:198–211.
- Yamada, S. B. 1977. Geographic range limitation of the intertidal gastropods *Littorina sitkana* and *L. planaxis*. *Marine Biology* 39:61–65.
- Victor, B. C., and G. M. Wellington. 2000. Endemism and the pelagic larval duration of reef fishes in the eastern Pacific Ocean. *Marine Ecology Progress Series* 205:241–48.
- Vucetich, J. A., and T. A. Waite. 2003. Spatial patterns of demography and genetic processes across the species range: Null hypotheses for landscape conservation genetics. *Cons. For. Genet.* 4:639–45.
- Wares, J. P., S. D. Gaines, and C. W. Cunningham. 2001. A comparative study of asymmetric migration events across a marine biogeographic boundary. *Evolution* 55:295–306.

- Wellington, G. M., and B. C. Victor. 1989. Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). *Marine Biology* 101:557–68.
- Zacherl, D., S. D. Gaines, and S. I. Lonhart. 2003. The limits to biogeographical distributions: Insights from the northward range extension of the marine snail, *Kelletia kelletii* (Forbes, 1852). *Journal of Biogeography* 30:913–24.
- Zacherl, D. C., P. H. Manriquez, G. Paradis, R. W. Day, J. C. Castilla, R. R. Warner, D. W. Lea, and S. D. Gaines. 2003. Trace elemental fingerprinting of gastropod statoliths to study larval dispersal strategies. *Marine Ecology Progress Series* 248:297–303.