

The Biogeography of Marine Communities

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Marine biogeography originated in the mid-1800s as a descriptive science that attempted to chart the current and past geographic distributions of taxa (Dana 1853). Classic biogeographers focused on mapping distributional provinces of species, genera, and other taxonomic groups (reviewed by Briggs 1974), and thus the field was “systematic and historical, rather than ecological, in its approach” (Hedgpeth 1957). The biogeography of ecological units (i.e., communities) was rarely considered until many years later (Hedgpeth 1957; Thorson 1957), and even then, understanding progressed slowly. Robert MacArthur’s pioneering book *Geographical Ecology* was one of the first significant attempts to integrate biogeography and ecological theory (MacArthur 1972). Next, Geerat Vermeij, who began his career as an undergraduate student with MacArthur, further integrated biogeography and ecology by considering morphological adaptations of marine taxa along abiotic and biotic gradients. His book *Biogeography and Adaptation* provided a global perspective on the evolution of biological pattern, process, and diversity (Vermeij 1978). Nearly 20 years later, James Brown’s book *Macroecology* furthered the case for interdisciplinary synthesis and encouraged ecologists to consider patterns and processes that occur over the broader spatial and temporal scales traditionally studied by biogeographers (Brown 1995).

When Brown’s book was published in 1995, marine community ecologists were primed to embrace its messages, as the field was in the midst of rediscovering the openness of marine ecosystems and the importance of large-scale processes such as larval recruitment (Dayton and Tegner 1984; Underwood and Denley 1984; Roughgarden et al. 1988). Since that time, marine ecologists have increasingly focused on questions related to large-scale ecological patterns and processes. Substantial progress in addressing some of these questions is highlighted in the book *Marine Macroecology* (Witman and Roy 2009).

This chapter focuses on understanding how and why assemblages of interacting marine species vary over large geographic scales. The accurate description of biogeographic patterns is a necessary starting point for these investigations (Underwood et al. 2000). Until recently, there have been few high-resolution data sets that describe how the composition and structure of marine communities vary over large spatial scales. Biogeographic treatments of marine fauna and flora generally illustrate range endpoints of species’ distributions, but seldom include information regarding spatial variation in population abundances or community composition. On the other hand, most marine ecologists have historically worked at one or a few field sites, gaining little insight into variation in community structure over broader spatial scales.

Fortunately, the number of studies conducted across latitudinal gradients has increased in the past decade. Much of this research has been on benthic community

structure, and some studies have included multiple sites spanning thousands of kilometers (e.g., Broitman et al. 2001; Witman et al. 2004; Connolly et al. 2005; Schoch et al. 2006; Connell and Irving 2008; Blanchette et al. 2008, 2009; Smale et al. 2010; Schiel 2011; Wieters et al. 2012). These studies have provided unprecedented detail on how community structure varies across broad spatial scales. In the tradition of classic biogeography, many of these biotic patterns have been correlated with gradients in abiotic factors, including temperature, wave energy, and coastal upwelling (e.g., Schoch et al. 2006; Blanchette et al. 2008; Schiel 2011). However, these descriptions of community patterns also suggest that ecological processes, including dispersal, recruitment, population dynamics, and species interactions, may influence geographic differences among communities. For example, surveys of rocky intertidal communities along the coast of Chile documented latitudinal shifts in the abundances of functional groups (Broitman et al. 2001). Notably, kelps increased in abundance at higher latitudes, in association with cooler water temperatures. In contrast, the cover of crustose algae was inversely related to kelp abundance in the low intertidal zone, a finding that is consistent with competition between these two groups. The cover of corticated algae and kelps was negatively correlated with herbivore abundance, suggesting that geographic differences in algal assemblages might be affected by variation in herbivory. Finally, there was a biogeographic break in the abundance of mussels along the coast, suggesting a potential influence of recruitment on latitudinal variation in community structure (Broitman et al. 2001).

An integration of approaches from marine biogeography and community ecology has begun to provide mechanistic insight into the processes that might drive these and other latitudinal patterns. This chapter considers ecological, physiological, evolutionary, and oceanographic processes that contribute to patterns of geographic variation in benthic marine communities, with a focus on four questions. First, what processes set and maintain species' geographic range boundaries? These processes constrain which species belong to a given assemblage and thus provide a critical foundation for understanding the biogeography of marine communities. Second, how and why do population abundances vary across a species' geographic range? Surveys suggest that patterns of population abundance along a species' range can take a variety of forms (e.g., Sagarin and Gaines 2002a; Schoch et al. 2006). For example, some species reach higher abundance in the center of their range, whereas others have their peak abundance near the edge of their range. The processes that influence species' range boundaries and population abundances influence the composition and structure of local species assemblages and set the stage for the final two questions. The first of these asks, what are the causes and consequences of latitudinal variation in species interactions? A growing number of comparative experiments

conducted across large spatial scales have provided new insights into geographic variation in the strength of competition, facilitation, predation, and herbivory. The final section of this chapter considers whether these species interactions are sufficient to explain local species richness, or whether there is an additional role for large-scale historical and evolutionary processes. In particular, does the size of the regional species pool influence the species richness of local communities? Recent work in these four areas highlights an integration of marine biogeography and community ecology that seeks to move beyond descriptive patterns to understand the underlying ecological and evolutionary processes driving geographic variation in marine communities.

Species' Geographic Range Limits

Mapping the geographic distributions of taxa has been a central focus of marine biogeography for over 150 years (reviewed by Hedgpeth 1957; Briggs 1974). Multiple species often share the same geographic range boundaries within narrow regions of coastline (Dana 1853), allowing taxa with similar geographic distributions to be grouped into biotic provinces (**Figure 7.1**; Schenck and Keen 1936; Briggs 1974). The association between species' range boundaries and environmental gradients has also been a traditional focal point of marine biogeography. Historically, biogeographers relied on correlational approaches, mapping latitudinal distributions of biotic provinces onto charts of temperature isotherms (Dana 1853; Hedgpeth 1957; Briggs 1974). These studies were largely descriptive, and little effort was made to determine the mechanisms through which ocean temperature might set the range limits of marine species.

A more mechanistic focus began to develop following a landmark paper by Hutchins (1947). Hutchins hypothesized that temperature sets the range boundaries of marine species primarily through two general mechanisms. First, range limits may occur where temperatures beyond the edge of the range are too physiologically stressful for individuals to survive. In this scenario, equatorward range boundaries are set by an intolerance of high temperatures, whereas poleward range boundaries are set by low temperatures. This mechanism was supported primarily by anecdotal evidence, such as observations that southern species recruited regularly to Cape Cod, Massachusetts, during the summer but were killed by severe winter conditions (Allee 1923). Second, Hutchins hypothesized that in some cases, range limits reflect critical temperatures required for successful reproduction. For example, a minimum temperature could be necessary for successful production of gametes, the initiation of spawning, or larval development (Orton 1920). Hutchins proposed that the poleward and equatorward boundaries of a given species might be set by either one of these two mechanisms (i.e., thermal constraints on survival or on reproduction). This

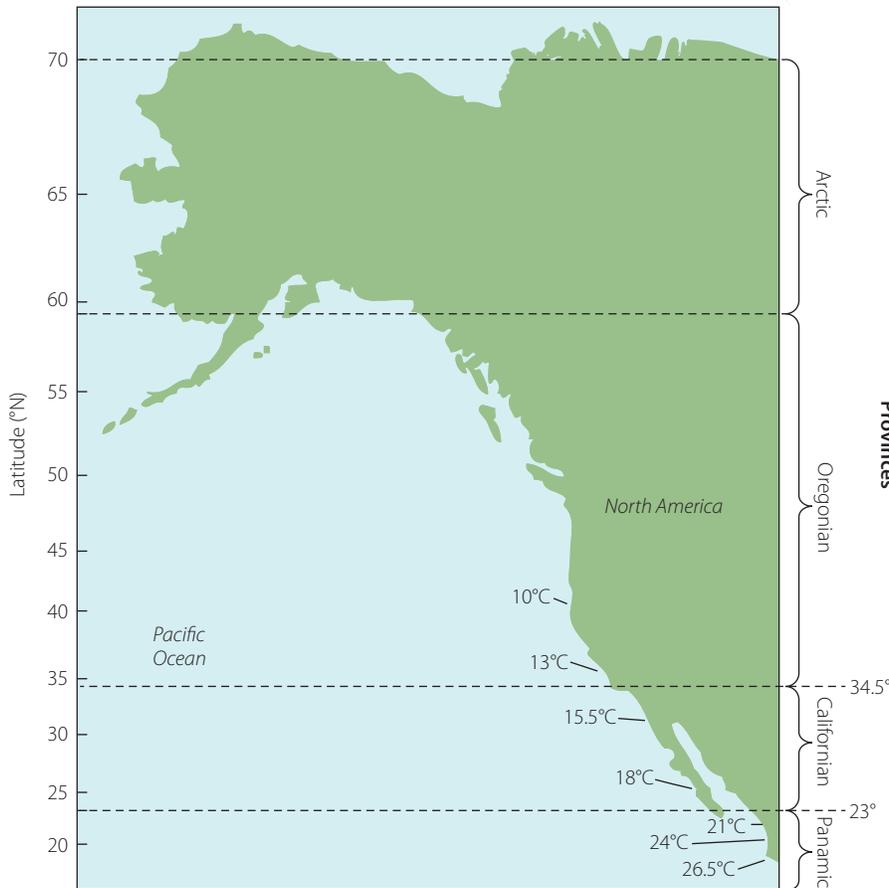


Figure 7.1 Example of a map of biotic provinces of distribution. In this scheme proposed by Dall (1909), four provinces of molluscs are recognized along the Pacific coast of North America, with the transition between the Oregonian and Californian provinces at Point Conception, California (34.5° N). Many alternative schemes have been proposed. Locations of isotherms are shown by the mean annual water temperatures marked along the coast. (After Schenck and Keen 1936.)

conceptual framework was adopted in a number of subsequent studies of marine species' distributions (Hedgpeth 1957; van den Hoek 1982).

The desire to predict shifts in species' distributions associated with climate change has sparked renewed interest in the factors controlling species' range boundaries (reviewed by Helmuth et al. 2006; Sexton et al. 2009). The resulting work has relied heavily on descriptions of past and present distributions of species and has remained grounded in the traditional correlational approaches of biogeography. However, marine ecologists have also begun to integrate surveys of species' distributions with laboratory and field experiments, physiological metrics, oceanographic data, weather records, and modeling to produce a more mechanistic understanding of range boundaries.

Niche-based modeling

Given the strong correlation between temperature and species' range boundaries, species are generally expected to shift poleward as global temperature increases (Parmesan and Yohe 2003). Bioclimate envelope modeling (also known as ecological niche modeling) has emerged as a promising tool to predict such shifts in geographic ranges. This approach has been adopted widely in terrestrial systems, but has only recently been applied to marine species (e.g., Lima et al. 2007; Cheung et al. 2009;

Martínez et al. 2012). Bioclimate envelope models assume that the current geographic distribution of a species reflects the environmental conditions preferred by that species (i.e., its ecological niche). Shifts in a species' distribution and range are modeled by combining these niche requirements with predicted spatial changes in environmental conditions generated by climate models. Although bioclimate interactions can contribute to maintaining the range boundaries of some marine species (e.g., Wetthey 2002; deRivera et al. 2005), most marine ecosystems contain some spatial and temporal refuges from competition and predation. Therefore, it seems likely that

hard barriers, such as the lethal effects of temperature, may be the primary drivers of species' absences beyond their geographic ranges. The influence of temperature is the environmental driver most often considered in analyses of marine range shifts, but the effects of ocean currents and habitat distribution have also been incorporated into more detailed models (e.g., Cheung et al. 2009; Martínez et al. 2012). Although bioclimate envelope models have yielded valuable predictions, the merit of this approach has been debated due to the reliance of niche-based models on correlations that may or may not reflect the true causes of range boundaries (Helmuth 2009).

An alternative, more mechanistic modeling approach uses observational and experimental data to identify which environmental factor(s) interact with which phase of the life cycle to set an organism's range boundary (Bhaud et al. 1995; Helmuth et al. 2006). For example, field and laboratory data suggest that the poleward range boundary of the gray snapper (*Lutjanis griseus*) along the southeastern coast of the United States is set by winter mortality of juvenile fish exposed to cold temperatures (Wuenschel et al. 2012). Once this critical "weak link" is identified, this information can be incorporated into mechanistic predictions of future changes in range boundaries (e.g., Hare et al. 2012; Jones et al. 2012). This modeling approach is a form of "ecological forecasting" (Helmuth 2009) and can

be validated by testing whether hindcasts of past thermal conditions accurately predict historical changes in species' range boundaries. For example, survey data indicate that the southern range boundary of the intertidal barnacle *Semibalanus balanoides* has retracted poleward by 300 km along the coast of France since 1872. Wetthey and Woodin (2008) used records of past weather and a mechanistic simulation model of barnacle body temperatures to hind-cast changes in the thermal environment near this species' historical range limit. Their hindcasts supported the hypothesis that the observed shift in the range boundary was driven by warmer winters that impeded reproduction. The greatest source of uncertainty in mechanistic models of this type comes not from climate models, but rather from an incomplete knowledge of species' thermal limits and requirements (Helmuth et al. 2006; Hare et al. 2012). This suggests a critical need for additional experimental studies of physiological tolerances and the factors that control species' range boundaries.

Temperature effects on survival and reproduction: Mechanistic studies

Although it is clear that species' range boundaries are often correlated with temperature, major challenges remain in identifying which aspects of temperature constrain species' distributions and how these effects vary among different life stages and taxa (Helmuth et al. 2006; Sexton et al. 2009). Mechanistic studies of range boundaries are well suited to address these challenges and have become more common in marine systems (e.g., Zacherl et al. 2003; Gilman 2006; Sanford et al. 2006). For example, although adult gray snapper in the western Atlantic have a poleward range boundary near the central coast of Florida, juveniles are frequently observed over 1000 km north of this boundary (Wuenschel et al. 2012). Laboratory experiments demonstrated that juvenile snapper were negatively affected by chronic exposure to the low temperatures of northern estuaries during winter months (Wuenschel et al. 2012). Although the evidence is correlative, the strong agreement among thermal tolerances quantified in the laboratory, the spatial distribution of winter temperatures, and the distribution of adult fish suggest that the geographic range of gray snapper is set by overwinter survival of juveniles.

Mud fiddler crabs (*Uca pugnax*) also live along the Atlantic coast of the United States and have a poleward range boundary just north of Cape Cod. However, a field experiment in which juvenile male crabs were transplanted to intertidal enclosures just beyond their range boundary demonstrated that benthic fiddler crabs are tolerant of severe winter conditions, including prolonged exposure to temperatures below -1°C (Sanford et al. 2006). In contrast, laboratory experiments showed that few planktonic larvae were able to complete development at water temperatures below 18°C , a threshold that larvae experience regularly at the northern edge of their range during the summer season of reproduction. This result suggests that physi-

ological constraints on larval survival during the summer months, rather than survival of benthic juvenile stages during the winter, may set the poleward range boundary of fiddler crabs (Sanford et al. 2006). Similar studies have been conducted to explore what mechanisms set the equatorward range boundary of the blue mussel (*Mytilus edulis*) on the Atlantic coast of the United States (Wells and Gray 1960; Jones et al. 2009). In the field, small blue mussels transplanted to near the equatorward range boundary at Cape Hatteras, North Carolina, experienced high mortality, suggesting that thermal tolerances also set this boundary (Jones et al. 2009). These and other mechanistic studies (e.g., Jones et al. 2012) support the hypothesis that temperature often plays a key role in setting species' range boundaries (Hutchins 1947).

Biogeographic boundaries: Temperature or transport?

Species' range limits are often clustered at major headlands, such as Cape Hatteras and Point Conception in the United States (Dana 1853; Gaylord and Gaines 2000), or at other coastal features, such as the San Matías Gulf in Argentina (Wieters et al. 2012). These biogeographic boundaries are often locations where major poleward and equatorward currents collide (Gaylord and Gaines 2000). Such currents originate at different latitudes and depths and frequently differ sharply in temperature. As a result, these coastal features are characterized by strong thermal gradients (Figure 7.2). As discussed on p. 132, co-occurring range boundaries have traditionally been attributed to

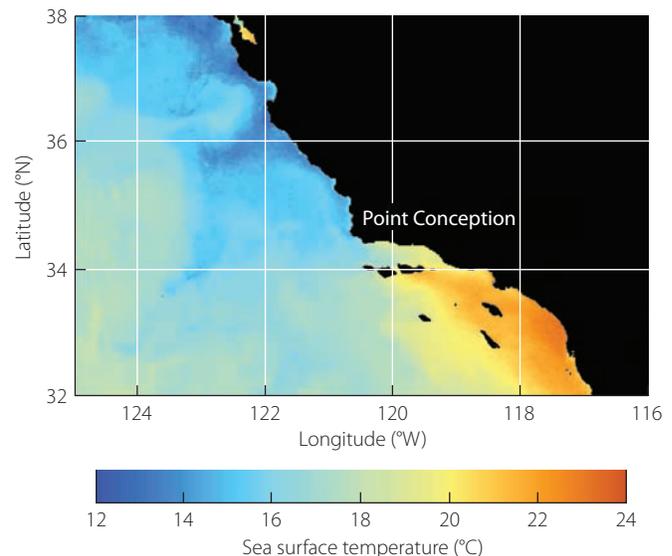


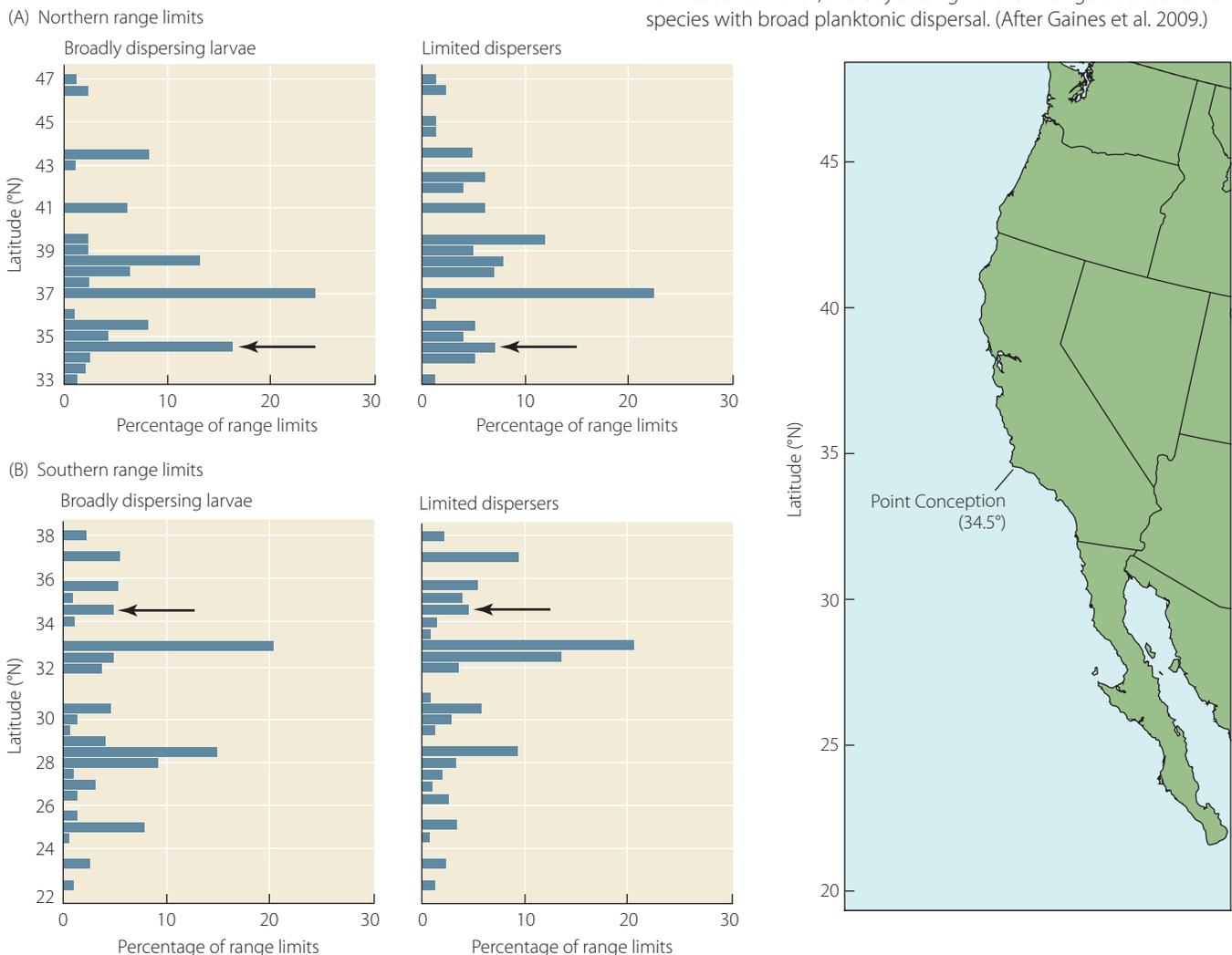
Figure 7.2 Satellite image showing sea surface temperatures ($^{\circ}\text{C}$) at Point Conception, California. Cool water is carried south along the coast by the California Current, which diverges from the shore at Point Conception. During the spring and summer, a recirculating eddy of warmer water often lies just south of the headland. This biogeographic boundary is thus characterized by both a strong temperature gradient and a convergence of currents. (Image from August 2012, courtesy of the National Oceanic and Atmospheric Administration.)

the effects of temperature in limiting survival or reproduction (Hutchins 1947). Gaylord and Gaines (2000) supported an alternative hypothesis that species' range limits at these locations might be due to strong advective currents that act as barriers to alongshore dispersal of planktonic larvae. Model results demonstrated that several configurations of flow fields could produce range boundaries in the middle of a linear coastline comprising otherwise suitable habitat. One scenario, an eddy circulation field, was found to create a one-way barrier to dispersal along the coast, such that equatorward transport was permitted while poleward transport was not. Point Conception, California, was proposed as a potential example of this type of flow field (Gaylord and Gaines 2000).

Gaines and colleagues investigated some of these predictions by assembling data on the distributions of intertidal invertebrates along the west coast of North America (Gaines et al. 2009). They hypothesized that if circulation patterns were responsible for faunal breaks, then species with different life histories should respond differently to flow-mediated dispersal barriers. In particular, species with broadly

dispersing larvae should have range boundaries clustered at major headlands where alongshore dispersal is interrupted by flow fields. In contrast, such circulation patterns should not directly affect the distributions of species with limited or no planktonic dispersal. On the other hand, if species' range limits were set predominantly by temperature, range boundaries should be concentrated at major headlands where sharp discontinuities in temperature occur, regardless of dispersal method. Results suggested a stronger role of dispersal than temperature at Point Conception, which was found to be a range boundary for many species with broad dispersal, but not for those with limited dispersal (Figure 7.3; Gaines et al. 2009). These data also supported

Figure 7.3 Distribution of intertidal invertebrate species' range limits ending at different latitudes along the Pacific coast of North America. Species are separated into broad dispersers (with a planktonic phase lasting days to months) and limited dispersers (with a very brief or nonexistent planktonic phase). Data for Point Conception (34.5° N) are highlighted with arrows, and its location is indicated on the map. These results are consistent with the hypothesis that circulation patterns near Point Conception impede larval transport from south to north, thereby setting northern range boundaries for species with broad planktonic dispersal. (After Gaines et al. 2009.)



their model predictions, which suggested this headland might function as a one-way barrier to larval dispersal, impeding transport from south to north, but not from north to south (Gaylord and Gaines 2000). For those species with broadly dispersed larvae, Point Conception was often found to be a northern range limit for southern species, but it was seldom a southern range boundary for northern species.

These model results and analyses focused attention on the neglected role that circulation and other oceanographic processes might play in influencing dispersal patterns and range boundaries. Improved tools and methods have helped spur investigations of these processes. For example, oceanographic data from high-frequency radar and other instruments are now available to map surface currents and explore the nearshore processes that influence larval dispersal (Paduan and Washburn 2013). Rapid advances in molecular techniques have also increased the availability of genetic sequence data, providing new opportunities to test ideas about dispersal, gene flow, and population connectivity. For example, Wares and colleagues analyzed patterns of gene flow among populations of four marine invertebrates that spanned the coastline north and south of Point Conception (Wares et al. 2001). For the three species with planktonic larvae, they found differential gene flow, with a greater proportion of migration events from north to south than from south to north. These patterns suggested diminished transport of larvae northward around Point Conception, which is consistent with the hypothesis that this headland is a one-way barrier to planktonic dispersal (Gaylord and Gaines 2000). In contrast, in a dogwhelk species without planktonic dispersal, there was no evidence of asymmetrical migration (Wares et al. 2001).

In related studies of gene flow along the California coast, Dawson (2001) and Kelly and Palumbi (2010) tested whether phylogeographic gaps within species (i.e., regions of restricted gene flow among populations) co-occur at Point Conception. Phylogeographic breaks were found to be clustered in specific regions, but did not coincide with Point Conception, indicating high gene flow and bidirectional dispersal of fish and invertebrate larvae across this biogeographic boundary (Dawson 2001; Kelly and Palumbi 2010). Southward transport of larvae is expected given the prevailing direction of the California Current, but relaxations of upwelling and altered circulation patterns during El Niño events might also permit the periodic transport of planktonic larvae northward around Point Conception (Kelly and Palumbi 2010).

These population genetic studies suggest that, for many species, gene flow and dispersal around Point Conception occur in both directions. This suggestion is not that surprising, because although Point Conception is a biogeographic boundary for some species, there are many other species with distributions that span Point Conception and end elsewhere (Dawson 2001). Thus Point Conception is perhaps best viewed as a broad transition zone between northern and southern taxa, rather than an impenetrable

barrier created by advective currents or extreme changes in temperature (Dawson 2001; Blanchette et al. 2008).

Indeed, Gaylord and Gaines (2000) recognized that Point Conception was not a barrier to all species with planktonic dispersal, and they suggested that a species' response to flow-induced range boundaries was likely to be modulated by its life history and physiology. Analyses of phylogeographic breaks in coastal species from several other regions of the world, including Australia (Ayre et al. 2009), South Africa (Teske et al. 2006), and Chile (see discussion by Brante et al. 2012), suggest that major biogeographic boundaries are seldom obstacles to dispersal for all species and that dispersal potential often determines susceptibility to these barriers. Thus this work (Gaylord and Gaines 2000; Gaines et al. 2009) has stimulated additional efforts to understand where and when transport and dispersal limitation might contribute to geographic range boundaries.

Dispersal limitation and range boundaries

While most studies of range boundaries in marine species have focused on the effects of temperature, evidence suggests that a large fraction of marine species may have ranges influenced by dispersal limitation. For example, detailed field studies of an intertidal limpet (*Lottia scabra*) on the west coast of the United States found little evidence that adult performance (i.e., survival, growth, gonad development) was reduced in populations near the poleward range edge compared with those closer to the range center (Gilman 2006). However, recruitment declined sharply across the same spatial gradient, dropping to very low levels in populations closest to the range edge. Although the cause of recruitment limitation remains uncertain in this limpet, the species has a relatively short planktonic larval duration, so frequent stretches of sandy coast more than 50 km long might be a considerable barrier to dispersal in this region (Gilman 2006). Indeed, both *Lottia scabra* and its congener *L. insessa* reach their poleward range boundaries at Cape Arago, Oregon, which is located at the southern edge of a 300 km stretch of sandy coastline (Gilman 2006; Kuo and Sanford 2013). Largely uninterrupted stretches of sand (130–300 km in length) and complex local currents also appear to impede larval dispersal and contribute to range boundaries in Portugal (Lima et al. 2007), along the subtropical east coast of Australia (Poloczanska et al. 2011), and at the southeastern corner of Australia (Ayre et al. 2009).

A similar role for dispersal limitation was suggested by a study of the barnacle *Chthamalus montagui* on the south coast of England (Figure 7.4; Herbert et al. 2009). Adult fitness was assessed along a gradient from the edge of the geographic range to more interior populations. There was no evidence that reproduction, growth, or survival were affected negatively at the range edge. However, recruitment was very low close to the range boundary, and oceanographic barriers to dispersal and suboptimal habitat were proposed as the primary causes (Herbert et al. 2009).

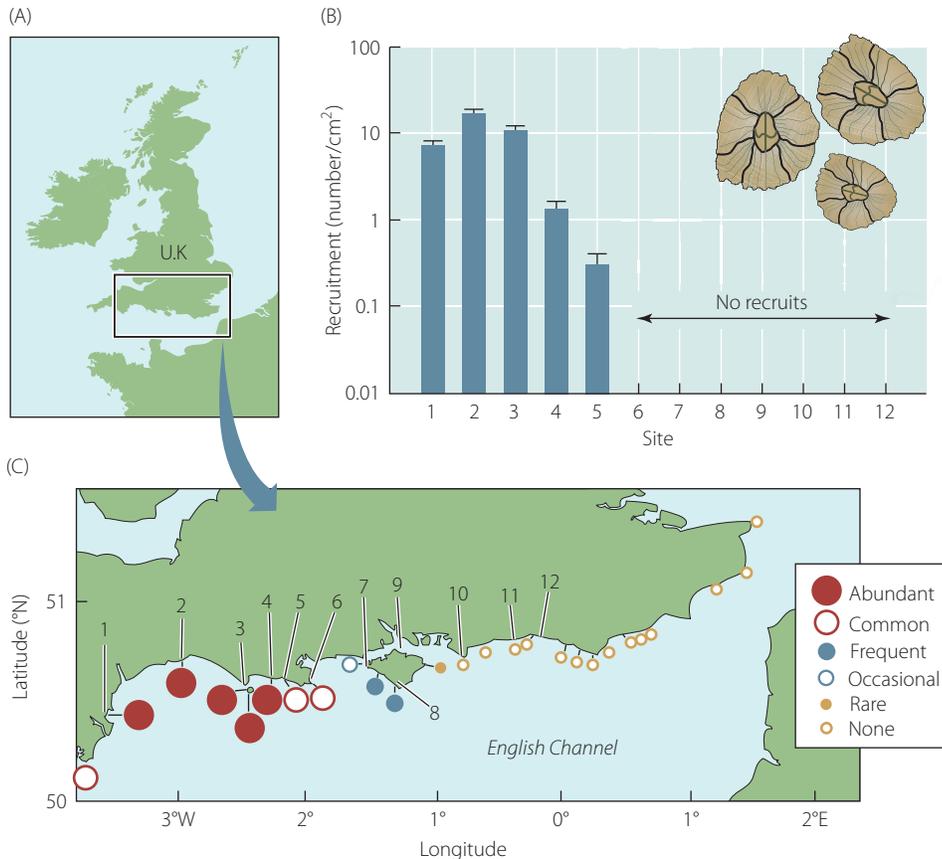


Figure 7.4 Distribution of the barnacle *Chthamalus montagui* near its range boundary on the central south coast of England. (A) Map of the United Kingdom and study region. (B) Mean recruitment of settling *Chthamalus* to cleared plots at 12 intertidal locations along the English Channel in 1999 (site numbers are shown in C). Error bars show standard errors (SE). (C) Maximum abundance of adult *Chthamalus* observed at 26 sites along the south coast during 1999–2008. The species' range boundary is associated with low recruitment near the edge of the range. (After Herbert et al. 2009.)

Studies of range expansions have also been informative in elucidating the role of dispersal limitation. For example, Zacherl and colleagues (2003) studied a marine whelk (*Kelletia kelletia*) whose distribution had recently expanded poleward 325 km beyond its historical range boundary at Point Conception. Surveys of whelk populations suggested limited dispersal in the extended portion of the range, with a higher frequency of older, larger individuals than in the historical range. The authors hypothesized that warmer temperatures and altered circulation patterns might have acted synergistically to facilitate this range expansion. In particular, circulation changes associated with El Niño events might have increased poleward dispersal of larvae, and the warmer temperature of the water might have increased larval settlement and juvenile survival in the new portion of the range (Zacherl et al. 2003). Indeed, similar processes are suggested for the poleward range expansion of a sea urchin (*Centrostephanus rodgersii*) in southeastern Australia (Ling et al. 2009), where in the past 60 years the Eastern Australian Current (EAC) has strengthened considerably, leading to a greater poleward penetration of warmer water. The effects of these changes on the range expansion of the sea urchin appear to be twofold: winter temperatures in the newly colonized range now exceed the lower threshold for successful larval development in this species, and the poleward expansion of the EAC provides larval transport to formerly inac-

cessible regions (Ling et al. 2009; Banks et al. 2010; see also Chapter 14).

Interactive effects of temperature and dispersal on range boundaries

These studies of range expansion highlight an emerging realization that the question of whether range boundaries are controlled by temperature or by circulation patterns may sometimes assume a false dichotomy. In the two range expansions just summarized, changing currents appear to have facilitated poleward transport while warmer temperatures permitted successful larval development. A model by Byers and Pringle (2006) further highlights the potential interactions between temperature and transport. This model demonstrates that several life history strategies related to the timing of larval release and the release of multiple broods of larvae might be favored as adaptations to avoid larvae being carried downstream by a mean equatorward current. In addition, the model highlights the role that cooler temperatures near the poleward edge of a range may play in limiting dispersal. In particular, cooler water temperatures are known to slow development rates and increase planktonic larval durations in most marine species (reviewed by O'Connor et al. 2007). As planktonic durations increase, it becomes less likely that temporary flow reversals will result in the net transport of larvae in the poleward direction. Thus cooler

temperatures near a poleward range edge may impede poleward larval transport against the mean current, eventually reducing recruitment to zero at the range boundary (Byers and Pringle 2006).

Such processes may contribute to the poleward range boundary of the mud fiddler crab north of Cape Cod. Similar to the conditions of the Byers and Pringle model, the prevailing flow in this region is equatorward from the Gulf of Maine, with temporary flow reversals during the summer. Culturing experiments demonstrated that the planktonic larval duration of fiddler crabs increased exponentially as temperature decreased, from 24–27 days at 20°C to 52–81 days at 16°C (Sanford et al. 2006). This lengthy planktonic period at 16°C (a common summer temperature near the range edge) probably reduces poleward transport of larvae against the prevailing current. In addition, there was a striking decrease in rates of larval survival as temperatures dropped from 18°C to 16°C (Sanford et al. 2006), suggesting that the direct effects of cooler temperatures on larval physiology play a major role in setting this range boundary.

These considerations suggest a mechanism through which ocean warming associated with climate change could facilitate poleward range expansions in some species. In particular, warmer temperatures are expected to shorten planktonic larval durations and increase larval survival, increasing the probability of net transport poleward during temporary flow reversals (Byers and Pringle 2006; Sanford et al. 2006). Interestingly, these effects might arise through temperature increases during the spring and summer, when invertebrate and fish larvae are often released as plankton. This dispersal-based mechanism differs fundamentally from the traditional view that global warming will facilitate poleward range expansions by easing cold stress during the winter. Incorporating these contrasting mechanisms into predictive models might yield different projections regarding the influence of climate change on range boundaries.

Evolutionary processes and range boundaries

Theory suggests that evolutionary processes can also play an important role in setting geographic range boundaries. In particular, if the range boundaries of some species are set wholly or partly by thermal tolerances, why doesn't selection favor the evolution of greater tolerances in populations at the edge of the range? At least two mechanisms have been proposed to explain why a species might fail to adapt to environmental conditions beyond its range boundary (reviewed by Sexton et al. 2009; Dawson et al. 2010; Kelly et al. 2012). These mechanisms depend on whether dispersal into populations at the edge of the range is high or low (Dawson et al. 2010). In the first case, a high rate of dispersal from central populations leads to antagonistic gene flow of maladapted alleles that overwhelm the potential for local adaptation in range-edge populations. In the second case, a low dispersal rate from central populations reduces genetic variation in edge

populations, limiting their capacity for adaptation (i.e., the genetic impoverishment hypothesis). In theory, edge populations should thus have very different characteristics depending on which of these two mechanisms is in operation: high gene flow and high genetic diversity in the first case, and low gene flow and low genetic diversity in the second (Dawson et al. 2010). A synthesis found that 64% of the studies addressing these patterns have documented lower genetic diversity in range-edge than in central populations, although these differences are seldom large (Eckert et al. 2008). However, the vast majority of these studies were conducted in terrestrial species. Few marine studies have documented how patterns of genetic variation differ across a species' geographic range.

Two exceptions are studies that examined patterns of gene flow and genetic diversity associated with poleward range expansions. In California, populations of an intertidal barnacle (*Tetraclita rubescens*) within a recently expanded portion of its geographic range were characterized by very high gene flow and high genetic diversity (Dawson et al. 2010). Similarly, there was no evidence of reduced genetic diversity in newly established populations of the sea urchin *Centrostephanus rodgersii* within its recently expanded range in southeastern Australia (Banks et al. 2010). In both studies, genetic results suggested high dispersal of planktonic larvae to range-edge populations from more central populations within the historical range.

These results are consistent with the hypothesis that high gene flow to range-edge populations might contribute to setting species' range boundaries by impeding local adaptation to more extreme environments (Dawson et al. 2010). Several caveats should be noted, however. First, both of these studies focused on species with long planktonic durations and high dispersal potential. Second, both species had recently undergone relatively rapid range expansions over long distances (>300 km). Whether similarly high levels of genetic diversity are apparent in marine species with shorter dispersal distances or older, more stable edge populations remains to be determined. Finally, these studies examined variation in neutral markers, and it is unknown whether similar patterns of variation occur in quantitative traits that influence thermal tolerance (Eckert et al. 2008).

Few studies of marine species have tested whether environmental tolerance limits differ in populations located at the edge versus the interior of a range (e.g., Schultz et al. 1998; Sanford et al. 2006; Gaston et al. 2009). Even fewer have tested whether scope for adaptation is diminished at the edge of a geographic range, as predicted by the genetic impoverishment hypothesis (Hoffmann et al. 2003). Kelly and colleagues (2012) addressed this question using eight populations of a tide pool copepod (*Tigriopus californicus*) spanning over 1800 km of its geographic range along the west coast of North America. In the laboratory, these populations were exposed to ten generations of strong selection to test their capacity to evolve increased thermal tolerance. As predicted by the genetic impoverishment hypothesis,

heritable variation in thermal tolerance was low in southern range-edge populations. However, contrary to prediction, it was also low in some populations throughout the species' range (Kelly et al. 2012). There is a strong need for additional studies to address these evolutionary hypotheses regarding geographic range boundaries by quantifying patterns of dispersal, gene flow, and adaptive variation across a species' range (Hoffmann et al. 2003; Eckert et al. 2008; Gaston et al. 2009; Sexton et al. 2009; Kelly et al. 2012).

Finally, there is also growing interest in the role that macroevolutionary history may play in constraining species' range limits. In particular, theory suggests that closely related taxa might share similar range boundaries because aspects of their fundamental niches are conserved within clades (Wiens and Graham 2005). For example, paleontological and biogeographic analyses of marine bivalves in the northeastern Pacific and western Atlantic suggest conservatism in range limits within both genera and families (Roy et al. 2009). The conserved traits that underlie similar range boundaries within bivalve clades are presently unknown, but might include physiological or morphological traits that influence dispersal success or thermal tolerance (Roy et al. 2009).

Implications and future directions

An integration of approaches from biogeography, ecology, evolutionary biology, and oceanography has led to advances in our understanding of species' range boundaries in the sea. The historical focus on correlating range boundaries with temperature isotherms has been supplanted by more mechanistic studies that integrate laboratory and field experiments, physiological and oceanographic data, and modeling. One of the most unexpected conclusions based on these efforts is that dispersal limitation may often contribute to setting the range boundaries of marine species. The underlying causes of low dispersal and recruitment to populations near range boundaries remain poorly understood and will be an important focus of future research. Possible causes include reduced larval production, temperature thresholds for larval development, oceanographic currents that impede larval transport, scarcity of suitable habitat, and phenotype–environment mismatches (Gaylord and Gaines 2000; Gilman 2006; Sanford et al. 2006; Marshall et al. 2010). Several studies suggest that altered circulation patterns and increased temperature may interact synergistically to increase dispersal during geographic range extensions (Zacherl et al. 2003; Byers and Pringle 2006; Ling et al. 2009). Through its influence on gene flow, the magnitude of dispersal into populations near the edge of a range is also likely to shape local adaptation and other evolutionary processes that influence range boundaries (Dawson et al. 2010). New methods in population genetics and genomics, coupled with more detailed studies of coastal oceanography, promise to advance our understanding of the interactions among currents, larval dispersal, gene flow, and adaptation across species' ranges. Improving our understanding

of these processes is essential to predicting how climate change will alter the range boundaries and geographic distributions of marine species.

The Geography of Abundance

In mapping geographic distributions and range boundaries, biogeographers historically focused on the presence or absence of species rather than on their abundance. On the other hand, ecologists often addressed processes influencing abundance, but seldom worked across large spatial scales (Brown et al. 1995). James Brown highlighted this disciplinary division and suggested that the geographic range of a species could be more effectively conceptualized as a complex three-dimensional surface, where two dimensions map the spatial extent of the distribution and the third dimension represents the abundance of each population (Brown et al. 1995). This view emphasizes the connection between the processes shaping the boundaries of a geographic distribution (the traditional domain of biogeography) and those regulating population abundance (the traditional domain of ecology). This perspective has stimulated considerable interest in the geography of abundance in marine species.

The abundant-center hypothesis

In considering the geography of abundance, Hengeveld and Haeck (1982) and Brown (1984) observed that species were frequently most abundant near the center of their geographic ranges and less abundant toward the edges. The idea that this pattern might be a general rule became known as the “abundant-center hypothesis.” The basis for this hypothesis is the classic ecological concept of the multidimensional niche (Hutchinson 1957). Brown (1984) argued that a species should be most abundant at the center of its geographic range because that is where abiotic and biotic variables are ideal for individual fitness. Moreover, if environmental variables tend to be spatially autocorrelated, population abundance should be approximated by a normal distribution, with abundance declining smoothly from the range center toward the margins (Brown 1984).

The majority of the data that were initially available to formulate and test the abundant-center hypothesis came from studies of terrestrial plants, birds, and insects (Hengeveld and Haeck 1982; Brown 1984; Sagarin and Gaines 2002b). This bias toward terrestrial systems motivated Sagarin and Gaines (2002a) to test whether abundant-center patterns of distribution were characteristic of marine species. They surveyed the abundance of twelve rocky intertidal invertebrates at 42 sites spanning most of the species' geographic ranges along the west coast of North America. Only two species had distributions consistent with the abundant-center hypothesis, whereas six species had high densities near one of their range edges, and the other four species showed no clear patterns of spatial variation in abundance (**Figure 7.5**). Based on these sur-

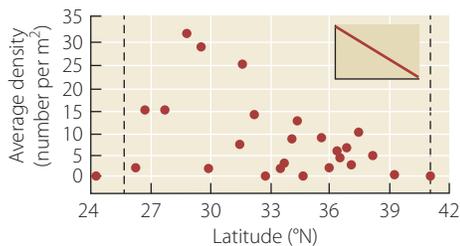
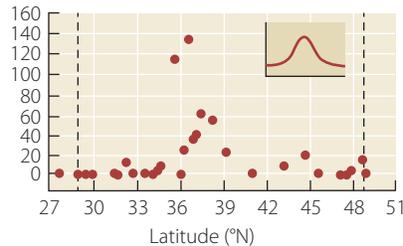
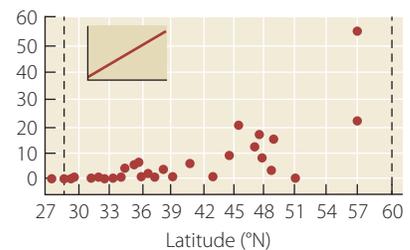
(A) *Anthopleura sola*(B) *Chlorostoma funebris*(C) *Anthopleura xanthogrammica*

Figure 7.5 Geographic distributions of abundance for three intertidal invertebrates along the west coast of North America. Each data point is the mean density at one sampling location. Dashed vertical lines indicate range limits. The results shown are representative of distributions seen in a study of twelve species, including (A) The sea anemone *Anthopleura sola* (abundance increases towards the southern range limit, referred to as “ramped south”), (B) the turban snail *Chlorostoma (Tegula) funebris* (abundant center), and (C) the sea anemone *A. xanthogrammica* (ramped north). Only two of the twelve species showed an abundant-center distribution. (After Sagarin and Gaines 2002a; photos courtesy of Jackie Sones.)

veys and a review of the literature, Sagarin and Gaines (2002a,b) concluded that abundant-center distributions were uncommon.

This work stimulated a number of studies investigating the abundant-center hypothesis in other marine species and in a variety of geographic regions. These studies have supported the conclusion that the abundant-center distribution is far from a universal rule, occurring in only about a third to a half of the species examined (Table 7.1). This conclusion has prompted researchers to ask why abundant-center distributions are not more common. Addressing this question has required moving beyond the description of abundance distributions to testing the assumptions of Brown’s model and exploring the processes and mechanisms that underlie geographic patterns of abundance (Sagarin et al. 2006).

Role of environmental heterogeneity

The abundant-center hypothesis assumes that the environmental factors driving individual fitness vary

predictably with latitude along gradual, monotonic gradients (Brown 1984). Several authors have challenged this assumption and suggested that departures from the idealized abundant-center distribution might arise in marine systems because many coastlines are characterized by heterogeneous mosaics of environmental conditions (Sagarin and Gaines 2002a; Gilman 2005; Sagarin et al. 2006; Tam and Scrosati 2011). A study of demersal fishes along the coast of southwestern Australia provides some support for this view (Langlois et al. 2012). In this system, a striking 15 out of 20 species examined exhibited a unimodal abundance distribution. The authors suggested that abundant-center distributions are common along the coast of southwestern Australia because of a consistent thermal gradient and a low level of productivity. They noted that, in contrast, the majority of marine studies examining geographic patterns of abundance have been conducted in regions of coastal upwelling, where complex spatial mosaics of temperature and productivity might obscure unimodal patterns of abundance (Langlois et al. 2012). For example, on the west coast of North America, water temperature and productivity can vary over relatively small spatial scales (tens to hundreds of kilometers) with the intensity of coastal upwelling and the location of rocky headlands (Menge et al. 1997; Caselle et al. 2011). Along the west coast of North America, the aerial body temperatures of organisms within the intertidal zone also vary in a non-monotonic pattern due to differences in the timing of low tides during the warmest months of the year (Helmuth et al. 2002). These complex patterns of alongshore variation in temperature might generate considerable patchiness in the geographic distribution of physiologically optimal habitat.

TABLE 7.1 Results from studies testing the abundant-center hypothesis in marine species

REFERENCE	LOCATION	SCALE	TAXA	ABUNDANCE DISTRIBUTIONS ^a		
				TOTAL SPECIES TESTED	ABUNDANT-CENTER	RAMPED
Sagarin and Gaines 2002a	NE Pacific (N. America)	4500 km	Intertidal invertebrates	12	2	5
Gilman 2005	NE Pacific (N. America)	700 km	Intertidal limpet	1	0	0
Fenberg and Rivadeneira 2011	NE Pacific (N. America)	1800 km	Intertidal limpet	1	1	0
Ebert 2010	NE Pacific (N. America)	2600 km	Intertidal sea urchin	1	1	0
Rivadeneira et al. 2010	SE Pacific (Chile)	2600 km	Intertidal crabs	5	2	1
Hidas et al. 2010	SE Australia	600 km	Intertidal invertebrates	3	1	0
Tuya et al. 2008	SW Australia	1400 km	Fishes	8	3	2
Langlois et al. 2012	SW Australia	1500 km	Fishes	20	15	4
Tam and Scrosati 2011	NW Atlantic (N. America)	1800 km	Intertidal invertebrates	3	2	1

Source: After Langlois et al. 2012.

^aThese columns show the total number of species tested and the number of those species found to have an abundant-center distribution or a ramped distribution (i.e., increasing abundance near a range edge). Note that data fits to abundant-center and ramped models were tested statistically in many, but not all, cases.

Indeed, Brown and colleagues recognized that spatial heterogeneity in the environment was probably much more complex than envisioned in their initial hypothesis. Therefore, they refined their initial ideas and suggested that the ranges of most species will contain many “cool spots” where a species is relatively rare, interspersed with “hot spots” where favorable conditions allow the species to become more abundant (Brown et al. 1995). Results from surveys of marine species are consistent with this view. For example, Blanchette and colleagues (2008) reported geographic patterns of abundance for 22 common species of sessile invertebrates, macroalgae, and seagrass from surveys conducted at 67 rocky intertidal sites ranging from Baja California, Mexico, to Alaska. For most species, “cool spots” and “hot spots” were interspersed across the geographic range, including adjacent sites separated by tens of kilometers. Similar variation in abundance among closely spaced populations is apparent in almost all surveys of marine species (e.g., Sagarin and Gaines 2002a; Gilman 2005; Schoch et al. 2006). However, although environmental heterogeneity may prevent smooth declines in abundance as one moves from range center to range edge, the question of whether hot spots of abundance tend to be concentrated near the center of the range, as predicted by the revised version of the abundant-center hypothesis (Brown et al. 1995), remains to be addressed.

Role of dispersal in uncoupling habitat favorability and local abundance

Numerous authors have suggested that peaks in local abundance will not necessarily be concentrated near the center of marine species’ ranges because many marine

species have high dispersal rates (Sagarin and Gaines 2002a; Gilman 2005; Lester et al. 2007; Ebert 2010; Hidas et al. 2010). As noted on p. 139, an assumption underlying the abundant-center hypothesis is that favorable conditions increase per capita reproduction and subsequently drive local increases in abundance. This assumption may be violated, however, if planktonic dispersal decouples habitat favorability, reproductive output, and local abundance (Sagarin and Gaines 2002a; Gilman 2005; Lester et al. 2007; Ebert 2010; Hidas et al. 2010). In such species, adults living in optimal habitat may have high reproductive output, but the resulting offspring may be dispersed to less favorable sites, decoupling abundance from local environmental conditions. There is some evidence to support this contention. In the eastern Pacific, no relationship was found between the abundance of predators and habitat favorability (i.e., the local abundance of prey) for predators with long planktonic dispersal periods, such as sea stars (**Figure 7.6A**; Wieters et al. 2008). In contrast, predatory dogwhelks, which lack planktonic dispersal, showed a strong correlation between their local abundance and the recruitment of their prey (**Figure 7.6B**; Wieters et al. 2008). Although abundant food increases reproductive output in both taxa, enhanced reproduction may not translate into increased local abundance of sea stars because of their planktonic dispersal.

While planktonic dispersal should tend to decouple habitat favorability from local abundance, this conclusion comes with some caveats. Growing evidence suggests that, contrary to the conventional wisdom of the past, planktonic larvae may often remain in the neighborhood of their natal sites as a result of larval behavioral or oceanographic

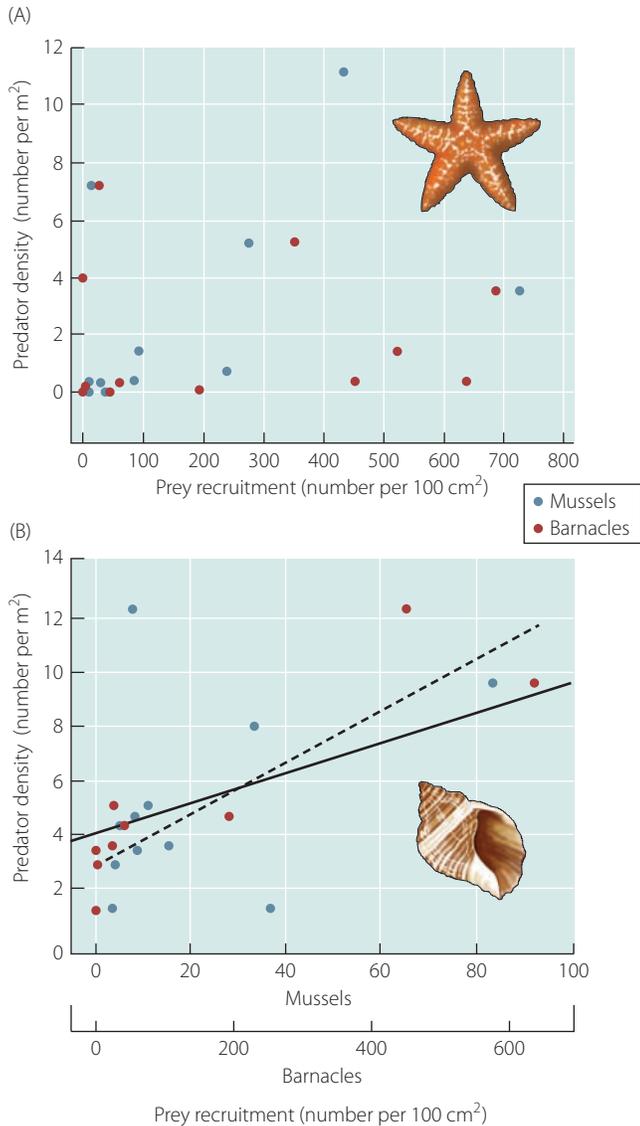


Figure 7.6 Relationship between prey recruitment (a measure of habitat favorability) and predator abundance for two intertidal predator species with different dispersal potential. (A) Prey recruitment did not predict the density of the sea star *Pisaster ochraceus* ($p > 0.05$), a species with planktonic dispersal. (B) Mean density of the dogwhelk *Nucella emarginata*, which lacks planktonic dispersal, increased with mean barnacle recruitment (dashed line) and mean mussel recruitment (solid line). Note the different scales of prey recruitment for barnacles (lower x-axis) and for mussels (upper x-axis). Data were collected on the west coast of North America. (After Wieters et al. 2008.)

features that retain them close to their origin (see Chapter 4). If this is the case, then optimal conditions that favor high reproductive output (e.g., conditions near the center of a geographic range) might still lead to high population abundance at the broader scale over which larvae are transported (i.e., the dispersal kernel). Such regional processes are suggested by a study of temporal changes in sea star abundance in the Gulf of Maine. Following a

massive recruitment of subtidal mussels, reproduction of sea stars (*Asterias* spp.) was temporarily enhanced, resulting in an increase in the larval recruitment of sea stars throughout the entire region (Witman et al. 2003). This result is consistent with the view that a positive correlation between habitat favorability (i.e., prey abundance in this case) and the abundance of predators is expected to occur as one approaches the dispersal scale of the predator (Wieters et al. 2008).

Postsettlement mortality is a second process through which habitat favorability may influence local abundance, even in species with planktonic dispersal. Postsettlement mortality is frequently high in marine species (Marshall et al. 2010), and thus the early juvenile phase often acts as a population bottleneck. To the extent that favorable habitat conditions (e.g., optimal temperature and abundant food) enhance the postdispersal survival of recent settlers, patterns of adult abundance can reflect environmental gradients even in species with planktonic dispersal. Thus, despite a tendency for planktonic dispersal to weaken links between local conditions and local abundance, dispersal does not necessarily invalidate the basis of the abundant-center hypothesis.

Geographic variation in individual performance and demographic processes

These considerations emphasize the importance of an integrated perspective that examines how individual performance and multiple demographic processes vary over large spatial scales to influence population abundance (Gilman 2006; Sagarin et al. 2006; Lester et al. 2007; Gaston 2009; Rivadeneira et al. 2010). Integrating biogeography and ecology in this context provides mechanistic insight into geographic variation in abundance. For example, in sandy beach communities along the coast of South America, yellow clams appear to have an abundant-center distribution (Fiori and Defeo 2006). Performance and demographic parameters were quantified in yellow clam populations over about a thousand kilometers, covering the southern half of the species' range (Figure 7.7; Fiori and Defeo 2006). Clam abundance decreased smoothly from the range center to the range edge. This geographic pattern of abundance was closely matched by variation in recruitment and growth rates, both of which also declined monotonically with decreasing temperature from the range center to the range edge. Recruitment occurred throughout the year near the range center, but was highly seasonal near the range edge (Fiori and Defeo 2006). These demographic patterns provide a possible mechanistic basis for the abundant-center distribution observed in this species.

Along the west coast of North America, the distribution of purple sea urchin abundance was also found to be roughly unimodal, although peak abundance was skewed slightly toward the equatorward end of the geographic range (Figure 7.8, Figure 7.9A; Ebert 2010). However, geographic variation in performance did not follow a similar

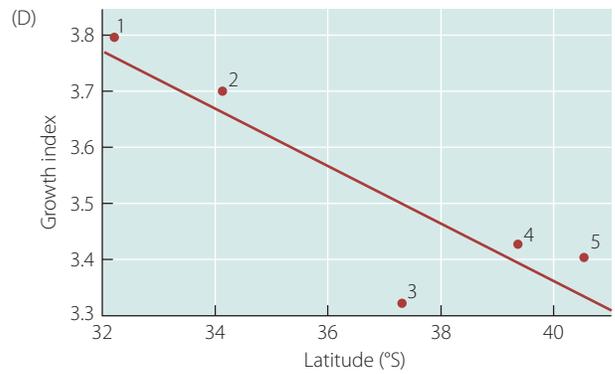
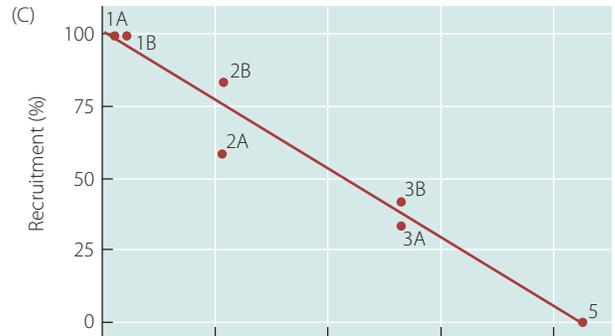
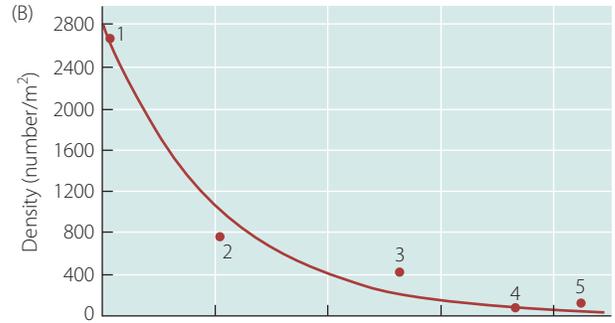
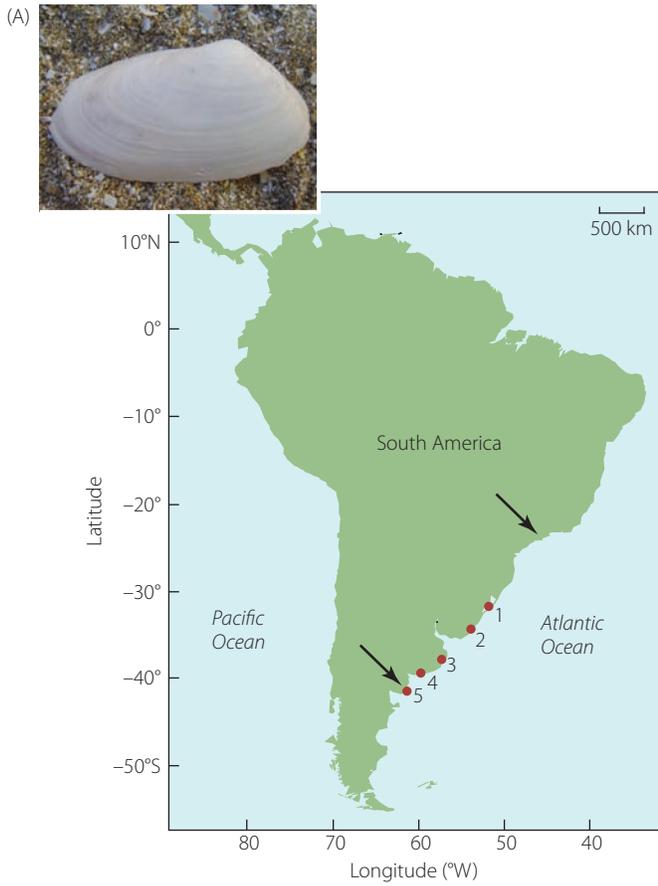


Figure 7.7 Abundance and performance of the yellow clam (*Mesodesma mactroides*) in the southern half of its geographic range in South America. (A) Locations of the five study sites and the endpoints of the geographic range (arrows). (B) Latitudinal variation in mean density of clams. (C) Latitudinal variation in recruitment (percentage of months in the year with clams less than 5 mm long in samples). A and B labels represent data collected at a site in two different years. (D) Growth (estimated by the growth performance index, ϕ'). (After Fiori and Defeo 2006.)



Figure 7.8 Purple sea urchins (*Strongylocentrotus purpuratus*) in a tide pool in northern California. Several size classes of urchins are visible. The proportion of individuals that are 1 year old or less can be used as an index of recruitment (1-year-old urchins are generally 2 cm or smaller in test diameter). (Courtesy of Jackie Sones.)

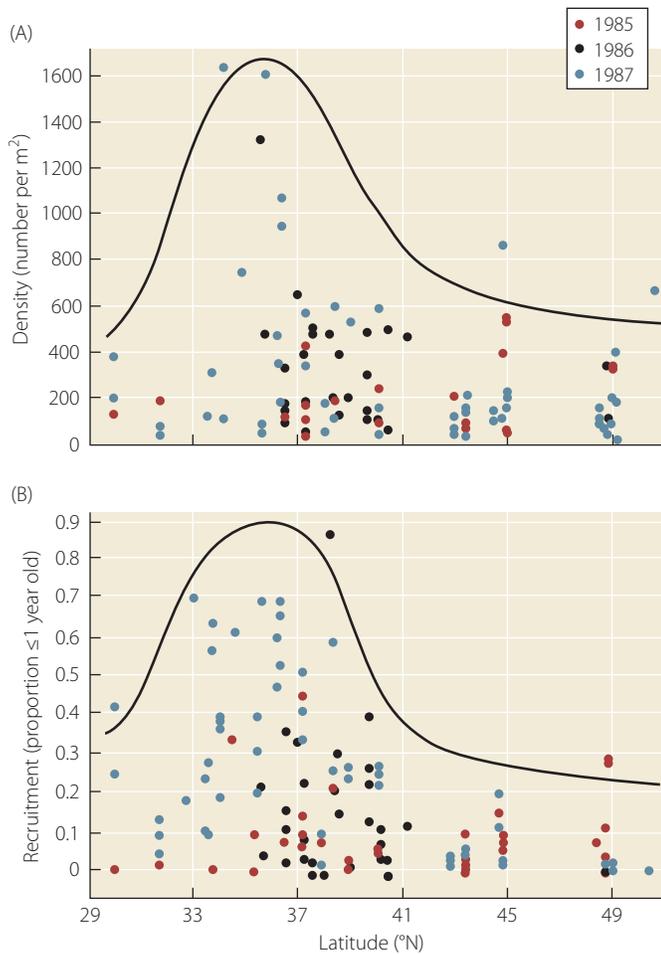


Figure 7.9 Latitudinal variation in abundance and recruitment of purple sea urchins (*Strongylocentrotus purpuratus*) along the west coast of North America. (A) Population density of sea urchins, calculated based on the surface area of pools or crevices and adjusted to number of individuals per m². (B) Recruitment, based on the proportion of small urchins. Curves were fitted by eye by the author to illustrate general trends. Peak abundance of sea urchins along the coast generally matched geographic variation in recruitment. (After Ebert 2010.)

recruitment? At the present, these questions remain unresolved. However, these studies suggest that geographic patterns of abundance might sometimes be coupled to one demographic parameter (e.g., recruitment) despite being largely unrelated to other aspects of performance (e.g., growth and per capita reproduction). These and several related studies (Lewis 1986; Hidas et al. 2010; Lathlean et al. 2010; Wethey et al. 2011) point to the importance and challenges of identifying critical demographic bottlenecks, determining how they are influenced by environmental factors, and understanding how these processes vary both geographically and among species.

Role of plasticity in physiological and life history traits

By defining the center of a geographic range as the “optimal” environment, the abundant-center hypothesis assumes that all populations of a species respond in a similar way to a given set of environmental conditions. However, if individuals in geographically separated populations exhibit plasticity in their physiological performance, departures from an idealized abundant-center distribution might occur (Sagarin et al. 2006). Many marine organisms are capable of physiological acclimatization, which can allow individuals far from the range center to be buffered against environmental conditions that would otherwise be suboptimal (Dahlhoff and Somero 1993; Stillman and Tagmount 2009). For example, metabolic compensation for latitudinal changes in temperature has been documented in a variety of marine ectotherms and is reflected by high-latitude populations that have higher metabolic rates than those at low latitudes when measured at a common temperature (Clarke 1993; Whiteley et al. 2011).

Plasticity in life history strategies might also alter the predicted associations among environmental variation, individual fitness, and local population abundance (Fiori and Defeo 2006; Martone and Micheli 2012). For example, although individuals at cooler temperatures near the poleward edge of a range may grow more slowly and have lower annual reproductive output than individuals near the range center, these individuals often have lower annual mortality, a longer life span, and reach a larger body size (Lewis 1986; Fiori and Defeo 2006). Theory suggests that such trade-offs among life history traits might complicate the expectations of ecological niche theory that predict a simple correspondence between environmental

unimodal pattern. In fact, estimates of growth and annual survival showed no consistent pattern of variation with latitude and were highly variable over small spatial scales (≤ 100 km). There was also no consistent pattern of latitudinal variation in gonad production over a broad spatial scale of more than 2300 km (Lester et al. 2007; Ebert et al. 2012). Gonad production varied across small spatial scales (tens of kilometers) and was higher in small bays than on coastal headlands, perhaps because these embayments had abundant drift kelp that fueled increased urchin reproduction (Lester et al. 2007). The lack of evidence for decreased performance (i.e., growth, reproduction, survival) at the edge of this species’ range is clearly not consistent with the assumptions of the abundant-center hypothesis. Recruitment, however, was unimodal, reaching a peak within roughly the same region of the coast as the abundance of adults (**Figure 7.9B**; Ebert 2010). Thus, in purple sea urchins, geographic patterns of abundance appear to be more closely correlated with recruitment than with growth, gonad production, or adult survival.

Does this region of peak urchin recruitment have a consistently favorable environment that maintains low rates of postsettlement mortality in juvenile urchins? Or might there be positive feedback, such that larger adult populations in this region contribute to a greater larval pool for

gradients and fitness (Gaston 2009; Martone and Micheli 2012). Examining geographic variation in a single metric of performance may therefore be misleading because investment in one trait (such as growth rate) may be accompanied by a decrease in allocation to another trait (such as reproduction; Gaston 2009; Martone and Micheli 2012). For example, turban snails in two regions of Baja California experienced different water temperatures and invested differently in growth and reproduction, but these two life history strategies yielded similar age-specific fecundities (Martone and Micheli 2012). If such plasticity in life history strategies is common, it may dampen the influence of environmental gradients on individual fitness and contribute to relatively consistent population abundances over broad geographic scales. Important feedbacks might also occur among local density, life history traits, and population processes (Defeo and Cardoso 2004). For example, in a study of California sheephead, those populations with the highest densities were composed of smaller fish, and had lower per capita and total reproductive output, than the population with the lowest density (Caselle et al. 2011).

Although plasticity in life history traits may weaken the predicted link between latitudinal gradients and population abundance, environmental constraints on life history traits may contribute to abundant-center distributions in some species. For example, Rivadeneira and colleagues (2010) found evidence of abundant-center distributions in two of five intertidal species of porcelain crabs sampled over much of their geographic ranges along 2500 km of the Chilean coast. Population sex ratios also followed a unimodal pattern, with a bias toward females near the center of the range and a scarcity of females near the range edges (see also Defeo and Cardoso 2002). These patterns may reflect differential costs experienced by the sexes across the geographic range. For example, the costs of egg production and brooding for female porcelain crabs might be higher near the edges of the range, where temperatures are far from optimal (Rivadeneira et al. 2010). In one porcelain crab species (*Allopetrolisthes angulosus*) with an abundant-center distribution, not only were there far fewer females in populations near the range edge, but the frequency of females that were brooding was considerably less than in range center populations (Figure 7.10). To the extent that these patterns influence larval production and recruitment, environmental constraints on life history traits might contribute to the abundant-center pattern observed in this species. Interestingly, those porcelain crab species that conformed to the expectations of the abundant-center hypothesis also tended to be those that were small-bodied and less abundant locally (Rivadeneira et al. 2010). Whether these traits are causally related to the very different geographic patterns of abundance observed among the five species of porcelain crabs remains uncertain, but comparative studies such as this one are a promising avenue for exploring the mechanistic drivers of abundance patterns.

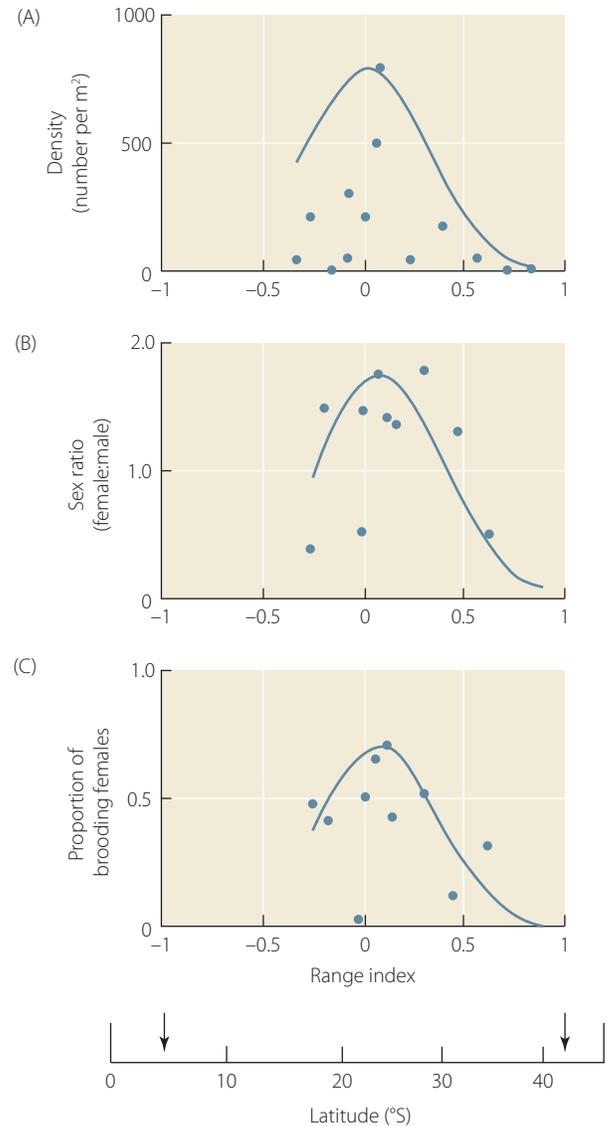


Figure 7.10 Latitudinal variation in the abundance and life history of the porcelain crab *Allopetrolisthes angulosus* across its geographic range in Chile. (A) Population density. (B) Sex ratio (females:males). (C) Proportion of females brooding embryos. Curves are the best model fits. Range index varies from -1 to 1 ; 0 indicates the range center. Latitude is shown on the lower x-axis; arrows indicate range limits. Both the ratio of females present and the proportion of females brooding declined near the range edges, perhaps contributing to lower population densities there relative to the range center. (After Rivadeneira et al. 2010.)

Role of evolutionary processes

In addition to showing phenotypic plasticity, populations distributed across geographic ranges may be locally adapted to persistent environmental conditions. Given the perceived openness of marine systems, most marine species were historically regarded as collections of genetically homogeneous populations with little potential for adaptive divergence. Evidence suggests, however, that

local adaptation may be more common in marine species than is traditionally recognized (Conover et al. 2006; Sanford and Kelly 2011). A variety of fish and marine invertebrates have evolved patterns of countergradient variation in growth rates in response to latitudinal gradients in temperature (reviewed by Conover et al. 2006; Sanford and Kelly 2011). For example, along the east coast of the United States, Atlantic silversides (*Menidia menidia*) show a clear pattern of countergradient variation: high-latitude populations, which experience cooler water temperatures, show faster growth rates than do low-latitude populations when held under common conditions (Conover and Present 1990; Hice et al. 2012). In this case, local adaptation dampens the influence of the environmental gradient on performance, potentially contributing to departures from an abundant-center distribution.

Similarly, populations of dogwhelks (*Nucella canaliculata*) along the west coast of the United States exhibit a complex geographic mosaic of genetic variation in thermal tolerance (Kuo and Sanford 2009). The upper thermal limits of laboratory-reared, second-generation snails were found to differ among populations, suggesting genetic differences in thermal tolerance. Counterintuitively, newly hatched snails from central California were less heat tolerant than those from higher-latitude populations. However, this geographic pattern of variation is consistent with the mosaic of potential thermal stress that occurs along this coast, where high-latitude sites can experience longer exposure to stressful midday low tides than sites at lower latitudes due to variation in the timing of low tides (Helmuth et al. 2002). Latitudinal variation in the thermal tolerance of tide pool copepods follows a similar non-monotonic pattern along this coastline, in which populations from northern California show less heat tolerance than those from higher latitudes (Figure 7.11; Kelly et al. 2012). Whether these genetic differences in thermal tolerance influence demographic processes in these species has yet to be determined. However, if local adaptation tends to equalize performance and individual fitness across a species' range, geographic patterns of abundance may fail to conform to the idealized normal distribution.

Implications and future directions

Although there is little evidence that abundant-center distributions are a general rule in marine species, efforts to describe these spatial patterns have focused attention on the ecological and evolutionary processes underlying geographic variation in abundance. There appear to be multiple reasons why abundant-center distributions are less common in marine systems than predicted by the general model of Brown and colleagues (1995). Strong environmental heterogeneity, especially in coastal upwelling systems, may cause departures from the idealized normal distribution of abundance. Marine species with planktonic dispersal might also have population abundances that are decoupled from the influence of the local environment on per capita

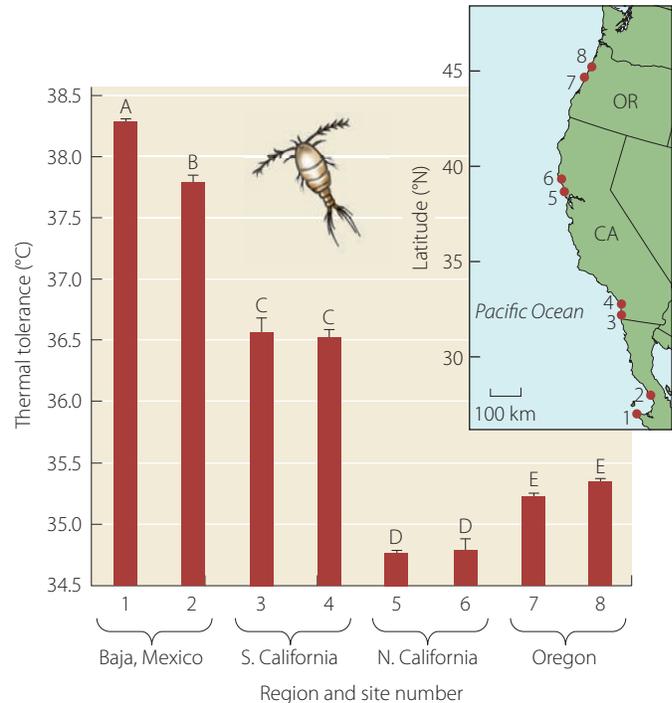


Figure 7.11 Geographic variation in the thermal tolerances of tide pool copepods (*Tigriopus californicus*). The inset map shows the locations of the eight study sites in North America. Bars are mean thermal tolerances (LT₅₀, the lethal temperature for 50% of the individuals tested; +SE) of laboratory-reared, second-generation copepods (adult males). Thermal tolerances differed among populations (analysis of variance, ANOVA, $p < 0.001$). Shared letters above bars indicate populations whose means do not differ (Tukey-Kramer, $p > 0.05$). Low-latitude populations had the highest thermal limits, but thermal tolerances in northern California were lower than those in Oregon. (After Kelly et al. 2012.)

reproduction. Finally, phenotypic plasticity and local adaptation to environmental gradients might dampen the influence of latitudinal variation on life history traits, individual fitness, and local abundance. Nevertheless, clear abundant-center distributions have been documented in some marine species, challenging marine ecologists to understand why these patterns emerge in some species and ecosystems but not in others. An integrated approach that considers geographic variation in performance and multiple demographic processes may provide the most promise for finding general explanations for this variability.

The mechanisms that drive geographic variation in population abundance constitute a research area with important implications for marine community ecology and conservation (Sagarin et al. 2006). The abundance of species can have a strong effect on the strength of species interactions and on community dynamics. In addition, an understanding of the processes that drive geographic variation in abundance has a number of important conservation applications, including fisheries management and the design of marine reserve networks (Caselle et al. 2011; Hamilton et al. 2010).

Latitudinal Variation in Species Interactions

The first two sections of this chapter have considered species within a community as largely independent units. However, by influencing the composition and structure of local species assemblages, the processes that influence species' range boundaries and population densities help set the stage for considering latitudinal variation in species interactions and species diversity. Latitudinal variation in the strength of species interactions has historically been an important component of several ecological theories (e.g., Paine 1966; Pianka 1966) and has received attention from marine ecologists in the context of several recent hypotheses and research goals. First, over mesoscales (i.e., hundreds of kilometers), species interactions are predicted to vary in intensity along coastal gradients of environmental stress, productivity, and recruitment (Menge et al. 1997, 2003; Connolly and Roughgarden 1999; Pennings et al. 2003). Many of these predictions are logical extensions of community regulation models (Menge and Sutherland 1987; Menge and Olson 1990; Bertness and Callaway 1994) that were initially developed and tested primarily through experiments conducted over small spatial scales, such as across intertidal gradients of stress (Menge and Sutherland 1987; Bertness and Leonard 1997). Second, there is a growing interest in defining the spatial scales over which the strengths of species interactions vary (Benedetti-Cecchi et al. 2001). Traditionally, marine ecologists have conducted controlled experiments at one or a few local field sites, and whether results from these experiments can be extrapolated to broader spatial scales has been an open, and sometimes a contentious, question (Foster 1990; Paine 1991; Estes and Duggins 1995; Pennings et al. 2003). Determining the factors that drive the context dependency of species interactions over latitudinal spatial scales has emerged as an important challenge for improving the predictive capacity of ecology. Finally, at global scales, several long-standing hypotheses propose that species interactions are more intense at tropical than at temperate latitudes, promoting greater species diversity in the tropics (Dobzhansky 1950; Pianka 1966; Vermeij 1978, 2005). These hypotheses have received renewed attention among marine ecologists (e.g., Freestone et al. 2011; Poore et al. 2012).

An effective tool for addressing how and why species interactions vary with latitude is a comparative–experimental approach in which identically designed experiments are replicated across large spatial scales (reviewed by Sanford and Bertness 2009). This experimental design provides insight into how species interactions vary along abiotic gradients that are not amenable to manipulation. Dayton (1971) pioneered this approach with his studies on rocky intertidal shores, and it has since been used in a variety of marine ecosystems. Comparative experiments have been conducted to quantify species interactions over

two large, but very different, spatial scales. In some cases, the interaction between a focal species and one or more other species has been investigated over a large portion of the focal species' geographic range (e.g., over many hundreds of kilometers). In other cases, species interactions within a given ecosystem (e.g., rocky intertidal reefs or eelgrass beds) have been investigated over even broader geographic scales (thousands of kilometers), including tropical versus temperate comparisons. At this second scale, the communities being compared have evolved independently and generally contain very few, if any, of the same species (e.g., Paine et al. 1985). This section begins by considering studies of interaction strength across a species' geographic range, and it concludes by examining broader, global comparisons among tropical versus temperate communities.

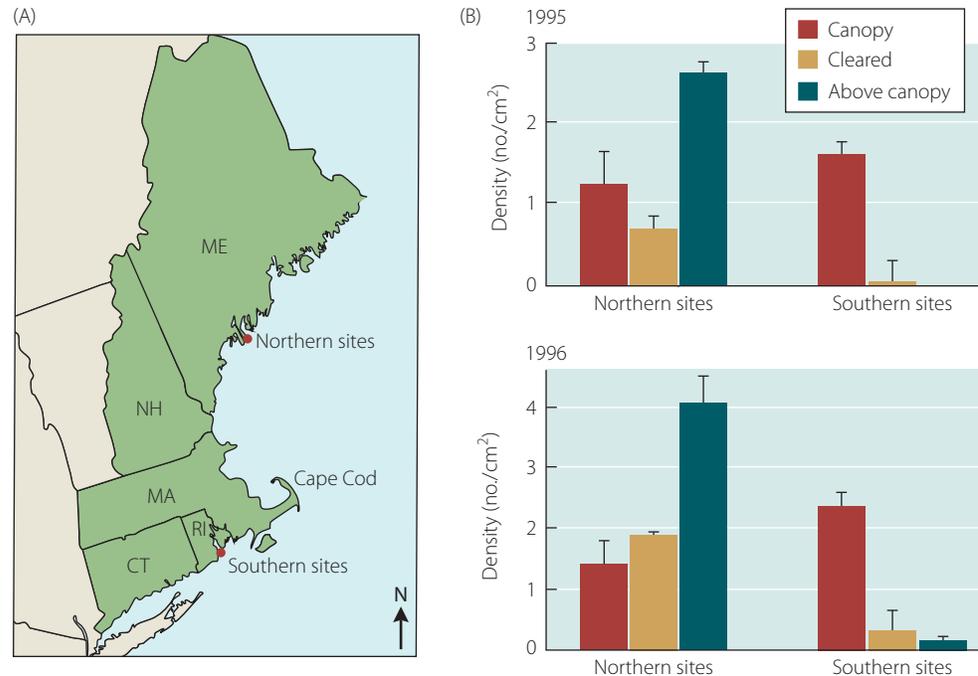
Environmental stress gradients and the strength of competition and facilitation

Theory developed primarily from experiments conducted over local spatial scales suggests that the relative importance of competition and facilitation should vary predictably along latitudinal gradients of environmental stress (Menge and Sutherland 1987; Bertness and Callaway 1994). Specifically, these theories predict that competitive interactions will decline along a latitudinal gradient of increasing environmental stress, whereas the strength of facilitation will increase.

Efforts to address these predictions are illustrated by several experiments conducted at intertidal sites spanning Cape Cod on the Atlantic coast of the United States. In the first of these, Wethey (1984, 2002) tested whether competition between two intertidal barnacle species varied predictably along a coastal gradient of heat and desiccation. His experiments demonstrated that north of Cape Cod, the northern barnacle species *Semibalanus balanoides* rarely experienced thermal stress during low tides and was able to competitively exclude the more southern species (*Chthamalus fragilis*). South of Cape Cod, however, where thermal stress was greater, *Semibalanus* was often eliminated from the high intertidal zone and was unable to outcompete *Chthamalus* (Wethey 2002).

Similarly, Leonard (2000) tested the hypothesis that differences in thermal stress north and south of Cape Cod modified the interaction between an intertidal canopy-forming alga (*Ascophyllum nodosum*) and the barnacle *Semibalanus* (Figure 7.12). Identical high intertidal plots were established at four sites, two north and two south of Cape Cod, and the algal canopy was removed from half of the plots at each site. At the southern sites, where maximum rock temperatures were often several degrees warmer, survival of barnacle recruits was largely dependent on facilitation by the algal canopy. In contrast, barnacles at the northern sites survived equally well in canopy plots and in cleared plots. These results suggested that the importance of *Ascophyllum* in buffering against heat and desiccation varied predictably along the coast (Leonard

Figure 7.12 Geographic variation in the interaction between the canopy-forming alga *Ascophyllum nodosum* and the barnacle *Semibalanus balanoides*. (A) Map of study sites in the northeastern United States. (B) The mean density of barnacle recruits (+SE) was monitored in plots with an algal canopy, with algae cleared, and directly above the canopy. At warmer sites south of Cape Cod, few barnacles survived without the canopy. At cooler northern sites, survival of barnacles was not dependent on the canopy. The experiment was replicated in 1995 and 1996. (After Leonard 2000.)



2000). Subsequent experiments conducted in this region indicated that the interaction of barnacles with *Ascophyllum* germlings was different from their interaction with the adult canopy (Kordas and Dudgeon 2011). In the more southern regions, where the water was warmer, barnacles grew faster and sometimes had strong competitive effects on algal germlings, especially in the early spring. In contrast, in northern regions, where the water was colder, barnacles grew more slowly, and competitive effects on algal germlings were weaker, sometimes even switching to facilitative effects (Kordas and Dudgeon 2011).

The observation that species interactions can shift from negative to positive along latitudinal gradients is further supported by experiments conducted in salt marshes located north and south of Cape Cod (Bertness and Ewanchuk 2002). Interspecific competition plays a major role in structuring salt marshes in New England. Facilitation can also be important, however, because the shade produced by neighboring plants can reduce soil evaporation and thus prevent the development of potentially lethal hypersaline conditions (see Chapter 11). Bertness and Ewanchuk (2002) hypothesized that the sign of interactions between salt marsh plants would shift along a latitudinal gradient of solar radiation. In particular, facilitation was predicted to occur at lower latitudes, where greater solar radiation drives increased surface evaporation and salt stress. In contrast, competition was expected to occur at higher latitudes, where temperatures were cooler and solar radiation was weaker. To test this hypothesis, salt marsh plants were transplanted into plots with and without neighbors at sites north and south of Cape Cod. As predicted, plants generally benefited from neighbors in warmer southern

marshes. In contrast, in cooler northern marshes, interactions were neutral or competitive (Bertness and Ewanchuk 2002).

Influence of temperature on per capita predation and herbivory

Many species experience gradual latitudinal changes in temperature across much of their geographic range. Although these subtle changes in temperature may be well within a species' tolerance limits, they may have important influences on species interactions. Almost all marine fishes and invertebrates are ectotherms, so thermal variation in their environment has an enormous influence on their rates of metabolism, respiration, locomotion, and feeding (Clarke 1993; Hochachka and Somero 2002). An increase in body temperature of 5°C typically increases rates of biological processes by about 40–75% (given a typical Q_{10} of 2 to 3). These rate effects are well known to physiologists, but have been neglected in marine ecology, where temperature differences of a few degrees have often been considered inconsequential to community processes (reviewed by Sanford 2002). However, given the pervasive influence of temperature on animal physiology, per capita rates of consumption are predicted to increase with decreasing latitude.

Surprisingly few field studies have measured per capita feeding rates of marine consumers across latitudinal gradients. A study of the herbivorous ocean surgeonfish (*Acanthurus bahianus*) that compared individuals in Panama, Florida, and Brazil found that, as predicted, feeding rates (bites per minute) decreased with decreasing water temperature (Floeter et al. 2005). Similarly, observations

suggested that temperature might play a role in driving geographic variation in the feeding rates of the crown-of-thorns sea star (*Acanthaster planci*). Massive outbreaks of *Acanthaster* can devastate coral reefs in the Pacific, but the intensity of predation appears to vary geographically with water temperature. In Hawaii, where water temperatures are often below 25°C, an outbreak of *Acanthaster* spread little and had minimal effects on coral reefs. In contrast, in Guam, where temperatures are typically 28°C to 29°C, an *Acanthaster* outbreak killed 90 percent of corals inhabiting 38 km of coastline in less than 2 years (Birkeland and Lucas 1990). Additional studies showed that individual sea stars in Guam consumed about twice as much coral tissue as, and had movement rates five times greater than, sea stars in Hawaii (Birkeland and Lucas 1990).

Along the west coast of the United States, per capita feeding rates of a keystone predator, the sea star *Pisaster ochraceus*, were quantified at 14 rocky intertidal sites by transplanting standardized clumps of mussels into the low zone (Menge et al. 2004). There was no evidence of a latitudinal trend in per capita feeding rates along this coastline, where water temperatures were 5°C to 8°C warmer in southern California than at northern sites. Previous field and laboratory experiments had demonstrated that per capita feeding rates of *Pisaster* within a single region responded strongly to short-term changes in water temperature of 3°C to 4°C associated with wind-driven upwelling events (Sanford 1999). The absence of a latitudinal influence of temperature on *Pisaster* feeding suggests that this sea star might acclimatize to differing temperature regimes. In response to persistent differences in temperature in different portions of their geographic range, ectotherms may sometimes undergo physiological changes to minimize the influence of temperature on biological processes (Clarke 1993). Such acclimatization might dampen the influence of latitudinal gradients in temperature on rates of predation and herbivory. The observation that geographic variation in temperature appears to influence per capita rates of predation strongly in one sea star (*Acanthaster*), but not in another (*Pisaster*), raises unanswered questions about variation within and among taxa in the scope for acclimatization and the influence of this physiological process on species interactions.

Population density, community composition, and context dependency

Beyond the direct effects of gradients in temperature and other abiotic factors, latitudinal variation in the strength of species interactions is shaped by local differences in population densities and the structure of the surrounding community. Clearly, geographic variation in the abundances of interacting species plays a major role in driving density-mediated shifts in interaction strength. For example, in the study of *Pisaster* described above, the density of sea stars was found to be the primary determinant of total predation intensity at a given site (Menge et al. 2004).

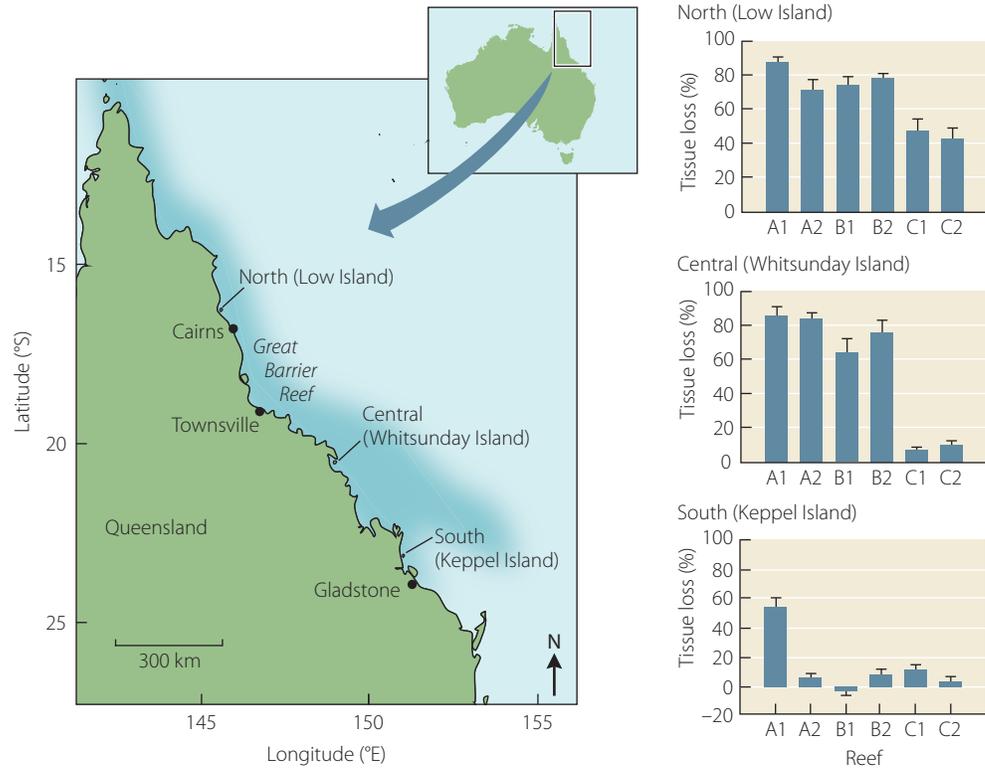
The abundance of *Pisaster* is patchy and highly variable along the west coast of North America, even among sites separated by tens of kilometers (Paine 1976; Sagarin and Gaines 2002a; Menge et al. 2004). These abundance patterns appear to be stable over long time intervals (Paine 1976), suggesting consistency in the factors that maintain “hot spots” of abundance in this species (see p. 141). Given the community importance of this keystone predator, there is a strong need to understand the mechanisms that drive and maintain among-site variation in its abundance across its geographic range (Menge and Sanford 2013).

Likewise, the abundance of prey can play an important role in driving geographic variation in interaction strength. For example, Paine’s classic experiments on the coast of Washington State established that *Pisaster* could play a keystone role by controlling the competitively dominant mussel *Mytilus californianus* (Paine 1966). Paine (1980) speculated, however, that in Torch Bay, Alaska, located over 1100 km to the north, *Pisaster* was “just another starfish.” The geographic change in this sea star’s role was attributed to *M. californianus* becoming increasingly less abundant near its poleward geographic range boundary. In the absence of a strong trophic link to an abundant, competitively dominant prey species, the community importance of *Pisaster* appeared to be diminished considerably in Alaska (Paine 1980).

In some cases, latitudinal variation in the intensity of predation or herbivory can arise through differences in the species composition of the consumer assemblage. For example, cordgrass (*Spartina alterniflora*) dominates the mid- and low intertidal zones of salt marshes along most of the Atlantic coast of the United States. Field surveys of grasshopper feeding damage and snail enclosure experiments demonstrated that herbivory on cordgrass was higher in salt marshes at lower latitudes (Pennings and Silliman 2005). These latitudinal differences were in part due to differences in the composition of the herbivore assemblages. For example, the most common snail at the northern sites (*Melampus bidentatus*) was found not to graze on cordgrass. In contrast, cordgrass was grazed heavily at the southern sites by a snail (*Littoraria irrorata*) that did not occur at the northernmost sites (Pennings and Silliman 2005).

Finally, a study of coral reef fish herbivory illustrates how geographic variation in a focal species interaction can be influenced by differences in the surrounding community (Bennett and Bellwood 2011). Experimental assays were used to measure rates of fish herbivory on a brown alga (*Sargassum*) in three regions spanning 900 km of the Great Barrier Reef, Australia (Figure 7.13). Rates of fish herbivory declined dramatically from low- to high-latitude sites. This decline in herbivory was unrelated to a gradient of water temperature, since the timing of the experiments was staggered slightly so that mean temperatures in all regions were 26°C to 27°C. The four most common herbivorous fishes were also identical in each of the regions. The latitu-

Figure 7.13 Geographic variation in fish herbivory on the Great Barrier Reef, Australia. Bars show the mean percentage of algal tissue (*Sargassum*) consumed (+SE) in the field during 4.5-hour assays. Experiments were conducted on three fringing reefs in a northern, central, and southern region. On each reef, assays were conducted in two replicate locations (e.g., A1 and A2). Herbivory was significantly lower in the southern region. (After Bennett and Bellwood 2011.)



dinal variation in herbivory appeared to be driven by differences in the propensity to feed; at higher latitudes, fish were three to four times less likely to feed when they approached the transplanted algae. This difference in feeding behavior appeared to be shaped by geographic differences in the surrounding community, such as the presence or absence of other algal species or the topographic complexity and protection provided to fish by the local coral assemblage (Bennett and Bellwood 2011).

The role of variation in recruitment

A growing number of comparative experiments like those described on pp. 147–150 demonstrate the sources of context dependency that shape geographic variation in a given species interaction. A consistent conclusion from many of these studies is that geographic variation in the effects of consumers can depend less on differences in their feeding rates than on variation in the recruitment or growth of their prey. For example, after being hunted to near-extinction in the North Pacific, sea otters recolonized the Aleutian Islands and Southeast Alaska, two regions separated by over 2500 km. Estes and Duggins (1995) found that the return of sea otters to Southeast Alaska led to massive declines in their sea urchin prey, followed by large increases in kelp density. In contrast, sites in the Aleutian Islands supported dense sea urchin populations whether otters had recolonized them or not, and kelp density showed little change following the return of otters. This geographic variation in the outcome of the sea otter–urchin interaction was attributed to large differences in the recruitment of sea urchins. Small sea urchins were abundant throughout the Aleutian Islands, and urchins

reached high population densities even in the presence of sea otters. In contrast, small urchins were virtually absent from Southeast Alaska, where recruitment appeared to be highly episodic, perhaps due to unknown differences in oceanographic processes (Estes and Duggins 1995).

Prey recruitment appears to have an analogous influence on latitudinal variation in the effects of intertidal predators along the coast of Chile (Navarrete et al. 2005). To quantify predation by sea stars (*Heliaster helianthus*) and whelks (*Concholepas concholepas*), standardized clumps of mussels were transplanted into the intertidal zone at seven sites spanning 900 km on the central coast of Chile (Figure 7.14A). Rates of predation on the transplanted mussels were found to be similar across all sites (Figure 7.14B). After experimental exclusion of predators, however, mussels increased rapidly at southern sites, but were nearly absent from northern sites (Figure 7.14C). This difference in the effects of predators appeared to result from a latitudinal gradient in mussel recruitment (Broitman et al. 2001). In particular, mussel recruitment was orders of magnitude higher at southern sites than at northern sites. This break corresponded to an oceanographic discontinuity in upwelling at 32° S latitude, as lower mussel recruitment was associated with stronger and more persistent coastal upwelling in the northern region (Navarrete et al. 2005).

A final example of how recruitment can modulate the latitudinal effects of consumers is provided by experiments on limpet grazing conducted in Europe. To quantify variation in the effects of herbivorous limpets, identical experiments were conducted in five regions spanning over 1800 km (Coleman et al. 2006). Intertidal plots were estab-

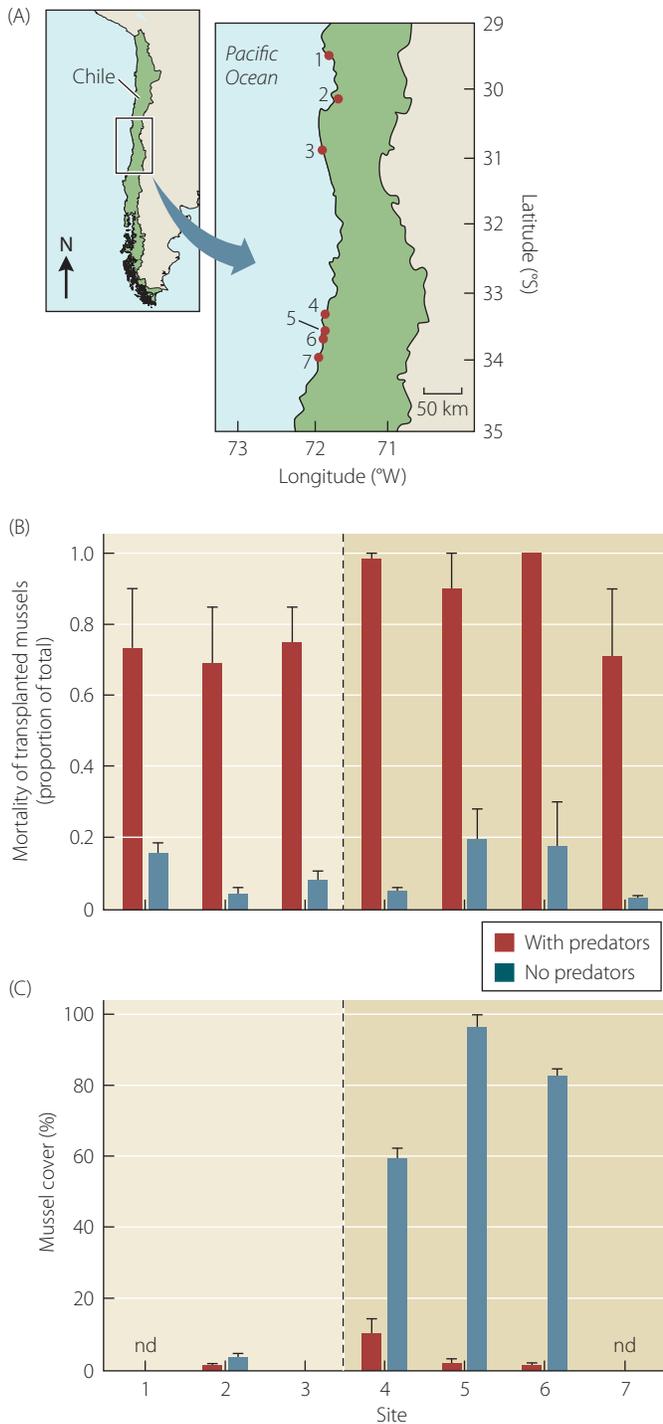


Figure 7.14 Geographic variation in effects of predators along the central coast of Chile. (A) Map of the seven study sites, including sites north and south of a biogeographic break in mussel recruitment at 32° S. (B) Mean mortality (+SE) of clumps of mussels transplanted into the intertidal zone in the presence and absence of predators. (C) Effect of predator exclusion on the cover of mussels colonizing cleared plots after 3 months. Vertical dashed lines separate sites north and south of 32° S. nd = no data. Although predation rates were similar across all sites, removal of predators did not lead to an increase in mussels in the northern region, where mussel recruitment was low. (After Navarrete et al. 2005.)

lished, and limpets (*Patella* spp.) were excluded from some of the plots to quantify their influence on algal establishment relative to control plots. Limpet removal increased algal abundance at all sites, but this effect was strongest in northern regions, where limpet removal led to rapid proliferation of canopy algae. In contrast, the effects of limpet removal were minimal in southern regions (Coleman et al. 2006). This geographic difference in the effects of limpets was counter to patterns of grazing activity: as expected, feeding activity (i.e., radular scrapes) generally increased with water temperature from northern to southern regions (Jenkins et al. 2001). Limpet density was also the same or higher in southern regions than in northern regions (Jenkins et al. 2001; Coleman et al. 2006). However, fucoïd algae were sparse in southern regions, which was hypothesized to limit the supply of reproductive propagules (Jenkins et al. 2005; Coleman et al. 2006). Thus, although limpets were abundant and more active in warmer southern regions, release from intense limpet grazing did not trigger a rapid response in algal abundance, perhaps because of limited algal recruitment in this region. A similar role of algal recruitment in mediating regional variation in herbivore effects was also suggested by intertidal experiments conducted in the northwestern Mediterranean (Benedetti-Cecchi et al. 2001).

Geographic mosaics of selection

Although often neglected in marine community ecology, evolutionary processes can play an important role in shaping latitudinal variation in the interactions between a given pair of species (Thompson 1999; Sanford et al. 2003). The potential for selection to drive adaptive divergence among marine populations has not been well studied in marine systems, in part because of the historical view that population connectivity and gene flow among most populations is high. However, a growing body of evidence suggests that local adaptation occurs in a variety of marine fishes and invertebrates, including those with planktonic dispersal (reviewed by Conover et al. 2006; Sanford and Kelly 2011).

Terrestrial ecologists have led the way in exploring how spatial variation in natural selection across a landscape can shape the strength of species interactions (Thompson 1999). Theory and empirical results from terrestrial studies suggest that a geographic mosaic of varying physical and biotic conditions can create a landscape of “hot spots” and “cold spots” where selection on a given species interaction is either strong or weak (Thompson 1999). The most extreme cold spots frequently occur in regions where one member in a pair of interacting species is absent.

Such geographic mosaics of selection can also shape variation in species interactions in marine ecosystems (Stachowicz and Hay 2000; Sotka and Hay 2002; Sanford et al. 2003; Freeman and Byers 2006). For example, Sotka and Hay (2002) explored latitudinal variation in patterns of herbivory by the amphipod *Ampithoe longimana* along the Atlantic coast of the United States. In the southern portion

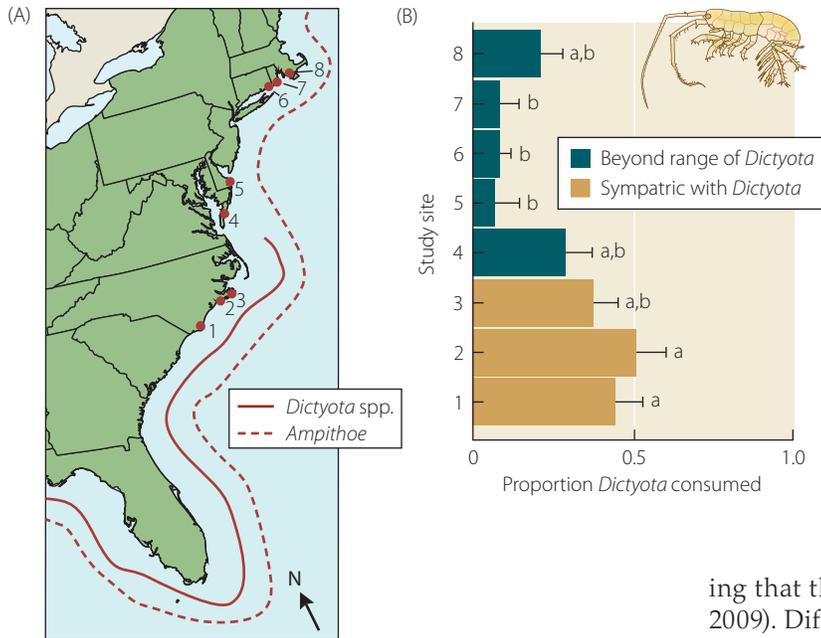


Figure 7.15 Geographic variation in the algal preference of the amphipod *Ampithoe longimana*. The map shows the locations of eight study sites along the Atlantic coast of the United States as well as the geographic ranges of *Ampithoe* and the chemically defended algae *Dictyota* spp. Bars show the mean proportion of *Dictyota* consumed (+SE) in laboratory assays in which *Ampithoe* were given an equal amount of a highly palatable alga (*Ulva* sp.). Shared letters to the right of bars indicate populations whose means do not differ (Tukey-Kramer, $p > 0.05$). Amphipods from southern populations generally consumed more *Dictyota* than those from northern populations beyond the range limit of the algae. (After Sotka et al. 2003.)

of its geographic range, *Ampithoe* avoids intense predation by omnivorous fishes by associating with the chemically rich alga *Dictyota menstrualis*. This algal species, however, is absent from the northern portion of the amphipod's geographic range, where fish predation is also less intense. Laboratory feeding assays demonstrated that amphipods from southern populations fed more readily on *Dictyota* (Figure 7.15) and were more tolerant of its defensive compounds than amphipods from northern populations (Sotka and Hay 2002; Sotka et al. 2003). Moreover, this difference among populations appeared to have a genetic basis, as it persisted after amphipods were reared through multiple generations in the laboratory. These results, and those of other studies (e.g., Stachowicz and Hay 2000; Freeman and Byers 2006), suggest that nonoverlapping geographic ranges of interacting species can create variation in the intensity of selection, which in turn can promote divergence in the strength of species interactions (Thompson 1999).

Theory and empirical results from terrestrial systems also suggest that the strength of selection on a given species interaction can be modified by the relative abundance of other species in the community (Benkman et al. 2001; Thompson and Cunningham 2002). A study of a marine predator–prey interaction is also consistent with this view (Sanford et al. 2003). Along the Pacific coast of the United States, predatory dogwhelks (*Nucella canaliculata*) live within beds of the intertidal mussel *Mytilus californianus*. Laboratory feeding assays and field surveys demonstrated that snails from southern populations readily drilled the thick-shelled *M. californianus*. In contrast, snails from northern populations were generally unable to drill this species and instead fed on acorn barnacles and blue mussels. These different drilling capacities persisted in snails reared through two generations in the laboratory, suggest-

ing that they are genetically based (Sanford and Worth 2009). Differences in drilling capacity among snail populations may reflect selection imposed by persistent spatial variation in prey recruitment along the coast. In particular, recruitment of preferred prey (acorn barnacles and blue mussels) was orders of magnitude lower at southern than at northern sites (Connolly et al. 2001). Therefore, the scarcity of preferred prey at southern sites may have selected strongly for snails able to drill large, thick-shelled *M. californianus*. A field experiment that reciprocally transplanted lab-reared whelks to enclosures at northern and southern sites supported this hypothesis and suggested that the capacity of southern whelks to drill *M. californianus* allows them to succeed in an oceanographic region where recruitment of alternative prey is consistently low (Sanford and Worth 2010). More broadly, these and other related studies in marine systems (e.g., Fawcett 1984; Trussell 2000; Freeman and Byers 2006) suggest that the strength of predator–prey interactions may vary geographically in response to spatially varying selection imposed by nonoverlapping geographic ranges and differing abundances of both the focal species and other members of the community.

Tropical–temperate comparisons of species interactions

At a global scale, several long-standing hypotheses suggest that predation and herbivory are more intense at low than at high latitudes, and that this difference may contribute to higher species diversity in the tropics (reviewed by Schemske et al. 2009). For example, Paine (1966) suggested that productivity is more stable in the tropics, promoting the evolution of a greater number of predator species. More predators in the tropics are expected to increase predation intensity, and over evolutionary time, stronger predation may reduce competitive exclusion among lower trophic levels, promoting speciation (Paine 1966). Several alternative hypotheses have also incorporated stronger biotic interactions as a driving force in the

evolution of greater species diversity in the tropics (Vermeij 2005; Schemske et al. 2009).

There have been relatively few empirical tests of whether predation is stronger in tropical than in temperate marine systems. Early comparative experiments conducted in rocky intertidal communities in Panama and New England generally supported this hypothesis. These experiments suggested that, in marked contrast to New England, prey in Panama relied on refuge microhabitats (holes and crevices) to avoid intense predation from fast-moving consumers (including fish) that foraged throughout the year (Menge and Lubchenco 1981; see also Heck and Wilson 1987; Freestone and Osman 2011). Additional experiments demonstrated that fish predation on intertidal gastropods was dramatically higher in Panama than in New England (Bertness et al. 1981). More recently, an experiment tested whether the influence of predation on fouling communities of sessile invertebrates was greater in tropical than in temperate systems (Freestone et al. 2011). Identically designed predator exclusion experiments were conducted in four regions distributed across 32 degrees of latitude along the west coast of the Atlantic. In each region, community development on settlement panels was quantified in the presence and absence of predators. Excluding predators had no effect on species richness in the temperate and subtropical regions, but species richness increased by two to more than ten times in the tropics when predators were excluded (Freestone et al. 2011).

Other studies have considered whether latitudinal patterns of algal species richness are related to geographic variation in the intensity of herbivory. The relationship between algal species richness and latitude varies among different regions of the globe, and sometimes between different sides of continents (Gaines and Lubchenco 1982; Santelices et al. 2009). For example, algal species richness increases at low latitudes on the east coast of North and Central America. In contrast, on the west coast of North and Central America, peak richness occurs at mid-temperate latitudes (Figure 7.16). Gaines and Lubchenco (1982) argued that these patterns were due in part to latitudinal variation in the strength of herbivory. They suggested that, overall, herbivory was greater in tropical than in temperate marine systems. However, they hypothesized that on the tropical east coast of North and Central America, extensive refuges from herbivores are common, promoting greater algal diversity. In contrast, on the tropical west coast, refuges from large foraging fish are rare, and the resulting intense herbivory may keep algal diversity low (Gaines and Lubchenco 1982).

Is there empirical support for stronger herbivory in the tropics? Poore and colleagues (2012) analyzed the published results of 613 field experiments that quantified the in situ effects of excluding marine herbivores in a variety of temperate and tropical marine ecosystems. As expected, herbivores were found to have strong negative effects on primary producers throughout the world. However,

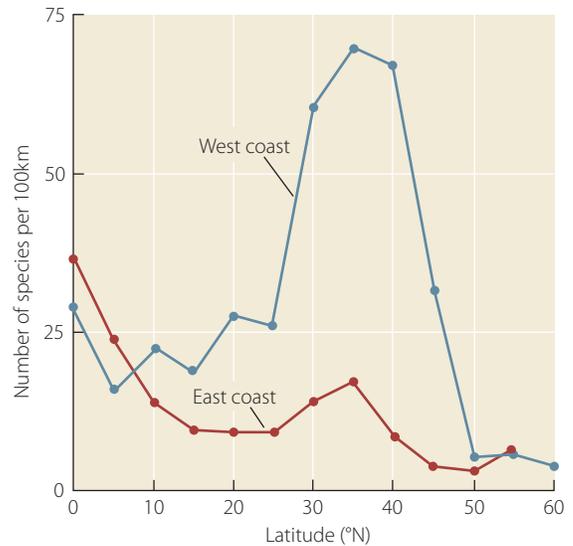


Figure 7.16 Latitudinal variation in algal species richness per 100 km of coastline on the east and west coasts of North and Central America. On the east coast, algal richness peaks in the tropics, whereas algal richness peaks at mid-temperate latitudes on the west coast. (After Gaines and Lubchenco 1982.)

the effect of herbivores actually decreased slightly from temperate to tropical latitudes, although this relationship was weak (Figure 7.17). Why did these analyses not suggest stronger herbivore effects in the tropics, given abundant evidence that grazers are more diverse, active, and

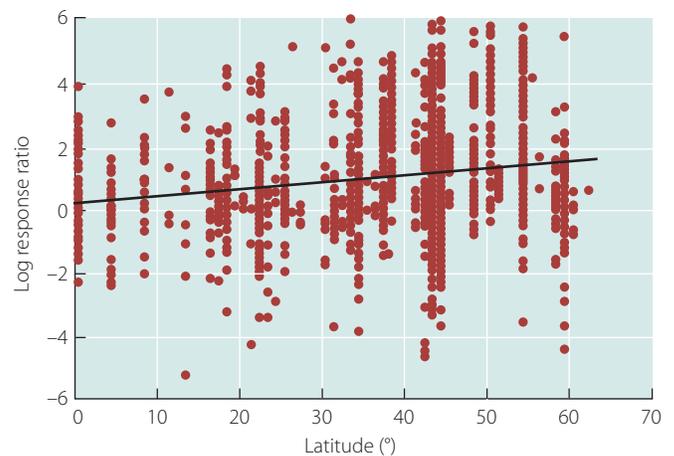


Figure 7.17 Latitudinal variation in the effects of excluding herbivores. Results are from a meta-analysis of 613 experiments. The log response ratio is calculated as $\ln(X_e/X_c)$, where X_e is the mean producer abundance from the grazer exclusion treatment and X_c is the mean producer abundance from the control (with herbivores present). Positive values of the log response ratio indicate that grazer exclusion increased producer abundance. The herbivore effect increased slightly with increasing latitude, although this relationship explained very little of the overall variance ($p < 0.001$, $R^2 = 0.02$). (After Poore et al. 2012.)

effective in tropical than in temperate regions (Vermeij 1978; Menge and Lubchenco 1981; Gaines and Lubchenco 1982)? One possible explanation is that these analyses examined the effect of grazers as the ratio of producer abundance in plots with grazers excluded versus grazers present. This ratio is influenced by both rates of herbivory and rates of producer growth. In temperate areas, where producers are often more abundant and nutrient levels are higher, there may be greater potential for a positive response of producers when grazers are removed. In addition, evidence suggests that over evolutionary time scales, intense herbivory has selected for increased chemical and morphological defenses among algae and plants found at lower latitudes (Gaines and Lubchenco 1982; Bolser and Hay 1996; Pennings et al. 2001). Therefore, well-defended producers at low latitudes may respond less strongly to the absence of grazers than would otherwise be expected (Pennings et al. 2001), a scenario that has been called “the ghost of herbivory past” (Poore et al. 2012). These results emphasize that evolutionary history and species traits can help shape variation in the outcome of species interactions over broad geographic scales (Vermeij 1978; Paine et al. 1985; Pennings et al. 2003; Poore et al. 2012).

Implications and future directions

A growing body of studies demonstrates that the strength and sign of species interactions can vary over the geographic ranges of marine species. In some cases, variation in interaction strength appears to be largely predictable based on latitudinal gradients of environmental stress. In other cases, patterns of geographic variation in species interactions are spatially complex and context dependent, driven by environmental mosaics and varying densities of consumers, their prey, and members of the surrounding community. Physiological acclimatization and local adaptation can also modify the local strength of species interactions, although these processes have not been well studied in marine systems.

Comparisons of species interactions in tropical versus temperate systems have quantified community responses to the removal of consumers (e.g., Menge and Lubchenco 1981; Poore et al. 2012), but the mechanisms underlying these responses are not well understood. For example, are greater effects of predator removals in tropical than in temperate systems due to higher per capita predation rates (e.g., related to warmer temperatures), or to a greater abundance or diversity of predators (Menge and Lubchenco 1981)? Or might differences in the colonization of bare plots following consumer removal be a function of latitudinal differences in the diversity, recruitment, growth, and defenses of algae and sessile prey (Edwards et al. 2010; Poore et al. 2012)? Although logistically challenging, additional experiments that tease these mechanisms apart would be informative.

From a conservation perspective, there is little doubt that the top-down effects of consumers can have a pro-

found influence on marine communities. The strength of these effects can vary greatly among geographically separated communities, however, presenting challenges for managers who may wish to apply research conclusions from distant sites to their local areas. With these thoughts in mind, future investigations of the ecological and evolutionary processes that modulate the strength of species interactions are likely to lead to more effective management of marine ecosystems (Estes and Duggins 1995; Sanford et al. 2003; Navarrete et al. 2005; Connell and Irving 2008).

Local versus Regional Effects on Species Richness

Marine community ecologists have long emphasized the influence of species interactions on the local species diversity of communities. This is not surprising, given that a large body of manipulative field experiments has demonstrated that predation, herbivory, competition, and facilitation can have striking effects on community structure. However, since the 1980s, it has been recognized that variation among marine communities can seldom be explained by differences in local species interactions alone (Dayton and Tegner 1984; Underwood and Denley 1984). For example, oceanographic processes operating over regional spatial scales can drive variation in larval recruitment and nutrient inputs, with profound effects on community structure (Roughgarden et al. 1988; Menge et al. 1997, 2003; Navarrete et al. 2005). In addition, ecologists have become increasingly aware that historical and evolutionary processes operating at large spatiotemporal scales can also shape community structure (Harrison and Cornell 2008).

Key to these considerations is the question of how strongly local diversity is influenced by the size of the regional species pool relative to local species interactions. The concept that local diversity is shaped by regional processes through dispersal has its roots in MacArthur and Wilson’s (1967) classic theory of island biogeography (Cornell and Harrison 2013). This theory emphasized that species diversity in a local community (in this case, an island) was partly a function of immigration from the regional species pool, which varied with distance from the mainland. More recently, plots of the relationship between local species richness in a community and regional species richness have been used to explore the relative importance of local species interactions (e.g., competition) versus regional-scale processes (e.g., the influence of history and macroevolution). Theory predicts that if species interactions have a controlling influence on species diversity, there should be an asymptotic relationship between local species richness and the size of the regional species pool (reviewed by Witman et al. 2004; Russell et al. 2006; Cornell et al. 2008). This relationship implies that with the inclusion of additional species, communities become saturated due to competition and the limits imposed by niche

packing. In contrast, a pattern in which local species richness increases as a linear function of the regional species pool suggests that communities are not saturated and that the regional species pool has an important influence on species diversity.

This theoretical approach has been criticized for a number of reasons, including methodological and statistical concerns as well as the existence of alternative explanations for relationships between local and regional richness (reviewed by Harrison and Cornell 2008). Many of these criticisms have been addressed through improved sampling designs and analyses (Cornell and Harrison 2013). In general, there is agreement that a positive relationship between local and regional richness provides evidence that local communities are open to regional enrichment, while not precluding the possibility that local interactions are also important (Witman et al. 2004; Cornell et al. 2008; Harrison and Cornell 2008). Exploration of the relationship between local and regional species richness provides an important foundation for additional investigations of the mechanisms influencing local community structure (Cornell et al. 2008).

Tests of community saturation and regional enrichment in marine systems

Compared with terrestrial systems, there have been relatively few tests of the relationship between local and regional species richness in marine systems (Hillebrand and Blenckner 2002). Two of the most thorough tests of this relationship are highlighted in this section. First, Witman and colleagues (2004) sampled the diversity of invertebrates on subtidal rock wall communities in twelve

regions distributed throughout much of the world (**Figure 7.18**, **Figure 7.19A**). Their study avoided many of the methodological criticisms that have been raised regarding experimental tests of community saturation. In particular, Witman and colleagues studied species found within a single habitat (subtidal rock walls), sampled at the small scale characteristic of competitive interactions among benthic invertebrates, and replicated their sampling in many regions of the globe to include regional pools of species richness that ranged from relatively small to very large. As expected, species richness was highest in the tropics and declined at higher latitudes (**Figure 7.19B**). Their analyses also revealed a striking linear relationship between the regional species pool and local species richness, with no evidence of saturation (**Figure 7.19C**). These results suggest that the number of species in local communities is influenced by the size of the regional species pool, and is not just a function of local species interactions such as competition (Witman et al. 2004).

A second important study of the influence of regional enrichment focused on coral diversity in the west-central Pacific (Cornell et al. 2008). This study was specifically designed to address concerns about the influence of sampling scale on the relationship between local and regional species richness (Rivadeneira et al. 2002; Russell et al. 2006). In particular, local species richness may be underestimated in species-rich regions if sampling in small plots often fails to capture rare species. Moreover, the regional species pool may be overestimated if local richness is sampled in a single habitat, but regional richness is drawn from taxonomic literature that compiles species diversity across multiple habitats, thereby including

groups of species that do not interact ecologically (Russell et al. 2006; Harrison and Cornell 2008). Saturating or curvilinear relationships between local and regional richness are more likely to arise as a sampling artifact when the local scale is small relative to the regional scale, a problem that has been termed “pseudosaturation” (Hillebrand and Blenckner 2002; Cornell et al. 2008). One solution to these challenges is to examine the relationship between local and regional richness at multiple spatial scales, thereby avoiding biases created by arbitrarily defining the local scale



Figure 7.18 A diverse community of invertebrates living at a depth of 15 m on a vertical rock wall at South Lion's Paw, a research site off the west coast of South Africa. Included in the photograph are soft corals, sponges, bryozoans, tube worms, sea anemones, and mussels. (Courtesy of Jon D. Witman.)

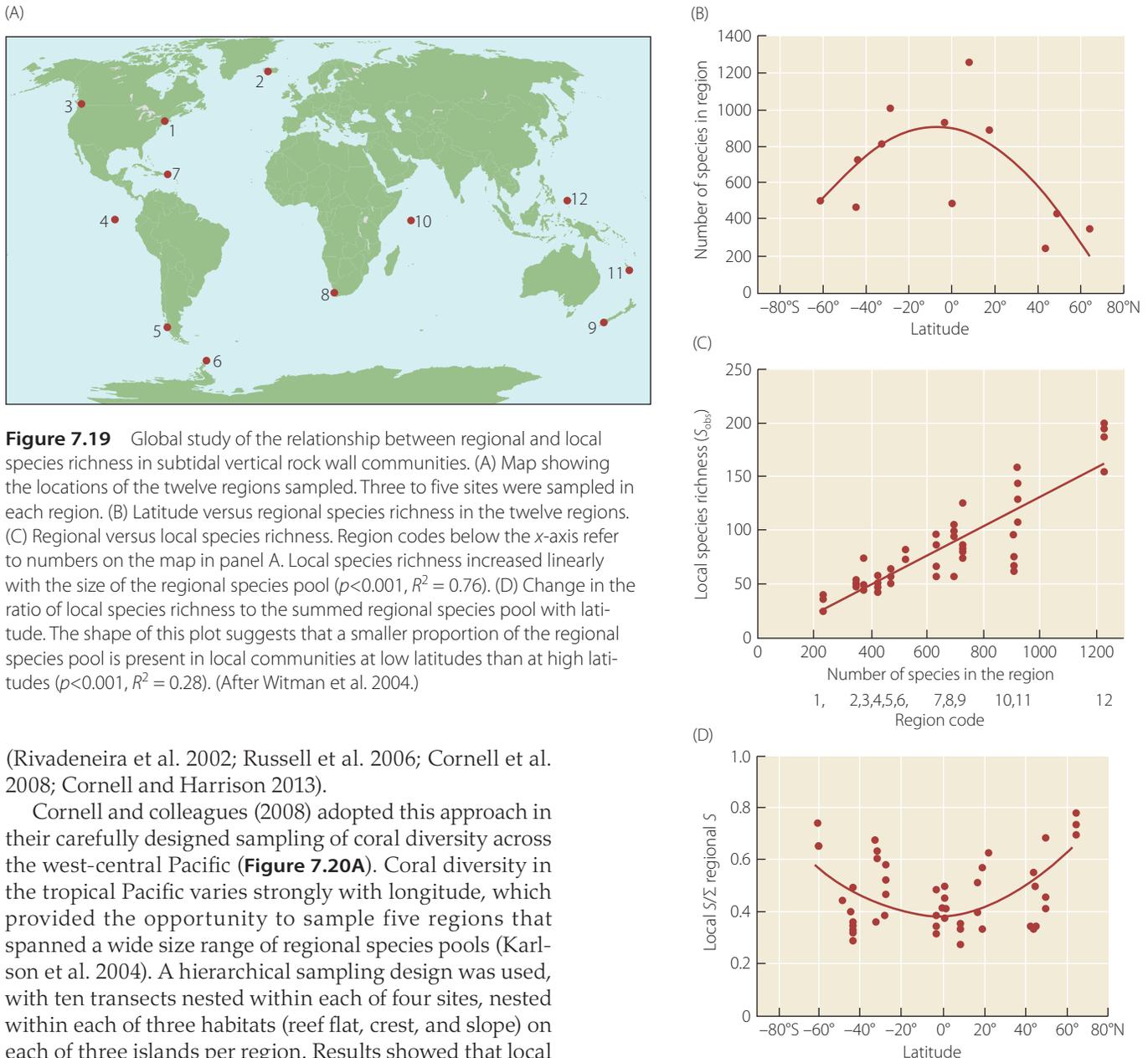


Figure 7.19 Global study of the relationship between regional and local species richness in subtidal vertical rock wall communities. (A) Map showing the locations of the twelve regions sampled. Three to five sites were sampled in each region. (B) Latitude versus regional species richness in the twelve regions. (C) Regional versus local species richness. Region codes below the x-axis refer to numbers on the map in panel A. Local species richness increased linearly with the size of the regional species pool ($p < 0.001$, $R^2 = 0.76$). (D) Change in the ratio of local species richness to the summed regional species pool with latitude. The shape of this plot suggests that a smaller proportion of the regional species pool is present in local communities at low latitudes than at high latitudes ($p < 0.001$, $R^2 = 0.28$). (After Witman et al. 2004.)

(Rivadeneira et al. 2002; Russell et al. 2006; Cornell et al. 2008; Cornell and Harrison 2013).

Cornell and colleagues (2008) adopted this approach in their carefully designed sampling of coral diversity across the west-central Pacific (**Figure 7.20A**). Coral diversity in the tropical Pacific varies strongly with longitude, which provided the opportunity to sample five regions that spanned a wide size range of regional species pools (Karlson et al. 2004). A hierarchical sampling design was used, with ten transects nested within each of four sites, nested within each of three habitats (reef flat, crest, and slope) on each of three islands per region. Results showed that local versus regional richness plots did not vary among the reef flat, crest, and slope habitats, so these data were pooled for analysis. The shape of the relationship between local and regional richness was evaluated at three scales: the island, the site, and a single transect (10 m line). The results were consistent and striking: at all scales, the relationship between local and regional richness was linear, with no saturation observed (**Figure 7.20B–D**). These results suggest that regional processes can influence local richness even in small areas (i.e., 10 m transects) within the most species-rich regions of the tropics (Cornell et al. 2008).

These findings (Witman et al. 2004; Cornell et al. 2008) suggest the need for a greater integration of community ecology and historical biogeography (Wiens and Donoghue 2004; Harrison and Cornell 2008). There is evidence

that modern coastal faunas bear a signature of historical events and evolutionary processes (e.g., Rex et al. 2005). For example, the size of the regional species pool is influenced by rates of basin-scale speciation, adaptive radiation, and extinction (Roy and Witman 2009). There has also been an increased focus on identifying the ancestral ecological niches of clades and their potential for niche evolution, along with the geographic origins of clades and their potential for dispersal from those origins (Wiens and Donoghue 2004). The influence of many of these processes on the size of the regional species pool can be addressed using improved phylogenetic and paleontological analyses (reviewed by Harrison and Cornell 2008; Roy and Witman 2009).

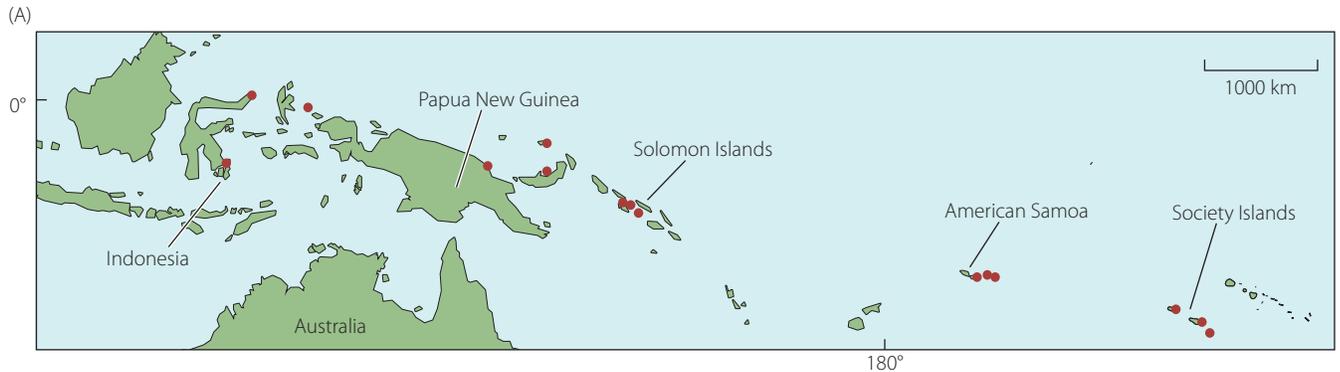
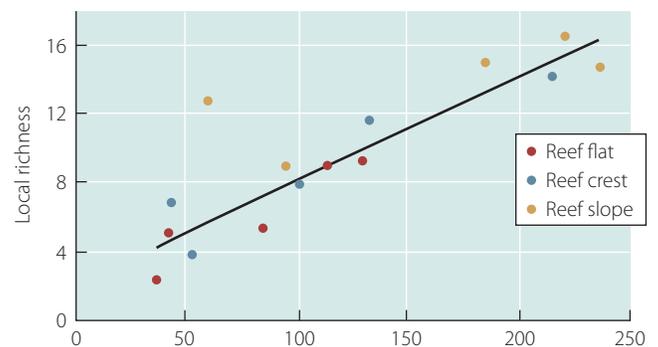


Figure 7.20 The relationship between regional and local species richness of corals across the west-central Pacific. (A) Map showing the three islands (red symbols) studied in each of five regions (from left to right): Indonesia, Papua New Guinea, the Solomon Islands, American Samoa, and the Society Islands of French Polynesia. (B–D) Relationships between the regional species pool and average local richness of corals plotted at three spatial scales: (B) 10 m transect, (C) site, and (D) island. Data points are coded by habitat type (reef flat, crest, or slope). All linear regressions were significant ($p < 0.001$), indicating regional enrichment of local diversity at all spatial scales. (After Karlson et al. 2004 and Cornell et al. 2008.)

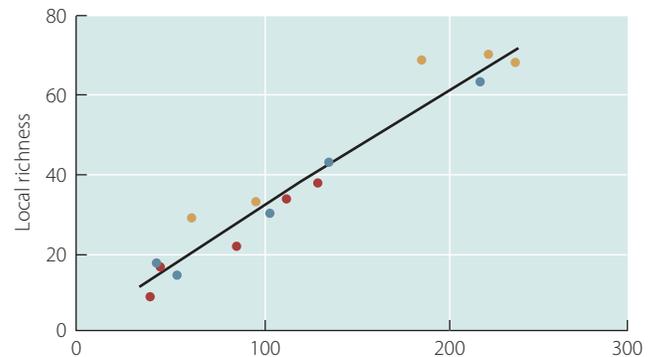
Latitudinal variation in local species interactions versus regional enrichment

Although they provide evidence of regional enrichment, the studies just summarized do not suggest that species interactions are unimportant in regulating local species richness. Indeed, analyses of rocky intertidal communities (Rivadeneira et al. 2002; Russell et al. 2006) suggest that the influence of the regional species pool diminishes at the small spatial scales characteristic of species interactions (although these are also the scales at which the potential for pseudosaturation is the greatest; Cornell et al. 2008). Interestingly, Witman and colleagues (2004) showed that regional enrichment of the local species pool was weaker in the tropics than at higher latitudes (**Figure 7.19D**). Although several alternative hypotheses have been proposed to explain this pattern, one explanation is that higher diversity in tropical systems leads to increased competitive interactions at local spatial scales, reducing the influence of the regional species pool (Witman et al. 2004). A recent field experiment conducted across 25 degrees of latitude supported the hypothesis that local species interactions are stronger at lower latitudes, leading to communities that are less open to enrichment from the regional species pool (Freestone and Osman 2011). However, the authors hypothesized that their results arose not from increased competition in the tropics, but rather from greater predation intensity, which limited community membership and thus reduced the potential for regional enrichment (Freestone and Osman 2011).

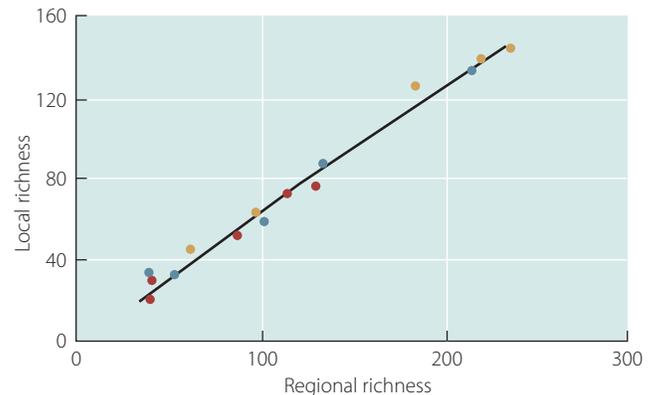
(B) Transect scale



(C) Site scale



(D) Island scale



Implications and future directions

Although the question is still being debated, evidence from marine systems suggests that the size of the regional species pool has an important influence on local species richness (Karlson et al. 2004; Witman et al. 2004; Cornell et al. 2008). This finding underscores the open nature of marine communities and highlights the need for increased attention to the historical and evolutionary processes that shape regional species pools. One of the most important results of this research is the observation that the relative influence of regional enrichment on local species richness varies with latitude (Witman et al. 2004). Given growing evidence that the strengths of species interactions often vary latitudinally as well (see p. 147, *Latitudinal Variation in Species Interactions*), these observations suggest intriguing hypotheses regarding interactions among latitude, species interactions, regional species pools, and local species richness (Witman et al. 2004). Russell and colleagues (2006) advocated comparative experiments that simultaneously quantify local interaction strengths and the size of the regional species pool, and results from such experiments have been informative (Freestone and Osman 2011). Historical data from highly invaded marine communities might also provide tests of whether increases in the regional species pool have led to concomitant increases in local species diversity (Sax and Gaines 2008). Future investigations of these questions promise to advance our understanding of the links among biogeography, regional processes, and the dynamics of local communities.

The discovery that regional processes have strong and pervasive influences on local species richness also has important implications for marine conservation (Witman et al. 2004; Karlson et al. 2004). If even diverse communities are rarely saturated, most marine communities may be susceptible to invasion (Witman et al. 2004). From a management perspective, the strong influence of regional processes on local communities suggests the importance of international coordination and cooperation (Karlson et al. 2004). Given increasing evidence that many local marine communities are linked by dispersal and function as metacommunities, management planning that considers local processes alone is likely to be insufficient and ineffective (Karlson et al. 2004; Connell and Irving 2008; Harrison and Cornell 2008).

CONCLUSIONS

This chapter highlights advances toward a new synthesis of marine biogeography and community ecology. The integration of approaches from biogeography, ecology, evolutionary biology, physiology, and oceanography has begun to yield novel insights into how and why marine communities vary over geographic spatial scales. It is worth noting that biogeography's traditional emphases on descriptions of spatial patterns and systematics continue to provide a critical foundation for this progress. In

recent decades, funding agencies, scientific journals, and even ecologists themselves have often downplayed the value of descriptive studies and taxonomy (for commentaries, see Underwood et al. 2000; Dayton 2003). However, taxonomic knowledge and accurate descriptions of how community structure varies over large spatial scales are essential precursors to addressing most of the ecological and evolutionary processes discussed in this chapter.

Four major themes emerge from this chapter. First, geographic variation at all levels of ecological organization, from individual performance to populations to communities, is often associated with environmental gradients. Recent work reaffirms biogeography's long-standing attention to latitudinal gradients in temperature. However, although temperature is undeniably influential, it is also clear that temperature is only one of many factors shaping geographic variation in marine communities. Mechanistic studies demonstrate the importance of variation in dispersal, life history, physiology, population demographics, species interactions, local adaptation, and evolutionary history in driving striking differences in marine communities over broad spatial scales.

This points to a second theme: the underappreciated role of dispersal in generating biogeographic patterns. Although it is challenging to study, the influence of dispersal appears to be pervasive and important. For example, recent studies suggest that many range boundaries may arise not from thermal limits, but from complex interactions among larval dispersal, temperature, coastal currents, habitat availability, life history, and population demographics (e.g., Gaylord and Gaines 2000; Zacherl et al. 2003; Gilman 2006; Sanford et al. 2006; Byers and Pringle 2006). Dispersal and gene flow among populations also shape the potential for local adaptation to abiotic and biotic variation across species' geographic ranges (Sanford and Kelly 2011). At the community level, geographic variation in dispersal and prey recruitment can determine the strength of key species interactions (Estes and Duggins 1995; Connolly and Roughgarden 2001; Navarrete et al. 2005). Evidence also suggests that dispersal links local communities to one another and to the regional species pool (Witman et al. 2004; Cornell et al. 2008). There is growing recognition that the size of the regional species pool is itself influenced by dispersal processes acting over evolutionary time scales as clades spread from their regions of origin (Wiens and Donoghue 2004). These observations suggest that a better understanding of dispersal in the sea, across a broad range of spatial and temporal scales, is essential to understanding geographic variation in marine communities. Despite the significant challenges of studying dispersal, new tools and approaches from larval biology, coastal oceanography, population genetics, and genomics offer hope for continued progress in this critical area (see Chapter 4).

Third, throughout this chapter, the importance of incorporating evolution into our understanding of biogeog-

graphic variation in communities is evident. Although frequently neglected in marine community ecology, evolutionary processes help shape geographic variation in marine communities at a variety of levels (Vermeij 1978). There is renewed interest in the role of evolutionary processes in maintaining species' range boundaries. Local adaptation to abiotic and biotic mosaics can also generate substantial divergence among geographically separated populations in physiology, life history, and feeding capacity, complicating attempts to extrapolate from local to broader spatial scales (Sanford and Bertness 2009). Over longer temporal scales, there is growing evidence that many marine communities retain a strong signature of evolutionary processes and historical events (Roy and Witman 2009). For example, niche conservatism within clades may influence the range boundaries of modern taxa (Roy et al. 2009) and their susceptibility to consumers (Poore et al. 2012). Similarly, rates of speciation can have a lasting influence on the regional species pool, with cascading effects on local communities (Vermeij 1978; Witman et al. 2004; Cornell et al. 2008).

A final theme to emerge from this chapter is the recognition that marine biogeography has often been neglected in marine conservation, but is of critical relevance in a number of areas. Representation of sites within different biogeographic provinces is increasingly considered in the design of marine reserve networks (Blanchette et al. 2008; Hamilton et al. 2010). In an era of climate change, an understanding of the processes that control species' range boundaries is essential to predicting how species distributions will shift along coastlines. In some cases, an understanding of biogeography has revealed that communities in different coastal regions are regulated by fundamentally different processes and may require contrasting management plans (Estes and Duggins 1995; Navarrete et al. 2005; Connell and Irving 2008). Finally, the growing recognition that local communities are interconnected by dispersal and influenced by regional processes requires management planning within a broader spatial context (Karlson et al. 2004). With these thoughts in mind, continued integration of marine biogeography and ecology promises to advance both our basic understanding of communities and the sustainable management of marine ecosystems.

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