

CHAPTER FIVE

MACROECOLOGICAL PATTERNS AMONG MARINE FISHES

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Introduction

Worldwide, there are over 28,000 species of fishes, which comprise more than 50 percent of all vertebrate species. Over 16,000 of these are marine for all or part of their lives, and fishes live in all parts of the world's oceans (Nelson 2006). "Fishes" represents a paraphyletic group that includes hagfishes (Myxini), lampreys (Petromyzontida), coelacanth, and lungfishes (Sarcopterygii), as well as the better known and much more diverse cartilaginous fishes (Chondrichthyes) and more recently evolved ray-finned fishes (Actinopterygii). They exhibit a considerable diversity of modes of reproduction, life cycles, and capacities for dispersal. The vast majority of marine ray-finned fishes have relatively small pelagic eggs and/or a pelagic larval phase, which, because it is spent in the water column away from adult habitat, enhances their capacity for dispersal and expansion of their geographic ranges (Leis and McCormick 2002). Cartilaginous fishes, in contrast, have large, benthic, or internally brooded eggs and lack a pelagic larval stage. However, their dispersal capabilities likely are enhanced by the large body size and mobility of adults, and these characteristics may have produced the large ranges many exhibit. The ancient origins of such species may also have given them more time than has been available to many recently derived teleost species to expand their ranges (Pyle 1999; Robertson, Grove, and

McCosker 2004). These fundamental differences in life histories of higher-level taxa can have important implications for distributional patterns and macroecology on both local and regional scales.

In marine environments, in contrast to terrestrial and freshwater environments, physical barriers to dispersal are thought to be weak and often absent (Briggs 1995). Coverage of most of the earth's surface by water, the continuity of such habitat over large distances, persistent transoceanic currents, intermittent large-scale oceanographic events (such as those due to the El Niño phenomenon) that produce extremes of variation in current flows, and the presence of pelagic larval stages should combine to increase dispersal potential, and produce high levels of gene flow and broad ranges for many species (Lessios and Robertson 2006). This combination of characteristics is likely to result in very different macroecological patterns among marine fishes compared to those observed in both terrestrial and freshwater species.

In this chapter, we briefly review current knowledge about patterns in the distribution and diversity of marine fish species in the context of the enormous spatial and temporal variation that results from oceanographic variability. We also discuss processes commonly implicated in controlling the distribution and regional diversity of marine fishes. This review necessarily depends on our current understanding of species-level diversity. Broader study of the genetics of putative species, especially widespread coral reef species (e.g., Muss et al. 2001) and open-ocean species (e.g., Miya and Nishida 1997) may reveal significantly greater cryptic species diversity. In addition, recent analysis indicates no decline in the rate of morphospecies descriptions of tropical shore-fishes in recent decades (Zapata and Robertson 2006). This review is also necessarily couched within the prevailing concept of species. Broader application of a phylogenetic species concept, recently advocated for coral-reef fishes (Gill 1999), would result in an increase in overall species diversity and a concomitant decrease in average species range (Agapow et al. 2004). Nonetheless, the predominant macroecological patterns for marine fishes discussed in this chapter are not expected to change significantly if that reorganization of the species concept were applied.

Global Patterns in Species Richness

Latitudinal Gradients

Latitudinal gradients in species richness represent the most widely argued about macroecological pattern relating to the large-scale spatial distributions of organisms (Willig, Kaufman, and Stevens 2003). In general, biological diver-

sity increases from polar to equatorial latitudes, a trend documented in a large array of terrestrial and marine taxa (e.g., Stehli, McAlester, and Newell 1969; Roy et al. 1998; Rex et al. 1993, 2005; Gaston and Blackburn 2000; Macpherson 2002; Hillebrand 2004; see also Valentine; and McClain et al., Roy and Witman, this volume). Although some exceptions exist that are associated with depth or habitat characteristics (e.g., Clarke 1992; Rohde 1999; Gray 2001), this gradient is one of the most predominant macroecological patterns known.

This latitudinal pattern of a peak of richness at the equator also holds for many assemblages of marine fishes (figs. 5.1 and 5.2), including not only pelagic and benthic species on each side of the Atlantic (Macpherson 2002), but also tropical reef-fishes in the Indo-Pacific (Connolly, Bellwood, and Hughes 2003; Mora et al. 2003). In the Indo-Pacific, a convex diversity pattern with latitude holds for tropical reef fishes (and corals) (Connolly, Bellwood, and Hughes 2003; Mora et al. 2003; Bellwood et al. 2005; figure 5.1, panel B). However, the extent to which the central peak results from overlap of widely distributed species rather than a concentration of local endemics with narrow ranges remains unclear (see Hughes, Bellwood, and Connolly 2002a and Mora et al. 2003, for opposing views).

The tropical eastern Pacific is a biogeographically discrete region with a high level of endemism: about 79 percent of the resident coastal fishes are regional endemics (Robertson and Allen 2002; Zapata and Robertson 2006). Mora and Robertson (2005a) found that the richness of endemic coastal fishes living on the continental shore has a generally bell-shaped latitudinal distribution that peaks in the center of that region (fig. 5.2, panel B). Broadly

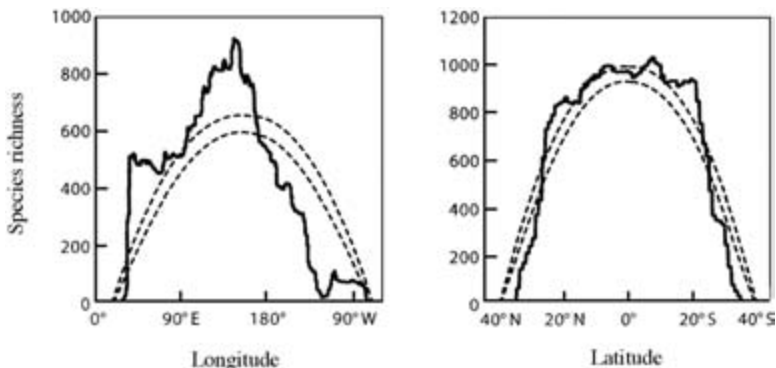


FIGURE 5.1 Longitudinal and latitudinal variation in the species-richness of reef fishes ($n = 1,766$) in the Indo-Pacific. Dotted lines represent the 99 percent of the values obtained from the randomizations (mid-domain model, reproduced with permission from Connolly, Bellwood, and Hughes 2003).

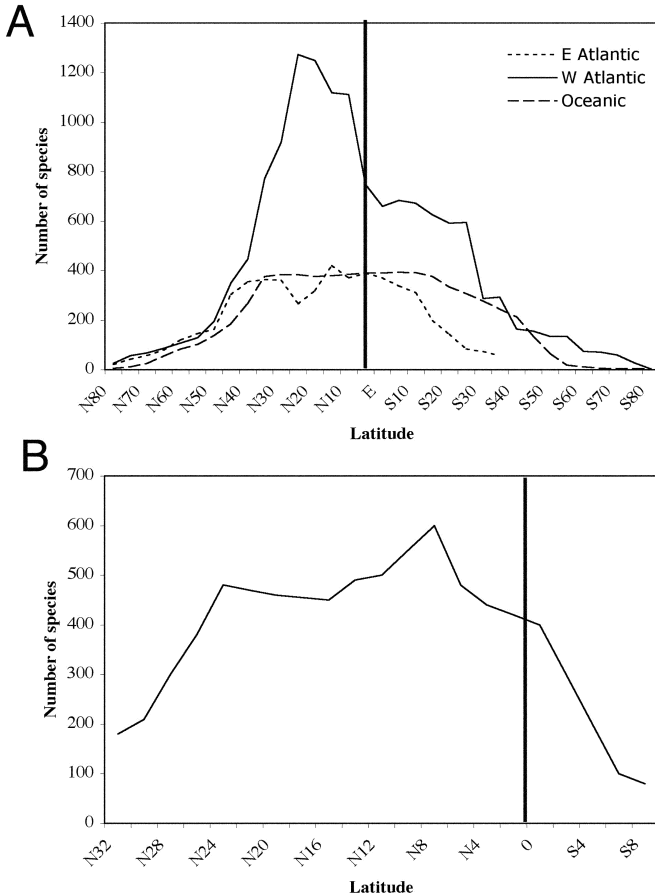


FIGURE 5.2 Latitudinal species richness gradients from (A) the Western and Eastern Atlantic fishes (solid line: coastal; dashed line: shelf-slope; dotted line: abyssal) and (B) Tropical Eastern Pacific shore-fishes (data from Macpherson, 2002, and Mora and Robertson, 2005a).

distributed species are largely responsible for that convex curve. Narrow-range species contribute the two small departures from that convexity, as they are concentrated in the two sections of the coast (Panama/Costa Rica and the Gulf of California) that have relatively large areas of habitat, an abundance of near-shore islands, and high habitat diversity.

In contrast to shore fishes, species assemblages in other habits, such as the continental slope and abyss, show a more homogeneous distribution of species richness with respect to latitude (Merrett and Haedrich 1997; Macpherson 2002; fig. 5.2, panel A). Departures from the general shallow-water pat-

tern can also occur at finer scales, within biogeographically discrete regions; for example, in the tropical eastern Pacific, species richness of endemic shorefishes peaks at about 8° N and declines not only northward but also southward, toward the equator (Mora and Robertson 2005a; fig. 5.2, panel B). Further latitudinal patterns of species richness of coastal benthic species are strongly influenced by major local hydrographic features. These include large upwelling areas, such as those off Benguela (Mas et al. 1991), and the Sahara coast (Binet 1997), and the points at which equator-bound cold temperate currents turn westward away from the equator in the eastern Pacific (Mora and Robertson 2005a). Marked declines in richness of many groups are associated with such features. For example, the freshwater and sediment outflow from the Amazon and nearby Orinoco rivers largely eliminate reef development and shallow coastal habitat for reef fishes along ~2,300 km of the equatorial coast of south America (Collette and Rutzler 1977), which provides a significant barrier to dispersal of reef organisms and probably is responsible for most of the endemism found in southern Brazilian coastal habitats (Joyeux et al. 2001; Rocha 2003). Consequently, in this part of the Atlantic Ocean, richness of coastal fishes does not peak on the equator itself, but well to the north of it in the Caribbean Sea, between 9–20° N (Macpherson 2002; fig. 5.2, panel A). Pelagic fishes are usually widely distributed, and few large faunal regions based on the distributions of these fishes have been defined (Briggs 1995). In general, these regions follow large-scale circulation patterns and discontinuities in oceanographic characteristics and hence are not influenced by river outflows and coastal upwellings (Longhurst 1998; Briggs 2003). In the Atlantic Ocean, there are strong poleward decreases in species richness among pelagic species at around 50°N and 40°S (Angel 1997; Macpherson 2002). These faunal breakpoints coincide with well defined transition zones between biogeochemically distinct oceanic provinces (see Longhurst et al. 1995).

While the fish faunas of temperate and polar seas generally are comparatively low in total diversity, those faunas tend to be dominated by clades that have undergone significant radiations (Briggs 2003). Conspicuous examples among fishes in the North Pacific include the scorpaenoids (e.g., *Sebastes* rockfishes and related genera; Love, Yaklovich, and Thorsteinson 2002) and cottoids (Bolin 1944). Consequently, coastal fish communities in the NE temperate Pacific are dominated by acanthopterygian fishes from both temperately and tropically derived lineages (Hobson 1994). Similarly, the Southern Ocean fish fauna is characterized by an overall low diversity and a high percentage of endemics with two striking radiations, those of nototheniids on the continental shelf and of liparids on the continental slope (Andria-

shev 1965, 1986; Gon and Heemstra 1990; Miller 1993; Eastman and Clarke 1998; Clarke and Johnston 2003). Although the diversity of Antarctic fishes is relatively low, that is not the case for other benthic taxa in the same waters. For groups such as filter feeders (e.g., sponges, bryozoans), Antarctic diversity is similar to that described for tropical areas (Brey et al. 1994). Frequent fluctuations in habitat availability originating from fluctuations in the extent of the continental ice sheet, together with the effects of the long-term cooling of sea water (Clarke and Crame 1997) may have been the main causes of the absence of many teleost families (through extinction) and the differences in the latitudinal clines in species richness between groups (Clarke and Johnston 2003). Thatje, Hillenbrand, and Larter (2005) suggest that differences in species richness between taxa can also be related to the extreme conditions faced by pelagic early life-history stages, which limited the capacity for recolonization by many species (e.g., teleost fishes and decapods) after the isolation of Antarctica ca. 34 million years ago, resulting in the loss of major taxonomic groups.

Latitudinal gradients are observed in the trophic structure of fish assemblages as well as in species richness. There are sharp declines in the abundance of herbivorous fishes with increasing latitude (Harmelin-Vivien 2002; Floeter et al. 2005). In general, tropical fish assemblages show a larger trophic spectrum, characterized by increased use of low-quality food resources, that is, algae, sponges, cnidarians (Hobson 1994). This may be associated to higher water temperatures facilitating digestive processes of low-caloric diets (Ebeling and Hixon 1991). More recently, Frank, Petrie, and Schackell (2007), using data from exploited ecosystems, found pronounced geographical variation in the type of trophic forcing (top-down or bottom-up) that was related to species richness and temperature. Their results suggest that this relationship has a strong influence on resilience to fishing, with cold and species-poor ecosystems with top-down control succumbing more readily (and recovering more slowly) than species-rich ecosystems from warmer areas, which normally experience fluctuating levels of top-down and bottom-up control.

While the general latitudinal gradient in species richness is well established (Gaston and Blackburn 2000; Willig, Kaufman, and Stevens 2003; Hillebrand 2004), more than thirty hypotheses that attempt to explain the pattern have been proposed (Rohde 1992). No single causal mechanism has proven sufficient to explain the overall pattern across a range of terrestrial and marine faunas and floras, although geographic area, productivity, ambient energy supply, Rapoport-rescue, the rates of speciation and extinction, and geometric constraints have been those most widely considered (Rohde

1992; Willig, Kaufman, and Stevens 2003). Some studies have found that habitat area does not explain the latitudinal pattern in benthic fish species richness on a large spatial scale (Rohde 1992; Roy et al. 1998; Macpherson 2002), while others working with different systems have reported habitat-area effects (e.g., for Indo-Pacific reef-fishes see Hughes et al. 2002b; Bellwood et al. 2005, and for tropical eastern Pacific shore-fishes see Mora and Robertson 2005a).

In Atlantic fishes, significant correlations exist between some environmental factors that represent proxies of energy input (sea surface temperature, nitrates and chlorophyll) and species richness of fishes, not only of pelagic and shallow-water benthic species, but also of species living at greater depths (Macpherson 2002). Because these variables provide indirect measures of energy input (Rohde 1992; Fraser and Currie 1996), those results support the view that the level of energy entering ecosystems (from solar energy and/or oceanographic events), and the way that this energy is used, plays an important role in determining the latitudinal distribution of fish diversity. However, Mora and Robertson's (2005a) assessment of potential effects of various major potential determinants of the latitudinal diversity gradient of coastal fishes within a single tropical biogeographic region (the tropical eastern Pacific) produced different results. Their analysis identified the mid-domain effect (MDE), which predicts such a distribution when the species ranges are randomly placed within a bounded geographical domain (e.g., Colwell and Lees 2000) as the major determinant of the distribution of broad-range species and habitat abundance and diversity as the main determinant for narrow-range species. They found no effects of energy supply (as indicated by temperature and primary production) or environmental variability, on the fauna as a whole or any of its components that they considered. However, the use of mid-domain and other null-models in biogeographic analyses remains controversial and there is no consensus about what really constitutes an appropriate null model for such assessments (Zapata, Gaston, and Chown 2005). Recent analyses have included effects of environmental gradients as well as domain boundaries (Connolly 2005). For example, Bellwood et al. (2005) demonstrated that the MDE and habitat area are both predictor variables of reef-fish species richness in the Indo-Pacific. These studies highlight the need for the testing of various hypotheses together, in order to take into account effects of collinearity among predictive variables (e.g., temperature covaries with the mid-domain effect), and for the use of techniques that cope with statistical effects of spatial autocorrelation within variables (see Mora and Robertson 2005a).

Thus marine biogeography, and biogeography in general, still lacks an

adequate general predictive theory of latitudinal gradients in species richness (Gaston and Blackburn 2000; Willig, Kaufman, and Stevens 2003, but see Allen, Brown and Gillooly 2002 and Gillooly et al. 2002, for a thermodynamic hypothesis for the species diversity gradient). Differences in the latitudinal patterns in species richness observed in Atlantic pelagic versus benthic fishes and in the relationship of each to different environmental factors indicate that a unique predictor of these gradients is unlikely (Macpherson 2002) and that gradients will be governed by different processes in different environments and parts of the world, as will gradients of different components of a single fauna. Indeed, Mora and Robertson (2005a) found quite different predictors of latitudinal patterns of species richness for tropical eastern Pacific shore-fishes with large and small geographic ranges. They pointed out that the so-called “Tropical Indo-Pacific” actually consists of a group of distinct subregions, with different processes likely influencing distributional patterns within each of those.

Longitudinal Patterns

Strong longitudinal variation in species richness is also evident both at the general level (Gaston and Blackburn 2000), and among tropical marine shore-fishes in particular (Briggs 1974; Bellwood and Hughes 2001; Connolly et al. 2003; Mora et al. 2003). The Indo-Australian Area (IAA) at the junction of the Pacific and Indian oceans has by far the greatest diversity of fishes of any part of the world (Briggs 1974; Randall 1998; Connolly, Bellwood, and Hughes 2003; Mora et al. 2003). In descending order of species richness, other global centers of diversity of tropical coastal fishes are the Greater Caribbean (within the tropical western Atlantic), the tropical eastern Pacific and the tropical eastern Atlantic (Briggs 1974).

Within the Indo-Pacific, species richness of reef-fish assemblages declines strongly with distance from the global hotspot of diversity in the IAA (Connolly, Bellwood, and Hughes 2003; Mora et al. 2003; fig. 5.1, panel A), which is centered on the Philippine Islands (Carpenter and Springer 2005). Two major processes contribute to this pattern. First, there are faunal losses due to reduction in habitat diversity that reflects the absence of continental habitats (e.g., estuaries, mangroves, large areas of shoreline influenced by river runoff), as one moves eastward onto the Pacific plate, where oceanic islands constitute the only habitat available (Randall 1998). Second, there is a decrease in species diversity within numerous lineages of coastal fishes (Springer 1982; Findley and Findley 2001; Allen 1975, 1979) that does not simply reflect declining habitat diversity. Much has been written concern-

ing this latter pattern (e.g., Briggs 1974, 1995, 2003; Randall 1998; Bellwood and Hughes 2001; Mora et al. 2003; Connolly, Bellwood, and Hughes 2003). Prominent hypotheses that attempt to account for the longitudinal diversity gradients in coastal fishes of the Indo-Pacific include the following. (a) Effects of habitat area: The amount of shelf area available to support a diversity of species declines as one moves from the center of diversity (Bellwood and Hughes 2001; Bellwood et al. 2005). (b) Environmental stability: The relative environmental stability of the IAA, especially with regard to environmental changes associated with Pleistocene glaciation events, has facilitated species survival relative to other regions that were more adversely affected, such as the Greater Caribbean (Chenoweth et al. 1998). (c) Increased potential for allopatric speciation: The geographic complexity of the Indo-Australian area, coupled with repeated cycles of exposure and submergence of land barriers during eustatic sea-level fluctuations, has facilitated allopatric speciation most in the IAA (Springer 1982; Springer and Williams 1990; Carpenter and Springer 2005). (d) Dispersal from a center of origin: Centers of high diversity, such as the IAA, have traditionally been thought to be the centers of origin for most extant species for a particular region (Briggs 1974, 1995, 2003). Some phylogenetic and genetic evidence supports the notion of such a pattern (Briggs 1995) and the view that colonization of the Pacific occurs mostly in an easterly direction (Lavery et al. 2004). Mora et al. (2003) argue that the decline in species richness from the center of diversity can be accounted for by variation in dispersal ability (as mediated by pelagic larval duration) outwards from a center of origin. (e) Center of accumulation: Effects of westward geostrophic flow in major ocean currents on the largest-scale directionality of dispersal of pelagic propagules may produce accumulations of species at the western boundaries of both the Pacific and Indian oceans basins, the IAA and E Africa, respectively (Jokiel and Marinelli 1992; Connolly, Bellwood, and Hughes 2003).

It seems likely that more than one, and quite possibly all, of these factors have played a role in building and maintaining the extraordinary diversity of fishes (and other organisms) at the junction of the Indian and Pacific oceans in the center of the Indo-Pacific. Historical biogeographic analyses that employ genetic techniques to identify the sites of origin and patterns of subsequent spread of taxa throughout the tropics should help resolve issues that are raised by (but cannot be resolved by) description and correlation alone (e.g., Palumbi 1997; Bernardi et al. 2003; Robertson, Grove, and McCosker 2004).

The Indian and Pacific oceans both have the greatest concentrations of reef-fish diversity on their western boundaries (Connolly, Bellwood, and

Hughes 2003). A similar pattern exists among shorefishes in the Atlantic basin, where diversity is greater on the western than eastern side (Briggs 1974). This pattern is consistent with most of the hypotheses described previously. In contrast, relatively few analyses of the distribution of diversity within the center of diversity in the Atlantic—the Greater Caribbean—are available (e.g., Robins 1971). Recently Smith, Carpenter, and Waller (2002) found, for a subset of the ichthyofauna, the highest diversity in two areas: (a) the Florida peninsula, and northern Cuba, and (b) the northern coast of South America. Thus, in longitudinal terms, diversity within the Greater Caribbean shows no evidence of a western-boundary concentration that could reflect the action of an accumulation process, despite the existence of a large-scale circulation pattern that might be expected to produce such a boundary effect. The predominant large-scale circulation pattern in the Greater Caribbean is thought to facilitate dispersal and gene flow throughout that region (e.g., Shulman and Bermingham 1995). However, there are counter-examples to panmixia within the Greater Caribbean, in which deep genetic breaks both occur over very short distances and show little correspondence to circulation patterns (Carlin, Robertson, and Bowen 2003; Taylor and Hellberg 2003; Rocha et al. 2005a). Planes (2002) provides similar examples in the central Pacific.

The tropical eastern Pacific (TEP) exhibits a very different diversity pattern to that of the tropical Indo-Pacific and tropical Atlantic. The shore-fish fauna of that region, with ~1,285 species, has a very high level of endemism: about 79 percent of the resident species and 16 percent of the genera occur nowhere else. Rates of endemism in equivalent sized areas in the Indo-Pacific are much lower (Connolly, Bellwood, and Hughes 2003; Mora et al. 2003), and the level of endemism in the Greater Caribbean, the sister biogeographic region of the tropical eastern Pacific, is only about one third that in the TEP (see Smith, Carpenter, and Waller 2002 for Caribbean data). The TEP has a long history of both isolation from the central Pacific (Grigg and Hey 1992) and close association with the Greater Caribbean. The latter connection was broken only relatively recently (~3 mya—see Coates and Obando 1996) by the final closure of the Isthmus of Panama. As a result, the coastal fish faunas of those two regions have strong taxonomic affinities: about 35 percent of the genera in the tropical eastern Pacific are shared with, and only with, the tropical western Atlantic (Rosenblatt 1967). The neotropics have a remarkable abundance of blennioid fishes, several families of which make major contributions to both faunas and occur primarily in the new world (Rosenblatt 1967; Robertson 1998). The eastern Pacific barrier (EPB), the world's widest deep-water barrier (5,000–7,000 km), has isolated the TEP

from the central Indo-Pacific for ~65 my (Grigg and Hey 1992). Normal currents across the barrier are sufficiently slow that transit times probably are beyond the larval durations of most species (Briggs 1961; Leis 1984). Consequently, demersal shore-fishes that have migrated eastward across the EPB constitute only 10 percent of the tropical eastern Pacific fauna. In contrast, almost all of the eastern Pacific epipelagic fishes and 25 percent of its in-shore pelagic fishes have successfully crossed the EPB (Robertson, Grove, and McCosker 2004). Among the demersal fishes, the transpacific migrants tend to be concentrated on the oceanic islands in the eastern Pacific, which have habitats similar to the islands from which they originated in the central Pacific. More than any other tropical region, the TEP is affected by oceanographic effects of El Niño events. While it is thought that greatly increased eastward current flow across the EPB during such events enhances eastward migration (e.g., Richmond 1990), there is little direct evidence to support that view (Robertson, Grove, and McCosker 2004). During El Niño events, however, there are temporary range expansions by shore-fishes both within the TEP and beyond the normal latitudinal bounds of that region (Lea and Rosenblatt 2000; Victor et al. 2001; Robertson, Grove, and McCosker 2004; Mora and Robertson 2005b).

Patterns of Variation in Species Range Sizes

The geographic area occupied by a fish species depends not only on its biological characteristics, such as habitat preferences, dispersal capabilities of larvae and adults, and interactions with competitors and predators, but also on the processes of speciation, extinction, and range fragmentation as a result of vicariant events (Briggs 1974; Connolly, Bellwood, and Hughes 2003).

HABITATS Not surprisingly, range size tends generally to be larger in pelagic and deep-sea fishes than in benthic and shallow-water species (Merret and Haedrich 1997; Macpherson 2003; fig. 5.3). Mora and Robertson (2005b) examined the distributions of range sizes among four groups of shorefishes endemic to the tropical eastern Pacific (fig. 5.4). Insular species have the smallest ranges, and species with small ranges are predominantly island forms. The range-size frequency distribution of continental species is bimodal, with most species having moderate to large ranges. Those authors argue that this pattern reflects a combination of (a) the paucity of existing barriers to dispersal on the continental shore, (b) a lack of intermittent barriers that appear and disappear with changing sea levels (i.e., like those that have repeatedly fragmented ranges in the Indo-Australian Area), and (c) the fact that those continental barriers affect primarily reef-fishes, which represent only 38

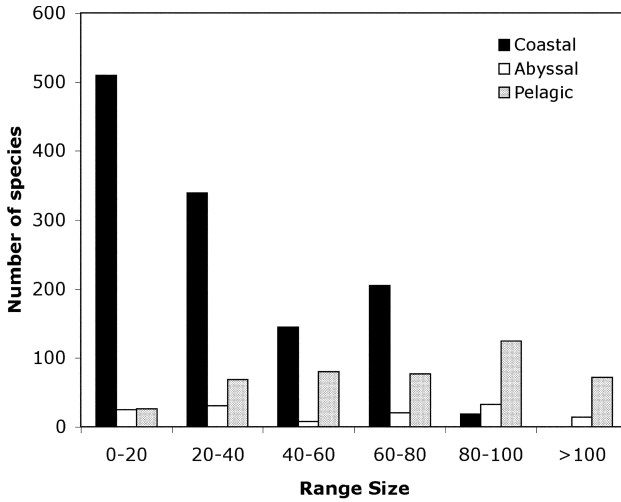


FIGURE 5.3 Frequency distributions of latitudinal range sizes for Western Atlantic coastal (0–100 m depth), abyssal (>1,000 m depth) and pelagic fishes (recorded in the water column). Range in degrees of latitude (see also Macpherson 2003).

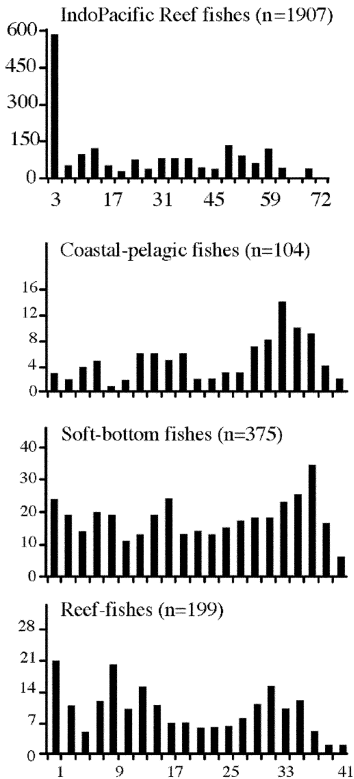


FIGURE 5.4 Frequency distributions (Y-axis, number of species) of latitudinal range sizes (X-axis, range size in degrees of latitude) three ecological groups of Tropical Eastern Pacific shore-fishes, plus Indo-Pacific reef fishes for comparison with the eastern Pacific reef fishes. (reproduced with permission from Mora and Robertson, 2005 B).

percent of the fauna. They found that, among continental species, range size decreases in the following hierarchy: pelagic species (continuous habitat) > benthic species living on soft bottoms (continuous habitat) > benthic species living on reefs (moderately discontinuous habitat) > species restricted to the oceanic islands (highly discontinuous habitat). They concluded that adult dispersal ability has the strongest effects on range size, and that isolation by open ocean barriers has stronger effects than isolation by habitat discontinuities on the continental shore. They also noted possible effects of variation in the geographic complexity of regions and the occurrence of intra-regional barriers on the structure of range-size frequency distributions in shore-fishes in different parts of the Atlantic and Indo-Central Pacific.

BARRIERS Large-scale oceanographic discontinuities are generally responsible for producing different pelagic biogeographic provinces in the open oceans (Longhurst 1998). Such discontinuities evidently also represent a major factor limiting the distributions of coastal as well as pelagic fishes, because the range limits of both often coincide with such oceanographic breakpoints (Ekman 1953; Briggs 1974; Zezina 1997; Macpherson 2003; Mora and Robertson 2005a). However, different types of species do not necessarily exhibit the same patterns of geographic structure, probably as a result of different patterns of colonization and dispersal capabilities and different ecological requirements. The frequency of occurrence on both sides of the eastern Pacific Barrier is much higher for oceanic pelagic species than for shore-fishes, and transbarrier species constitute a much greater percentage of the TEP fauna of pelagics than is the case for shorefishes (Robertson, Grove, and McCosker 2004). Other barriers include recently developed permanent land barriers, such as the central American isthmus, which finally severed longstanding connections between the tropical biotas of the west Atlantic and eastern Pacific some 3 mya (e.g., Coates and Obando 1996). They also include eustatically variable land barriers such as those in the Indo-Australian Area (Springer 1982; Springer and Williams 1990; Carpenter and Springer 2005). Major oceanographic processes also act as barriers (e.g., upwelling areas, river discharges, principal currents, oceanographic fronts), and pronounced discontinuities in the temperature, salinity, and productivity characteristics of water masses. In the Atlantic Ocean, the boundaries of ranges of pelagic fishes tend to coincide with transition zones between oceanic domains that have distinct biogeochemical properties and plankton communities, domains that were described by Longhurst et al. (1995) and Longhurst (1998). The distributions of range end-points in benthic taxa are mainly influenced by the Sahara and Benguela upwellings

in the eastern Atlantic, and by the boundaries of Labrador and Falkland currents and the Amazon/Orinoco river discharge in the western Atlantic. The zones on each side of these boundaries display marked differences in species richness. Furthermore, numerous species tend to become rarer toward their distributional limits, near these boundaries (Brown 1984; Macpherson 1989; Brown, Stevens, and Kaufman 1996). Rocha et al. (2002) showed how variation in the degree of genetic connectivity between the Caribbean and Brazilian populations of three members of a single genus is related to differences in habitat preferences that affect their ability to live within the 2,300 km wide Amazon barrier. The actions of such marine boundaries are also depth dependent because the effect of the oceanographic events marking biogeographic boundaries on the shelf and slope extends only as deep as the broad slope/rise. Consequently such boundaries are poorly defined on broad abyssal plain areas (Gordon and Duncan 1985; Haedrich and Merrett 1990; Macpherson 2003).

In the eastern Pacific, distributions of coastal species are strongly affected by pole-to-pole temperature gradients (Hubbs 1948), with notable break-points occurring where cold equator-bound currents turn westward and define the northern and southern limits of the centrally located tropical eastern Pacific (Briggs 1974; Hastings 2000; Mora and Robertson 2005b). Within the tropical part of the eastern Pacific the distribution of shallow coastal reef fishes is limited by effects of two large (300–750 km wide) “gaps” in the continental shore that lack reefs and consist entirely of sand and mud shorelines (Hastings 2000; Mora and Robertson 2005b).

ISLANDS AND SEAMOUNTS The few oceanic islands of the tropical Atlantic are widely scattered and support faunas that exhibit reduced species diversity, high levels of endemism, and other effects of isolation, including those due to greatly reduced habitat diversity (Briggs 1995; Robertson 2001). Considering that these islands vary in age and distance from adjacent coasts, comparative studies of their faunas can reveal considerable information about general patterns of evolution and distribution (Briggs 1995). Robertson (2001) analyzed the endemic shore-fish faunas of small, highly isolated tropical islands in the eastern Pacific and central Atlantic to assess whether they have unusual biological characteristics. He found that they have no particular characteristics in terms of body size, general dispersal capabilities, or taxonomic composition and concluded that shore-fishes in general are capable of maintaining persistent endemic populations on such islands if they can disperse to them.

The recent and continuing accumulation of genetic data on the shore-

fish faunas of those islands is providing insights into the origins and ages of island species and the extent of ongoing connections between island and mainland faunas (see Bernardi et al. 1999; Muss et al. 2001; Bowen et al. 2001; Rocha et al. 2002; Carlin, Robertson, and Bowen 2003; Rocha et al. 2005a, b; Robertson et al. 2006). Such work should eventually lead to a greatly enhanced appreciation of general patterns and processes governing the structure of island faunas and the extent to which they interact with mainland faunas, as well as the action of islands as stepping stones for transoceanic migration.

Seamounts tend to be dominated by species inhabiting neighboring areas (Rogers 1994). However, seamount faunas also show high levels of endemism (Wilson and Kaufmann 1987; Parin, Mironov, and Nesis 1997), and exhibit previously unsuspected high diversity (Richer de Forges, Koslow, and Poore 2000). Although there are few studies of seamount fish communities, results from various invertebrate groups indicate that seamounts likely are sites with high rates of speciation, as a result of reproductive and genetic isolation resulting from their geographic isolation both from other seamounts and continental shelf areas, and from hydrographic conditions that trap larvae that originated on a seamount and promote self-recruitment and sustaining local populations (Parker and Tunnicliffe 1994).

DEEP SEA There has been considerable improvement in our knowledge of the deep fish fauna in the last few decades. While those findings have provided some useful insights, logistical difficulties are such that the biota of the deep seas (>1,000 m) remains much more poorly known than that of shallower marine habitats (Haedrich 1997; Merret and Haedrich 1997). Differences in deep-sea community structure are thought to be associated with variation in productivity and levels of seasonal organic enrichment from sinking phytodetritus (Merret and Haedrich 1997; Rex, Stuart, and Coyne 2000). Despite their apparent isolation from immediate surface events, environmental changes associated with climatic fluctuations can also have significant effects on community structure in deep-sea habitats (Ruhl and Smith 2004). Deep pelagic species often associated with particular water masses, and, as a consequence, species composition and/or abundances often change rapidly along fronts between water masses (e.g., Backus, Craddock, and Shores 1969; Figueroa, Díaz de Astarloa, and Martos 1998). Among such fishes species diversity tends to be highest in mixing areas where species from neighboring water masses co-occur (e.g., Beamish et al. 1999).

The deep sea has unusual physico-chemical activity not found in shallow environments that has unique effects on associated biological communities.

Both hot and cold deep-sea hydrothermal vents, which are small, relatively short-lived and scattered, support unusual fish communities that are based on chemoautotrophic primary production (Van Dover 2000). There appears to be some interchange among these fish communities separated by long distances (ca. 1000 km), associated with high dispersal capabilities (Hashimoto et al., 1995), although the degree of local endemism is also high (Tunncliffe 1991; Tunncliffe and Fowler 1996). Mechanisms of colonization by vent organisms remain largely unknown for most of the mid-ocean ridge systems, although recent studies indicate that dispersal of invertebrate larvae occurs via deep-ocean currents (Van Dover et al. 2002).

The greatest diversity of such fishes occurs at mid-depths, near 1,500 m for demersal species (Rex et al. 1993; Haedrich 1997). However, depth trends in diversity vary geographically and among fish groups. At Porcupine Seabight (N Atlantic), for example, species richness peaks around 1,000 m and falls away steadily to the 2,400 m level, where it increases again (Haedrich and Merret 1997). Diversity in the NE Pacific is also bimodal, with peaks at 600–700 m and 2,000–2,100 m (Pearcy, Stein, and Carney 1982). Like the deep-sea benthic fishes, the greatest diversity of deep-sea pelagic fishes occurs at mid depths (Ebeling 1967; Haedrich 1997).

Although some demersal deep-sea fishes are widely distributed, many species appear to have small ranges (Haedrich and Merret 1988, 1990). As a consequence, similarities in demersal fish faunas between different areas within the deep sea usually are low (Haedrich 1997; Merret and Haedrich 1997). For example, the composition of deep-sea fish faunas in the N Atlantic and N Pacific are quite different, with <10 percent of species being shared (Haedrich and Merret 1988; Pearcy, Stein, and Carney 1982). The deep-sea fish fauna of SE Australia is more similar to that of the N Atlantic than that of the N Pacific (Koslow, Bulman, and Lyle 1994). While many pelagic deep-sea fishes are thought to have broad distributions encompassing one or more ocean basins (Haedrich 1997), detailed morphological analyses (e.g., Gibbs 1986) and recent genetic studies have revealed previously unrecognized cryptic diversity (e.g., Miya and Nishida 1997) calling this assumption into question.

RAPOPORT'S RULE The effect of latitude on species' range-size, known as Rapoport's rule, has been examined for many different groups since Stevens (1989) first discerned the tendency for range size to increase with latitude (Gaston, Blackburn, and Spicer 1998; Rohde 1999; Gaston and Blackburn 2000). Rapoport's rule is based on the rationale that greater environmental variation at higher latitudes selects for broad tolerance (and hence large

ranges) species, which can also live at less variable lower latitudes, where reduced variability also promotes the evolution of narrow tolerance (small range) species (Stevens 1989). Distributions of Atlantic fishes suggest that Rapoport's rule does hold, as species with distributions that reach latitudes nearest the poles do have the broadest ranges; however, this trend is relatively weak, suggesting that this rule is not the primary factor responsible for latitudinal patterns in range size (Macpherson 2003; see the following). Other studies (Rohde, Heap, and Heap 1993; Rohde and Heap 1996) indicate that Pacific fishes do not follow Rapoport's rule on a broad scale, though such a relationship may exist on a smaller scale. Mora and Robertson (2005a) found that latitudinal patterns of variation in range-size among regionally endemic tropical eastern Pacific shorefishes are consistent with Rapoport's Rule (fig. 5.5). However, they concluded that those patterns arise simply as corollaries of the mid-domain effect, which is the major determinant of the latitudinal distribution of species richness within that region. They also found opposite latitudinal patterns of variation in range size depending on whether average range-size in a latitudinal band was measured using either (a) the mean size of the ranges of all species present in that band (the original method of measurement—see Stevens 1989), or (b) the mean size of the ranges whose mid-points occur in that band (an alternative method developed by Rhode et al. 1993 to cope with a lack of statistical independence among measurements produced by the former method).

Many authors (e.g., Roy, Jablonski, and Valentine 1994; Gaston and Blackburn 2000) have considered various mechanisms that might explain latitudinal gradients in range size: climatic variability, area size, extinction rate, competition, and biogeographic boundaries. Pole-to-pole studies of latitudinal patterns in range size examine patterns that span multiple biogeographic provinces. Hence these largest-possible-scale latitudinal gradients may reflect the distinct environmental differences that separate adjacent provinces (e.g., temperature, salinity, and productivity), while there is greater constancy of environmental conditions within a given biogeographic province (Rutherford, D'Hondt, and Prell 1999). Consequently, the location of these oceanographic boundaries, the environmental conditions at the boundaries, and the ability of species to cross them may be the main factors that account for such largest-scale latitudinal gradients in range size (Roy, Jablonski, and Valentine 1994; Macpherson 2003; but see Mora and Robertson 2005a).

LARVAL DISPERSAL There is no clear relationship between range-size and larval dispersal capabilities among either tropical reef or temperate shore-

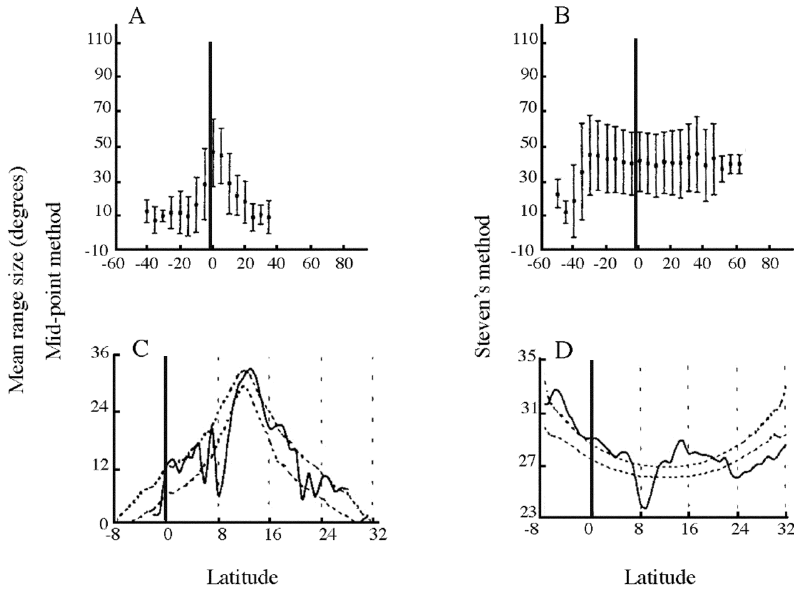


FIGURE 5.5 Rapoport's rule. A–B. Trends in mean range-size of teleost fishes from the Indo-Pacific. C–D. The same for the shorefishes of the Tropical Eastern Pacific. A and C: Mid-point method, using the midpoint of each species' latitudinal range as a single value, thus yielding a set of independent data points. B and D: Steven's method, where the mean distribution ranges of the species present in each 5° bin are calculated, and latitude is regressed on the mean range in each bin. Bars in figs. A–B are standard deviations; dotted lines in figs. C–D are the 95 percent confidence limits of the mean range size distributions generated by the mid-domain model. Equator marked by a vertical line. (A–B reproduced with permission from Rohde and Heap 1996, and C–D from Mora and Robertson 2005 A).

fishes, at least as measured by variation in the length of the pelagic larval life (e.g., Victor and Wellington 2000; Lester and Ruttenberg 2005; but see Mora et al. 2003). This suggests that range size is not set by a single mechanism, such as the length of the larval life. However, dispersal potential of such fishes may be influenced not only by larval durations, but also by whether larvae are restricted to nearshore habitats or range further offshore, and by their spawning characteristics (e.g., benthic or pelagic eggs, season of planktonic life; Shanks and Eckert 2005; Macpherson and Raventos 2006). Recent climate changes have affected the distributional pattern of numerous tropical and temperate marine fishes (e.g., Rocha et al. 2005b), to the extent that, in some cases, the position of a species' center of distribution has been significantly modified (Stenseth et al. 2002; Walther et al. 2002; Genner et al. 2004). It would be useful to analyze not only larval dispersal capabilities but

various other biological characteristics of such species, in order to better understand processes that facilitate such patterns of colonization and range modification.

DEPTH Geographic range size-frequency distributions vary strongly in relation to depth. In general, coastal species have smaller geographic ranges than species inhabiting the continental slope or abyssal plains (Briggs 1974; Stevens 1996; Macpherson 2003). Furthermore, there is a tendency for depth range to increase with depth of occurrence (e.g., Ekman 1953; Pineda 1993; Stevens 1996; Haedrich 1997; Merrett and Haedrich 1997; Smith and Brown 2002). These depth-range distributions of species are the bases for the recognition of depth provinces, the boundaries of which tend to lie around the edge of the continental shelf (300 m depth), the upper continental slope (300–1,000 m) and the abyssal domain (>1,000 m; Haedrich 1997; Merrett and Haedrich 1997; Macpherson 2003). However, separations between these depth provinces are less evident than those between latitudinal provinces. This is not surprising given that processes regulating the latitudinal distributions of species are unlikely to be the same as those regulating depth distributions (Macpherson 2003). The depth-domain boundaries tend to be related to a suite of oceanographic parameters, including discontinuities in temperature, discontinuities in productivity, sedimentary features, and hydrodynamics (Gordon and Duncan 1985; Haedrich and Merrett 1990). The extent of species depth ranges changes with latitude, because environmental conditions tend to be more uniform over depth at higher latitudes (Stevens 1996; Zezina 1997; Longhurst 1998). As a consequence, the depth-range frequency distributions of species are right-skewed near the equator, where most species have small depth ranges, and left-skewed near the poles, where most species have large depth ranges.

CLIMATE AND CHANGES IN DISTRIBUTION Sporadic shifts in the distributions of fish species have frequently been documented. In the tropical eastern Pacific two types of range-changes occur during El Niño events, when a surge of heated water moves eastward across the Eastern Pacific Barrier. The effects of that surge extend beyond the usual northern and southern limits of the region, which are defined by the westward turning points of cold equator-bound currents. First, many tropical species extend their ranges temporarily into adjacent temperate areas (northward extensions: Hubbs 1948; Lea and Rosenblatt 2000; southward extensions: Chirichigno and Velez 1998). Second, among species restricted entirely to the tropical eastern Pacific there are temporary range expansions within that area (Victor et al. 2001). A num-

ber of recent shifts in species ranges and changes in community structure in temperate areas have been attributed to climatic changes in both the north Pacific (e.g., Fields et al. 1993; McFarlane, King, and Beamish 2000; Zhang et al. 2000; Brooks, Schmitt, and Holbrook 2002; Beamish et al. 2004) and the north Atlantic and its sub-basins (e.g., Francour et al. 1994; Genner et al. 2004). Invasion of the tropical Atlantic by reef fishes has been linked to such environmental variation, with such changes providing insight into the effects of ongoing global climate change (Rocha et al. 2005b). Implications of global warming for tropical reef fishes have only begun to be explored (see Mora and Ospina 2001; Rocha et al. 2005a). In addition, the effects of climate change on even the remotest abyssal communities may be significant but remain poorly understood (Ruhl and Smith 2004).

Body Size Distributions

Many biological characteristics of species are related to, and often dependent on, body size (Peters 1983). Consequently, the distribution of body sizes of the species inhabiting an area has the potential to provide insights into mechanisms that determine the species composition of fish assemblages. Species' body-size distributions are mostly right-skewed (most species are small) in terrestrial animal communities, although skewness can change with geographical scale: from right-skewed at large scales to a variety of different shapes at local or regional scales (see Gaston and Blackburn 2000; Roy et al. 2000).

Body size is also related to metabolic rate, and large species consume more energy than small species, although they require less energy per gram of body weight (Peters 1983). The relationship between body size and abundance is one aspect of macroecology that has been assessed in numerous terrestrial organisms (e.g., Gaston and Blackburn 2000), but poorly studied in marine fishes. However, body size is a poor predictor of species abundance for SW Atlantic fishes (Macpherson 1989), as well as for Indo-Pacific reef fishes (Munday and Jones 1998; fig. 5.6). Furthermore, body-size and density relationships are different for smallest and largest size classes, probably associated with different patterns of resource acquisition (Ackerman, Bellwood, and Brown 2004). Biomass/size spectra (i.e., the biomass density of organisms belonging to different size classes—see Cyr, Peters, and Downing 1997) have been commonly employed in aquatic studies, to compare the structure of different nonfish communities (e.g., phyto- and zooplankton: Sheldon, Prakash, and Sutcliffe 1972; Rodriguez et al. 2001) and assess possible effects of system productivity on that size-spectral structure (Sprules and Munawar

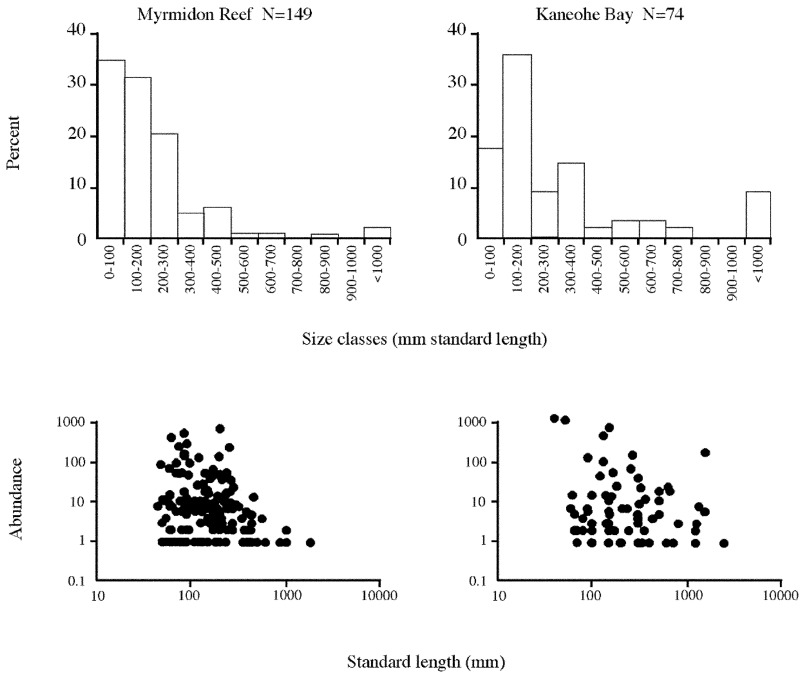


FIGURE 5.6 Body size distributions (upper panel) and body size versus abundance of each species (lower panel) of reef fishes from Hawaii and the Australian Great Barrier Reef (reproduced with permission from Munday and Jones 1996).

1986). Differences in the slopes of biomass/size spectra have been found to be associated with productivity: higher slope values tend to occur in areas of high productivity. That is, whereas high productivity areas have greater concentrations of biomass in smaller species (which have high turnover rates), in oligotrophic areas biomass is distributed more evenly among the different size classes, or may even be skewed toward the larger size classes (Sprules and Munawar 1986). There are few similar studies of body size distributions among fish communities (e.g., Merrett and Haedrich 1997; Munday and Jones 1998; Ackerman, Bellwood, and Brown 2004). As with the plankton, indications are that, among those fishes, there is greater biomass of large organisms in the more oligotrophic abyssal zone compared to the upwelling areas on the continental shelf, where the opposite relationship prevails (Macpherson and Gordo 1996). Furthermore, interesting patterns of variation in the diversity of large oceanic predators have recently been identified, with diversity being highest at intermediate latitudes (20–30°N and S), as well as near reefs, shelf breaks, and seamounts that can enhance local productivity and food supply (Worm, Lotze, and Myers 2003).

Unfortunately, industrial fisheries have produced significant disturbances to the relationship between size and abundance in many marine fish communities (Jennings and Kaiser 1998), as well as in life-history parameters and population characteristics such as average body size (Tittensor et al., this volume). These relationships may be more strongly altered in the deep sea (>1,000 m), an area virtually unknown, where new fishing technologies can have devastating consequences (Roberts 2002). Hence, future studies of natural size-distribution patterns among marine fishes would only be possible for unexploited communities in extremely large protected areas that have been established for a sufficiently long time that the ecosystem has recovered to an approximation of its original state (Marquet, Navarrete, and Castilla 1990; Jackson 2001). However, in some cases, highly disturbed marine communities may become irretrievably altered by settling into new stable states that are very different from the predisturbance condition (Knowlton 2004). Recently, fish body-size spectra and predator/prey body-mass ratios have been used to predict the original (pre-fishing) fish abundance and size-structure in the intensively fished North Sea. The results of that work suggest that the long-term depletion of large fishes through exploitation exceeds the level of depletion indicated by many short-term studies (Jennings and Blanchard 2004).

Conclusions

The availability of data on macroecological trends and processes in marine fishes is much as it is in other groups of marine organisms, with many large gaps (McClain et al., this volume; Santelices et al., this volume). Although the latitudinal and longitudinal distributions of species richness of fishes and invertebrates are largely concordant (e.g., Smith, Carpenter, and Waller 2002), species richness of some important nonfish groups, such as marine macroalgae, shows quite different latitudinal trends to that among marine fishes (Kerswell 2006; Santelices et al., this volume). Even so, it is likely that some mechanisms have similar influences on richness and range-size patterns among macroalgae, corals, and reef fishes. For example, distributions of diversity peaks in all three groups are consistent with predictions of accumulation patterns brought about by dispersal on large-scale ocean-current systems (Connolly, Bellwood, and Hughes 2003; Kerswell 2006). These studies provide new perspectives of drivers of observed diversity patterns. Further, rather than simply explaining declines in richness from the center by invoking processes that enhance richness in the center, Connolly, Bellwood, and Hughes (2003) examined those declines from the perspective of how environmental factors produce disproportionate changes in the centers and

endpoints of species distributions. They concluded that the distributions (directions and positions) of major ocean currents within both the Indian and Pacific basins explained much of both longitudinal and latitudinal patterns in corals and reef fishes. However, while mechanisms such as this are relevant to explaining patterns within ocean basins, for between-basin differences we must examine quite different processes. At that scale, major differences in historical processes become of primary importance (Briggs 1995; Rex et al. 2005). The global center of tropical marine diversity in the IAA at the western edge of the Pacific has been much more stable, and thus amenable to tropical organisms through evolutionary time than has the distinctly less diverse tropical west Atlantic, which was strongly influenced by repeated ice ages and is known to have suffered major extinction events of benthic taxa during the Pleistocene (Budd, Johnson, and Semann 1994).

The existence of similar spatial trends in diversity across a range of taxonomically distant groups of organisms that have very different larval and adult dispersal capabilities, that inhabit depth zones from the coastal zone down to the abyssal zone, and that include both pelagic and benthic forms, indicates that there are some general causal mechanisms that contribute to global macroecological gradients and patterns. That said, unfortunately, sufficient complexity has emerged from studies of macroecological patterns among marine fishes, other marine taxa, and terrestrial organisms over the last decade that biogeographers recognize that they are a long way from being able to claim we actually understand those causal mechanisms (Gaston and Blackburn 2000).

REFERENCES

- Ackerman, J. L., D. R. Bellwood, and J. H. Brown. 2004. The contribution of small individuals to density-body size relationships: Examination of energetic equivalence in reef fishes. *Oecologia* 139:568–71.
- Agapow, P. M., O. R. P. Bininda-Emonds, K. A. Crandall, J. L. Gittleman, G. M. Mace, J. C. Marshall, and A. Purvis. 2004. The impact of species concept on biodiversity studies. *Quarterly Review of Biology* 79:161–79.
- Allen, A. P., J. H. Brown, and J. F. Gillooly. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* 297:1545–48.
- Allen, G. R. 1975. *Damselfishes of the South Seas*. Neptune City, NJ: TFH Publications.
- . 1979. *Butterfly and angelfishes of the World 2*. MERGUS, Hans A. Baensch, Melle, Germany.
- Andriashev, A. P. 1965. A general review of the Antarctic fish fauna. In *Biogeography and ecology in Antarctica, Monography Biology, XV*, ed. P. van Oye and J. van Mieghem, 491–550. The Hague: Junk.
- . 1986. *Review of the snailfish genus Paraliparis (Scorpaeniformes: Liparididae) of the Southern Ocean*. Theses Zool. 7. Koenigstein: Koeltz Scientific Books.

- Angel, M. V. 1997. Pelagic biodiversity. In *Marine biodiversity: Patterns and processes*, ed. R. F. G. Ormond, J. D. Gage, and M. V. Angel, 35–68. Cambridge: Cambridge University Press.
- Backus, R. H., J. E. Craddock, and D. L. Shores. 1969. Mesopelagic fishes and thermal fronts in the western Sargasso Sea. *Marine Biology* 3:87–106.
- Beamish, R. J., A. J. Benson, R. M. Sweeting, and C. M. Neville. 2004. Regimes and the history of the major fisheries off Canada's west coast. *Progress in Oceanography* 60:355–85.
- Beamish, R. J., K. D. Leask, O. A. Ivanov, A. A. Balanov, A. M. Orlov, and B. Sinclair. 1999. The ecology, distribution, and abundances of midwater fishes of the subarctic Pacific gyres. *Progress in Oceanography* 43:399–442.
- Bellwood, D. R., and T. P. Hughes. 2001. Regional-scale assembly rules and biodiversity of coral reefs. *Science* 292:1532–34.
- Bellwood, D. R., T. P. Hughes, S. R. Connolly, and J. Tanner. 2005. Environmental and geometric constraints on Indo-Pacific coral reef biodiversity. *Ecology Letters* 8:643–51.
- Bernardi, G., D. R. Robertson, K. E. Clifton, and E. Azzuro. 1999. Ecology, biogeography and evolution of the Atlantic parrotfish genus *Sparisoma* inferred from mtDNA sequences. *Molecular Phylogenetics and Evolution* 15:292–300.
- Bernardi, G., G. Bucciarelli, D. Costagliola, D. R. Robertson, and J. B. Heiser. 2003. Ecology and evolution of the coral reef fish genus *Thalassoma* (Labridae): 1. Molecular phylogeny and biogeography. *Marine Biology* 144:369–75.
- Binet, D. 1997. Climate and pelagic fisheries in the Canary and Guinea currents 1964–1993: The role of trade winds and the southern oscillation. *Oceanologica Acta* 20:177–90.
- Bolin, R. L. 1944. A review of the marine cottid fishes of California. *Stanford Ichthyological Bulletin* 3:1–135.
- Bowen, B. W., A. L. Bass, A. I. Garcia-Rodriguez, L. A. Rocha, and D. R. Robertson. 2001. Phylogeography of the trumpetfish (*Aulostomus* spp.): A ring species complex on a global scale. *Evolution* 55:1029–39.
- Brey, T., M. Klages, C. Dahm, M. Gomy, J. Gutt, S. Hain, M. Stiller, W. E. Arntz, J. W. Wägele, and A. Zimmermann. 1994. Antarctic benthic diversity. *Nature* 368:297.
- Briggs, J. C. 1961. The East Pacific barrier and the distribution of marine shore fishes. *Evolution* 15:545–54.
- . 1974. *Marine zoography*. New York: McGraw-Hill.
- . 1995. *Global biogeography*. Amsterdam: Elsevier.
- . 2003. Marine centres of origin as evolutionary engines. *Journal of Biogeography* 30:1–18.
- Brooks, A. J., R. J. Schmitt, and S. J. Holbrook. 2002. Declines in regional fish populations: Have species responded similarly to environmental change? *Marine and Freshwater Research* 53:189–98.
- Brown, J. H. 1984. On the relationship between abundance and distributions of species. *The American Naturalist* 124:255–79.
- Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: Size, shape, boundaries and internal structure. *Annual Review of Ecology and Systematics* 27:597–623.
- Budd, A. F., K. G. Johnson, and T. A. Stemann. 1994. Plio-Pleistocene extinctions and the origin of the modern Caribbean coral reef fauna. In *Global aspects of coral reefs: Health, hazards and history*, ed. R. N. Ginsburg, 7–13. Miami: University of Miami Publications, Miami.
- Carlin, J. L., D. R. Robertson, and B. W. Bowen. 2003. Ancient vicariance and recent dispersal in the tropical Atlantic reef fishes *Epinephelus adscensionis* and *Rypticus saponaceus* (Percoidae: Serranidae). *Marine Biology* 143:1057–69.
- Carpenter, K. E., and V. G. Springer. 2005. The center of the center of marine shore fish biodiversity: The Philippine Islands. *Environmental Biology of Fishes* 72:467–480.

- Chenoweth, S. F., J. M. Hughes, C. P. Keenan, and S. Lavery. 1998. When oceans meet: A teleost shows secondary intergradation at an Indian-Pacific interface. *Proceedings of the Royal Society of London, B* 265 (1394): 415–20.
- Chirichigno, N. F., and J. D. Velez. 1998. Clave para indentificar los peces marinos del Perú. Perú: Instituto del Mar del Perú.
- Clarke, A. 1992. Is there a latitudinal diversity cline in the sea? *Trends in Ecology and Evolution* 7:286–87.
- Clarke, A., and J. A. Crame. 1997. Diversity, latitude and time: patterns in shallow sea. In *Marine biodiversity: Patterns and processes*, ed. R. F. G. Ormond, J. G. Gage, and M. V. Angel, 122–47. Cambridge: Cambridge University Press.
- Clarke, A., and N. M. Johnston. 2003. Antarctic marine benthic diversity. *Oceanography and Marine Biology. Annual Review* 41:47–114.
- Coates, A. G., and J. A. Obando. 1996. The geologic evolution of the Central American Isthmus. In *Evolution and environments in tropical America*, ed. J. B. C. Jackson, A. F. Budd, and A. G. Coates, 21–56. Chicago: University of Chicago Press, Chicago.
- Collette, B. B. and K. Rutzler. 1977. Reef fishes over sponge bottoms off the mouth of the Amazon River. Miami: Third International Coral Reef Symposium.
- Colwell, R. K., and D. C. Lees. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution* 15:70–76.
- Connolly, S. R. 2005. Process-based models of species distributions and the mid-domain effect. *The American Naturalist* 166:1–11.
- Connolly, S. R., D. R. Bellwood, and T. Hughes. 2003. Indo-Pacific biodiversity of coral reefs: Deviations from a mid-domain model. *Ecology* 84:2178–90.
- Cyr, H., R. H. Peters, and J. A. Downing. 1997. Population density and community size structure: Comparison of aquatic and terrestrial systems. *Oikos* 80:139–49.
- Darwin, C. 1872. *The origin of species by means of natural selection, 6th ed.* New York: Random House.
- Eastman, J. T., and A. Clarke. 1998. A comparison of adaptative radiations of Antarctic fish with those of non-Antarctic fish. In *Fishes of Antarctica: a biological overview*, ed. G. di Prisco et al., 3–26. Berlin: Springer-Verlag.
- Ebeling, A. W. 1967. Zoogeography of tropical deep-sea animals. *Studies in Tropical Oceanography* 5:593–613.
- Ebeling, A. W., and M. A. Hixon. 1991. Tropical and temperate reef fishes: comparisons of community structures. In *The ecology of fishes on coral reefs*, ed. P. F. Sale, 509–63. London: Academic Press.
- Ekman, S. 1953. *Zoogeography of the sea*. London: Sidgwick and Jackson.
- Fields, P. A., J. B. Graham, R. H. Rosenblatt, and G. N. Somero. 1993. Effects of expected global climate change on marine faunas. *Trends in Ecology and Evolution* 8:361–67.
- Figueroa, D. E., J. M. Díaz de Astarloa, and P. Martos. 1998. Mesopelagic fish distribution in the southwest Atlantic in relation to water masses. *Deep-Sea Research I* 45:317–32.
- Findley, J. S., and M. T. Findley. 2001. Global, regional, and local pattern in species richness and abundance of butterflyfishes. *Ecological Monographs* 71:69–91.
- Floeter, S. R., M. D. Behrens, C. E. L. Ferreira, M. J. Paddock, and M. H. Horn. 2005. Geographical gradients of marine herbivorous fishes: patterns and processes. *Marine Biology* 147:1435–47.
- Francour, P., F. C. Boudouresque, J. G. Harmelin, M. Harmelin-Vivien, and J. P. Quingnard. 1994. Are the Mediterranean waters becoming warmer? Information from biological indicators. *Marine Pollution Bulletin* 28:523–26.

- Frank, K. T., B. Petrie, and N. L. Schackell. 2007. The ups and downs of trophic control in continental shelf ecosystems. *Trends in Ecology and Evolution* 22:236–42.
- Fraser, R. H., and D. J. Currie. 1996. The species richness-energy hypothesis in a system where historical factors are thought to prevail: Coral reefs. *The American Naturalist* 148:138–59.
- Gaston, K. J., and T. M. Blackburn. 2000. *Pattern and process in macroecology*. London: Blackwell Science.
- Gaston, K. J., T. M. Blackburn, and J. I. Spicer. 1998. Rapoport's rule: Time for an epitaph? *Trends in Ecology and Evolution* 13:70–74.
- Genner, M. J., D. W. Sims, V. J. Wearmouth, E. J. Southall, A. J. Southward, P. A. Henderson, and S. J. Hawkins. 2004. Regional climatic warming drives long-term community changes of British marine fish. *Proceedings of the Royal Society of London, B* 271:655–61.
- Gibbs, R. J., Jr. 1986. The stomiid fish genus *Eustomias* and the oceanic species concept. Pelagic Biogeography. *UNESCO Technical Papers in Marine Science* 49:98–103.
- Gill, A. C. 1999. Subspecies, geographic forms and widespread Indo-Pacific coral-reef fishes species: A call for change in taxonomic practice. In *Proceedings of the 5th Indo-Pacific Fish Conference, Nouméa* ed. B. Séret and J.-Y. Sire, 79–87. Paris: Société Française d'Ichtyologie, 1999.
- Gillooly, J. F., E. L. Charnov, G. B. West, V. M. Savage, and J. H. Brown. 2002. Effects of size and temperature on developmental time. *Nature* 417:70–73.
- Gon, O., and P. C. Heemstra, eds. 1990 *Fishes of the Southern Ocean*. Grahamstown, South Africa: CTP Book Printers.
- Gordon, J. D. M., and J. A. R. Duncan. 1985. The ecology of the deep-sea benthic and benthopelagic fish on the slopes of the Rockall Trough, Northeastern Atlantic. *Progress in Oceanography* 15:37–69.
- Gray, J. S. 2001. Marine diversity: The paradigms in patterns of species richness examined. *Scientia Marina* 65, supplement 2:41–56.
- Grigg, R. W., and R. Hey. 1992. Paleooceanography of the tropical eastern Pacific Ocean. *Science* 255:172–78.
- Haedrich, R. L. 1997. Distribution and population ecology. In *Deep-sea fishes*, ed. D. J. Randall and A. P. Farrell, 79–114. Vol. 16. Fish Physiology series. London: Academic Press.
- Haedrich, R. L., and N. R. Merrett. 1988. Summary atlas of deep-living demersal fishes in the North Atlantic. *Journal of Natural History* 22:1325–62.
- . 1990. Little evidence for faunal zonation or communities in deep demersal fish fauna. *Progress in Oceanography* 24:239–50.
- Harmelin-Vivien, M. 2002. Energetics and fish diversity on coral reefs. In *Coral reef fishes. Dynamics and diversity in a complex ecosystem*, ed. P. F. Sale, 265–74. Amsterdam: Academic Press.
- Hashimoto, J., S. Ohta, K. Fujikura, and T. Miura. 1995. Microdistribution pattern and biogeography of the hydrothermal vent communities of the Minami-Ensei Knoll in the Mid-Okinawa trough, western Pacific. *Deep-sea Research I* 42:577–98.
- Hastings, P. A. 2000. Biogeography of the tropical eastern Pacific: Distribution and phylogeny of chaenopsid fishes. *Zoological Journal of the Linnean Society* 128:319–35.
- Hillebrand, H. 2004. Strength, slope and variability of marine latitudinal gradients. *Marine Ecology Progress Series* 273:251–67.
- Hobson, E. S. 1994. Ecological relations in the evolution of acanthopterygian fishes in warm-temperate communities of the northeastern Pacific. *Environmental Biology of Fishes* 40:49–90.
- Hubbs, C. L. 1948. Changes in the fish fauna of western North America correlated with changes in ocean temperature. *Journal of Marine Research* 7:459–82.

- Hughes, T. P., D. R. Bellwood, and S. R. Connolly. 2002a. Biodiversity hotspots, centres of endemism, and the conservation of coral reefs. *Ecology Letters* 5:775–84.
- Hughes, T. P., A. H. Baird, E. A. Dinsdale, V. J. Harriott, N. A. Moltchanivskij, M. S. Pratchett, J. E. Tanner, and B. L. Willis. 2002b. Detecting regional variation using meta-analysis and large-scale sampling: Latitudinal patterns in recruitment. *Ecology* 83:436–51.
- Jackson, J. B. C. 2001. What was natural in the coastal oceans? *Proceedings of the National Academy of Sciences* 98:5411–18.
- Jennings, S., and J. L. Blanchard. 2004. Fish abundance with no fishing: Predictions based on macroecological theory. *Journal of Animal Ecology* 73:632–42.
- Jennings, S., and M. J. Kaiser. 1998. The effects of fishing on marine ecosystems. *Advances in Marine Biology* 34:203–352.
- Jokiel, P., and F. J. Marinelli. 1992. The vortex model of coral reef biogeography. *Journal of Biogeography* 19:449–58.
- Joyeux, J. C., S. R. Floeter, C. E. L. Ferreira, and J. L. Gasparini. 2001. Biogeography of tropical reef fishes: The South Atlantic puzzle. *Journal of Biogeography* 28:831–41.
- Kerswell, A. P. 2006. Global biodiversity patterns of benthic marine algae. *Ecology* 87:2479–88.
- Knowlton, N. 2004. Multiple “stable” states and the conservation of marine ecosystems. *Progress in Oceanography* 60:387–96.
- Koslow, J. A., C. M. Bulman, and J. M. Lyle. 1994. The mid-slope demersal fish community off Southeastern Australia. *Deep-Sea Research I* 41:113–41.
- Lavery, S., T. Y. Chan, Y. K. Tam, and K. H. Chu. 2004. Phylogenetic relationships and evolutionary history of the shrimp genus *Penaeus* s.l. derived from mitochondrial DNA. *Molecular Phylogenetics and Evolution* 31:39–49.
- Lea, R. N., and R. H. Rosenblatt. 2000. Observations on fishes associated with the 1997–98 El Niño off California. *CalCOFI Report* 41:117–29.
- Leis, J. M. 1984. Larval fish dispersal and the East Pacific barrier. *Oceanography Tropical* 19:181–92.
- Leis, J. M., and M. I. McCormick. 2002. The biology, behavior and ecology of the pelagic, larval stage of coral reef fishes. In *Coral reef fishes. Dynamics and diversity in a complex ecosystem*, ed. P. F. Sale, 171–99. London: Academic Press.
- Lessios, H. A., and D. R. Robertson. 2006. Crossing the impassable: Genetic connections in 20 reef fishes across the Eastern Pacific Barrier. *Proceedings of the Royal Society of London, B* 273:2201–8.
- Lester, S. E., and B. I. Ruttenberg. 2005. The relationship between pelagic larval duration and range size in tropical reef fishes: A synthetic analysis. *Proceedings of the Royal Society of London B* 272:585–91.
- Longhurst, A. 1998. *Ecological geography of the sea*. San Diego: Academic Press.
- Longhurst, A., S. Sathyendranath, T. Platt, and C. Caverhill. 1995. An estimate of global primary production in the ocean from satellite radiometer data. *Journal of Plankton Research* 17:1245–71.
- Love, M. S., M. Yaklovich, and L. Thorsteinson. 2002. *The rockfishes of the Northeast Pacific*. Berkeley, CA: University of California Press.
- Macpherson, E. 1989. Influence of geographical distribution, body size and diet on population density of benthic fishes off Namibia (South West Africa). *Marine Ecology Progress Series* 50:295–99.
- . 2002. Large-scale species-richness gradients in the Atlantic Ocean. *Proceedings of the Royal Society of London B* 269:1715–20.

- . 2003. Species range size distributions for some marine taxa in the Atlantic Ocean. Effect of latitude and depth. *Biological Journal of the Linnean Society* 80:437–55.
- Macpherson, E., and A. Gordo. 1996. Biomass spectra in benthic fish assemblages in the Benguela system. *Marine Ecology Progress Series* 138:27–32.
- Macpherson, E., and N. Raventos. 2006. Relationship between pelagic larval duration and geographic distribution in Mediterranean littoral fishes. *Marine Ecology Progress Series* 327:257–65.
- McFarlane, G. A., J. R. King, and R. J. Beamish. 2000. Have there been recent changes in climate? Ask the fish. *Progress in Oceanography* 47:147–69.
- Marquet, P. A., S. A. Navarrete, and J. C. Castilla. 1990. Scaling population density to body size in rocky intertidal communities. *Science* 250:1125–27.
- Mas-Riera, J., A. Lombarte, A. Gordo, and E. Macpherson. 1990. Influence of Benguela upwelling on the structure of demersal fish populations off Namibia. *Marine Biology* 104:175–82.
- Merret, N. R., and R. L. Haedrich. 1997. *Deep-sea demersal fish and fisheries*. London: Chapman and Hall.
- Miller, R. G. 1993. *History and atlas of the fishes of the Antarctic Ocean*. Carson City, Nevada: Foresta Institute.
- Miya, M., and M. Nishida. 1997. Speciation in the open ocean. *Nature* 389:803–4.
- Mora, C., P. M. Chittaro, P. F. Sale, J. P. Kritzer, and S. A. Ludsin. 2003. Patterns and processes in reef fish diversity. *Nature* 421:933–36.
- Mora, C., and A. F. Ospina. 2001. Tolerance to high temperatures and potential impact of sea warming on reef fishes of Gorgona Island (tropical eastern Pacific). *Marine Biology* 139:765–69.
- Mora, C., and D. R. Robertson. 2005a. Causes of latitudinal gradients in species richness: A test with the endemic shorefishes of the Tropical Eastern Pacific. *Ecology* 86:1771–82.
- . 2005b. Factors shaping the range-size frequency distribution of the endemic fish fauna of the Tropical Eastern Pacific. *Journal of Biogeography* 32:277–86.
- Munday, P. L., and G. P. Jones. 1998. The ecological implications of small body size among coral-reef fishes. *Oceanography and Marine Biology. Annual Review* 36:373–411.
- Muss, A., D. R. Robertson, C. A. Stepien, P. Wirtz, and B. W. Bowen. 2001. Phylogeography of *Ophioblennius*: The role of ocean currents and geography in reef fish evolution. *Evolution* 55:561–72.
- Nelson, J. S. 2006. *Fishes of the world, 4th ed.* New York: Wiley.
- Palumbi, S. R. 1997. Molecular biogeography of the Pacific. *Coral Reefs* 16 (Suppl.): 47–52.
- Parin, N. V., A. N. Mironov, and K. N. Nesis. 1997. Biology of the Nazca and Sala y Gomez Submarine Ridges, an outpost of the Indo-West Pacific fauna in the eastern Pacific Ocean: Composition and distribution of the fauna, its communities and history. *Advances in Marine Biology* 32:145–242.
- Parker, T., and V. Tunnicliffe. 1994. Dispersal strategies of the biota on an oceanic seamount: Implications for ecology and biogeography. *Biological Bulletin* 187:336–45.
- Pearcy, W. G., D. L. Stein, and R. S. Carney. 1982. The deep-sea benthic fish fauna of the north-eastern Pacific Ocean on Cascadia and Tufts abyssal plains and adjoining continental slopes. *Biological Oceanography* 1:375–428.
- Peters, R. H. 1983. *The ecological implications of body size*. Cambridge: Cambridge University Press.
- Pineda, J. 1993. Boundary effects on the vertical ranges of deep-sea benthic species. *Deep-Sea Research* 40:2179–92.

- Planes, S. 2002. Biogeography and larval dispersal inferred from population genetic analysis. In *Coral reef fishes. Dynamics and diversity in a complex ecosystem*, ed. P. F. Sale, 201–20. Amsterdam: Academic Press.
- Pyle, R. L. 1999. Patterns of Pacific reef and shore fish biodiversity. In *Marine and coastal biodiversity in the tropical island Pacific region*, Volume 2: Population, development, and conservation priorities, ed. L. G. Eldredge, J. E. Maragos, P. F. Holthus, and H. F. Takeuchi, 157–75. Honolulu: Pacific Science Association.
- Randall, J. E. 1998. Zoogeography of shore fishes of the Indo-Pacific region. *Zoological Studies* 37:227–68.
- Rex, M. A., J. A. Crame, C. T. Stuart, and A. Clarke. 2005. Large-scale biogeographic patterns in marine molluscs: A confluence of history and productivity? *Ecology* 86:2288–97.
- Rex, M. A., C. T. Stuart, and G. Coyne. 2000. Latitudinal gradients of species richness in the deep-sea benthos of the North-Atlantic. *Proceedings of the National Academy of Sciences* 97:4082–85.
- Rex, M. A., C. T. Stuart, R. R. Hessler, J. A. Allen, H. L. Sanders, and G. D. F. Wilson. 1993. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature* 365:636–39.
- Richer de Forges, B., J. A. Koslow, and G. C. B. Poore. 2000. Diversity and endemism of the benthic seamount fauna in the southwest Pacific. *Nature* 405:944–47.
- Richmond, R. H. 1990. The effects of El Niño/Southern Oscillation on the dispersal of corals and other marine organisms. In *Global ecological consequences of the 1982-83 El Niño Southern Oscillation*, 153–90. Amsterdam: Elsevier.
- Roberts, C. M. 2002. Deep impact: The rising toll of fishing in the deep sea. *Trends in Ecology and Evolution* 17:242–45.
- Robertson, D. R. 1998. Do coral-reef fish faunas have a distinctive taxonomic structure? *Coral Reefs* 17:179–86.
- . 2001. Population maintenance among tropical reef-fishes: Inferences from the biology of small-island endemics. *Proceedings of the National Academy of Sciences* 98:5668–70.
- Robertson, D. R., and G. R. Allen. 2002. Shorefishes of the tropical eastern Pacific: An information system. CD-ROM. Balboa, Panama: Smithsonian Tropical Research Institute.
- Robertson, D. R., J. S. Grove, and J. E. McCosker. 2004. Tropical transpacific shorefishes. *Pacific Science* 4:507–65.
- Robertson, D. R., F. Karg, R. Moura, B. C. Victor, and G. Bernardi. 2006. Mechanisms of speciation and faunal enrichment in Atlantic parrotfishes. *Molecular Phylogenetics and Evolution* 40:795–807.
- Robins, C. R. 1971. Distributional patterns of fishes from coastal and shelf waters of the tropical western Atlantic. *FAO Fisheries Report* 72-2:249–255.
- Rocha, L. A. 2003. Patterns of distribution and processes of speciation in Brazilian reef fishes. *Journal of Biogeography* 30:1161–71.
- Rocha, L. A., A. Bass, D. R. Robertson, and B. W. Bowen. 2002. Adult habitat preferences, larval dispersal and the comparative phylogeography of three Atlantic surgeonfishes (Teleostei: Acanthuridae). *Molecular Evolution* 11:243–52.
- Rocha, L. A., D. R. Robertson, J. Roman, and B. W. Bowen. 2005a. Ecological speciation in tropical reef fishes. *Proceedings of the Royal Society of London B* 272:573–79.
- Rocha, L. A., D. R. Robertson, C. R. Rocha, J. L. Van Tassell, M. Craig, and B. W. Bowen. 2005b. Recent colonization of the Atlantic by an Indo-Pacific reef fish. *Molecular Ecology* 14:3921–28.
- Rodriguez, J., J. Tintore, J. T. Allen, J. M. Blanco, D. Gomis, A. Reul, J. Ruiz, V. Rodriguez,

- F. Echevarria, and F. Jimenez-Gomez. 2001. Mesoscale vertical motion and the size structure of phytoplankton in the ocean. *Nature* 410:360–63.
- Rogers, A. D. 1994. The biology of seamounts. *Advances in Marine Biology* 30:305–50.
- Rohde, K. 1992. Latitudinal gradients in species diversity: The search for the primary cause. *Oikos* 65:514–27.
- . 1999. Latitudinal gradients in species diversity and Rapoport's rule revisited: A review of recent work and what can parasites teach us about the causes of the gradients? *Ecography* 22:593–613.
- Rohde, K., and M. Heap. 1996. Latitudinal ranges of teleost fish in the Atlantic and Indo-Pacific oceans. *The American Naturalist* 147:659–65.
- Rohde, K., M. Heap, and D. Heap. 1993. Rapoport's rule does not apply to marine teleosts and cannot explain latitudinal gradients in species richness. *The American Naturalist* 142:1–16.
- Rosenblatt, R. H. 1967. The zoogeographic relationships of the marine shore fishes of tropical America. *Studies of Tropical Oceanography* 5:579–92.
- Roy, K., D. Jablonski, and J. W. Valentine. 1994. Eastern Pacific molluscan provinces and latitudinal diversity gradient: No evidence for "Rapoport's rule." *Proceedings of the National Academy of Sciences* 91:8871–74.
- . 2000. Dissecting latitudinal diversity gradients: Functional groups and clades of marine bivalves. *Proceedings of the Royal Society of London B* 267:293–99.
- Roy, K., D. Jablonski, J. W. Valentine, and G. Rosenberg. 1998. Marine latitudinal diversity gradients: Tests of causal hypotheses. *Proceedings of the National Academy of Sciences* 95:3699–3702.
- Ruhl, H. A., and K. L. Smith, Jr. 2004. Shifts in deep-sea community structure linked to climate and food supply. *Science* 305:513–15.
- Rutherford, S., S. D'Hondt, and W. Prell. 1999. Environmental controls on the geographic distribution of zooplankton diversity. *Nature* 400:749–53.
- Shanks, A. L., and G. L. Eckert. 2005. Population persistence of California current fishes and benthic crustaceans: A marine drift paradox. *Ecological Monographs* 75:505–24.
- Sheldon, R. W., A. Prakash, and W. H. Sutcliffe. 1972. The size distribution of particles in the ocean. *Limnology and Oceanography* 17:327–40.
- Shulman M. J., and E. Bermingham. 1995. Early-life histories, ocean currents, and the population-genetics of Caribbean reef fishes. *Evolution* 49:897–910.
- Smith, K. F., and J. H. Brown. 2002. Patterns of diversity, depth range and body size among pelagic fishes along a gradient of depth. *Global Ecology and Biogeography* 11:313–22.
- Smith, M. L., K. E. Carpenter, and R. K. Waller. 2002. An introduction to the oceanography, geology, biogeography, and fisheries of the tropical and subtropical western central Atlantic. In *The living marine resources of the western central Atlantic. Vol 1: Introduction, molluscs, crustaceans, hagfishes, sharks, batoid fishes, and chimaeras*, ed. K. E. Carpenter, 1–23. Rome: FAO.
- Springer, V. G. 1982. Pacific plate biogeography, with special reference to shorefishes. *Smithsonian Contribution of Zoology* 465:1–182.
- Springer, V. G., and J. T. Williams. 1990. Widely distributed Pacific plate endemics and lowered sea-level. *Bulletin of Marine Science* 47:631–40.
- Sprules, W. G., and M. Munawar. 1986. Plankton size spectra in relation to ecosystem productivity, size and perturbation. *Canadian Journal of Fishery and Aquatic Sciences* 43:1789–94.
- Stehli, F. G., A. L. McAlester, and C. E. Newell. 1969. Generation and maintenance of gradients of taxonomic diversity. *Science* 164:947–49.

- Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K. S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. *Science* 297:1292–96.
- Stevens, G. C. 1989. The latitudinal gradient in geographical range: How so many species co-exist in the tropics. *The American Naturalist* 133:240–56.
- . 1996. Extending Rapoport's rule to Pacific marine fishes. *Journal of Biogeography* 23:149–54.
- Taylor, M. S., and M. E. Hellberg. 2003. Genetic evidence for local retention of pelagic larvae in a Caribbean reef fish. *Science* 299:107–9.
- Thatje, S., C. D. Hillenbrand, and R. Larter. 2005. On the origin of Antarctic marine benthic community structure. *Trends in Ecology and Evolution* 20:534–40.
- Tunnicliffe, V. 1991. The biology of hydrothermal vents: Ecology and evolution. *Oceanography and Marine Biology Annual Reviews* 29:319–407.
- Tunnicliffe, V., and C. M. R. Fowler. 1996. Influence of sea-floor spreading on the global hydrothermal vent fauna. *Nature* 379:531–33.
- Van Dover, C. L. 2000. *The ecology of deep-sea hydrothermal vents*. Princeton, NJ: Princeton University Press.
- Van Dover, C. L., C. R. German, K. G. Speer, L. M. Parson, and R. C. Vrijenhoek. 2002. Evolution and biogeography of deep-sea vent and seep invertebrates. *Science* 295:1253–57.
- Victor, B. C., and G. M. Wellington. 2000. Endemism and the pelagic larval duration of reef fishes in the eastern Pacific Ocean. *Marine Ecology Progress Series* 205:241–48.
- Victor, B. C., G. M. Wellington, D. R. Robertson, and B. I. Ruttenberg. 2001. The effect of El Niño-Southern Oscillation event on the distribution of reef-associated labrid fishes in the eastern Pacific Ocean. *Bulletin of Marine Science* 69:279–88.
- Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: Pattern, process, scale and synthesis. *Annual Review of Ecology and Systematics* 34:273–309.
- Wilson, R. R., and R. S. Kaufmann. 1987. Seamount biota and biogeography. In *Seamounts, islands and atolls*, ed. B. H. Keating, P. Fryer, R. Batiza, and G. W. Boehlert, 319–34. Geophysical Monograph 43. Washington, DC: American Geophysical Union.
- Worm, B., H. K. Lotze, and R. A. Myers. 2003. Predator diversity hotspots in the blue ocean. *Proceedings of the National Academy of Sciences* 100:9884–88.
- Zapata, F. A., K. J. Gaston, and S. L. Chown. 2005. The mid-domain effect revisited. *The American Naturalist* 166:144–48.
- Zapata, F. A., and D. R. Robertson. 2006. How many species of shore fishes are there in the Tropical Eastern Pacific? *Journal of Biogeography* 34:38–51.
- Zeina, O. N. 1997. Biogeography of the bathyal zone. *Advances in Marine Biology* 32:389–426.
- Zhang, C. I., J. B. Lee, S. Kim, and J. Oh. 2000. Climatic regime shifts and their impacts on marine ecosystem and fisheries resources in Korean waters. *Progress in Oceanography* 47:171–90.