



CHAPTER 1

The History and Biogeography of Fishes on Coral Reefs

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I. Introduction

Coral reefs have been around since the Ordovician (Wood, 1999), and throughout their 450-million-year history they have shared the oceans with fishes. Modern scleractinian-dominated coral reefs and their associated fish faunas represent only the latest manifestation of a reefal ecosystem. It is almost self-evident that history is important to coral reefs, as the reefs build on the skeletons of past generations. But what of the associated fauna? Today, fishes form an integral part of reef communities, modifying benthic community structure and forming a major conduit for the movement of energy and material. Like the reefs, reef fish faunas have been shaped by history, but this historical influence may not be as apparent. Although it is becoming increasingly clear that history plays an important role in structuring local communities (Ricklefs and Schluter, 1993a), its influence on the ecology and biogeography of fishes on coral reefs remains largely unknown.

Most studies of reef systems have addressed the question of how biogeographic and ecological patterns

are maintained; relatively few consider how these patterns arose or their consequences. However, it is the combination of these two factors, origins and maintenance, that offers the clearest understanding of the nature of biogeographic patterns in reef organisms. Studies of the history of coral reefs have been largely restricted to documenting the history of the reef builders, which have left an outstanding fossil record (Wood, 1999). The history of associated faunas, and fish in particular, is less clear. However, this is changing, primarily as a result of phylogenetic analyses of reef fishes and from a reappraisal of the fossil record.

Until recently, historical considerations of reef fishes were restricted largely to studies by museum workers (e.g., Allen, Randall, Springer, Winterbottom) who examined the taxonomy, systematics, and biogeography of extant reef fishes. Paleontological information has likewise been confined to the works of specialists in museums. Workers such as Blot, Sorbini, and Tyler have provided a sound basis for the evaluation of the fossil record of reef fishes. The broader application of these findings to present-day ecology, community structure, and ecosystem function has only recently begun to be considered. Ecologists are looking increasingly at data from large temporal and spatial scales to provide a framework within which to interpret local patterns and small-scale experimental results. It is from this integration of systematics, biogeography, ecology, and paleontology that a new understanding of the nature of reef fishes is arising.

In this chapter we summarize our knowledge of the phylogenetics, paleontology, and biogeography of fishes on coral reefs and examine how these data, along with geological evidence, can aid our understanding of the role of historical factors in shaping modern coral reef fish faunas and their ecological attributes. In particular, we wish to address several specific questions:

1. What are coral reef fishes, when did they appear, and where did they come from?
2. Are Caribbean and Indo-Pacific reef fish assemblages comparable, and how do we explain major differences in reef fish assemblages across the Indo-Pacific?
3. How tight is the reef fish–coral reef association, and how do we evaluate the interaction between fishes and coral reefs?
4. What role have fishes played in the evolution of coral reefs, and is there any evidence of a change in this role over time?

II. Reef Fishes: Definitions and Distribution Patterns

Reef fishes are often seen as a distinctive and easily characterized group of fishes. However, though numerous texts and papers refer to “reef fishes,” the uniting characteristics of these assemblages are rarely defined. Although there have been several attempts to characterize the essence of a reef fish, none of these descriptions has proved to be diagnostic. Bellwood (1988a) provided a classification based on the degree of ecological association between the fish and reef, in terms of the reef’s role in providing food and/or shelter. A broader overview was given in Choat and Bellwood (1991), who described the ecological and taxonomic characteristics of reef fishes. In this scheme, they noted the abundance of small-gaped deep-bodied fishes on reefs, and the numerical dominance of a few families, including labrids, pomacentrids, chaetodontids, and acanthurids. Later Bellwood (1996a) established a more specific “consensus list” of reef fish families. This list comprised all families that one would find on a coral reef irrespective of its biogeographic location (i.e., Acanthuridae, Apogonidae, Blenniidae, Carangidae, Chaetodontidae, Holocentridae, Labridae, Mullidae, Pomacentridae, and Scaridae). These 10 families were regarded as characteristic reef fish families, the essence of a reef fish fauna; all are abundant and speciose on coral reefs (Fig. 1, but see Section VI below).

However, these studies have all looked at the similarities among reef fish faunas. They provide only a description of a reef fish fauna and are not diagnostic (Bellwood, 1998). Further examination of reef and non-reef areas has found that many of the characteristics of reef fish faunas may apply equally well to nonreefal fish faunas (Bellwood, 1998; Robertson, 1998b). In this chapter therefore, the term “reef fish” refers to those taxa that are found on, and are characteristic of, coral

reefs (i.e., the consensus list plus taxa characteristic of reefs in specific areas).

An understanding of the nature of the differences among reef fish faunas is critical to our understanding of the evolution of reef fishes and the role of history in determining the structure of modern reef fish assemblages. The dissimilarity between reef fish faunas can be seen in Fig. 1, which contrasts the species richness in a number of fish families at four biogeographically distinct reefal locations. Several features are immediately apparent:

1. Despite a more than threefold decrease in species numbers between the Great Barrier Reef (GBR) and the Red Sea, the basic pattern remains broadly comparable. The Red Sea reef fish fauna appears to be a random subset of a comparable high-diversity Indo-Pacific system such as the GBR. Indeed, there is no significant difference between the two faunas in terms of the distribution of species in families (χ^2 16.9; p , 0.46; df, 17).

2. Although overall the data for species/familial diversity are similar in the Caribbean and Red Sea (277/45 and 281/40, respectively), the familial composition and patterns of familial species richness vary markedly. In the Caribbean, the Lethrinidae, Pseudochromidae, Siganidae, Nemipteridae, and Caesionidae (Caesioninae) are absent. Together these families comprise approximately 7% of the species in the GBR fish fauna. However, several families are relatively well represented in the Caribbean, including the Serranidae, Haemulidae, and Sparidae and the regional (East Pacific/Caribbean) endemics, the Chaenopsidae and Labrisomidae.

3. Many of the characteristic reef fish families (e.g., Labridae, Pomacentridae) are present and abundant in New Zealand, a temperate region devoid of coral reefs. A similar pattern is seen in South Africa, South Australia, and western North America. Thus, although we readily recognize them as coral reef fish families, most of these characteristic reef fish families do not disappear when coral reefs stop. These taxa are characteristic of, but not restricted to, coral reefs.

If comparable data sets collected from a range of reefal and subtropical/temperate locations are examined using a Principal Component Analysis [PCA; modified after Bellwood (1997)] clear regional groupings are apparent (Fig. 2A, C), with high-, medium-, and low-diversity, low-latitude Indo-Pacific sites laying along the first axis. The decreasing diversity at these sites generally tracks a longitudinal shift away from

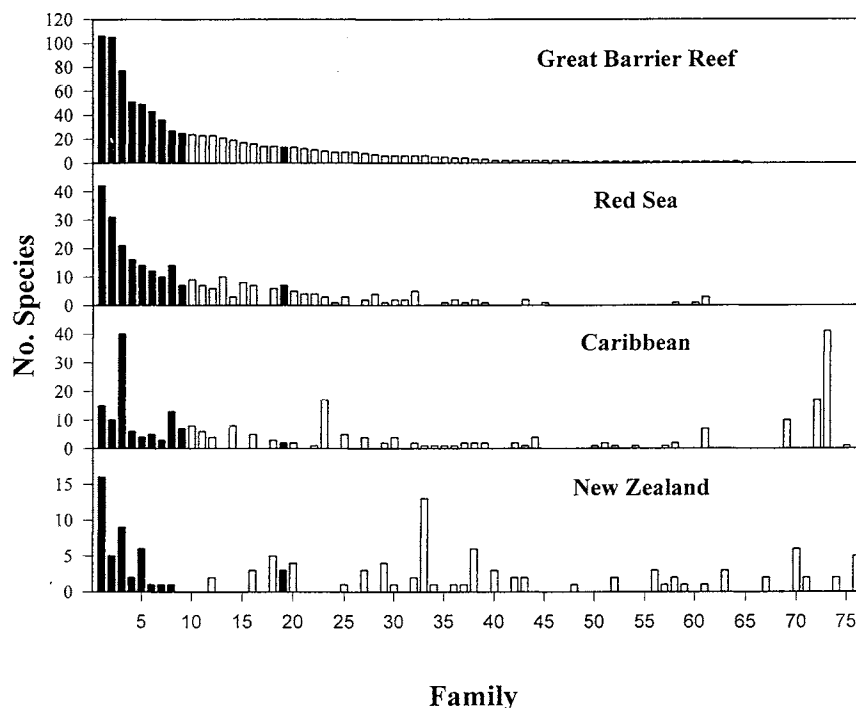


FIGURE 1 Species richness, by family, at four sites. The ranking of families at each site follows the Great Barrier Reef. Characteristic reef fish families are indicated by solid bars (after Bellwood, 1996a, 1997). Families: 1, Labridae; 2, Pomacentridae; 3, Serranidae; 4, Blenniidae; 5, Apogonidae; 6, Chaetodontidae; 7, Acanthuridae; 8, Scaridae; 9, Holocentridae; 10, Lutjanidae; 11, Pomacanthidae; 12, Scorpaenidae; 13, Lethrinidae; 14, Monacanthidae; 15, Pseudochromidae; 16, Balistidae; 17, Microdesmidae; 18, Tetraodontidae; 19, Mullidae; 20, Syngnathidae; 21, Siganidae; 22, Cirrhitidae; 23, Haemulidae; 24, Nemipteridae; 25, Ostraciidae; 26, Pinguipedidae; 27, Synodontidae; 28, Caesionidae; 29, Antennariidae; 30, Diodontidae; 31, Plesiopidae; 32, Sphyrnidae; 33, Tripterygiidae; 34, Callionymidae; 35, Ephippidae; 36, Malacanthidae; 37, Pempheridae; 38, Kyphosidae; 39, Priacanthidae; 40, Bythitidae; 41, Caracanthidae; 42, Gobiesocidae; 43, Mugilidae; 44, Opistognathidae; 45, Plotosidae; 46, Solenostomidae; 47, Trichonotidae; 48, Acanthoclinidae; 49, Aploactinidae; 50, Aulostomidae; 51, Batrachoididae; 52, Carapidae; 53, Centriscidae; 54, Centropomidae; 55, Chandidae; 56, Creediidae; 57, Dactylopteridae; 58, Echeinidae; 59, Eleotridae; 60, Fistulariidae; 61, Sparidae; 62, Teraponidae; 63, Uranoscopidae; 64, Xenisthmidae; 65, Zancidae; 66, Albulidae; 67, Aplodactylidae; 68, Berycidae; 69, Chaenopsidae; 70, Cheilodactylidae; 71, Clinidae; 72, Cynoglossidae; 73, Labrisomidae; 74, Odacidae; 75, Ogcocephalidae; 76, Pentacerotidae.

the Indo-Australian Archipelago. Examination of the family-vectors (Fig. 2B) suggests that the first axis is associated primarily with total species richness. However, principal component 1 (PC1) does not just measure species richness. The scores reflect similar numbers of species in those families exhibiting greatest variation in the data set. The strong correlation with total species richness reflects the congruence among families in the decrease in familial species richness. This pattern is seen in the relatively uniform orientation of family-vectors around PC1, which also suggests that

differences between high- and low-diversity sites are a result of the absence of taxa at low-diversity sites, i.e., there is no replacement. Low-diversity, low-latitude sites merely contain a lower number of species in the families found at high-diversity sites (as in Fig. 1). There are no “new” families that are characteristic of low-diversity sites (cf. Bellwood and Hughes, 2001).

The second axis explains only 12.3% of the variation but it appears to reflect changes in the relative composition of the assemblages in terms of temperate vs. tropical taxa (Fig. 2B). This axis separates high-latitude

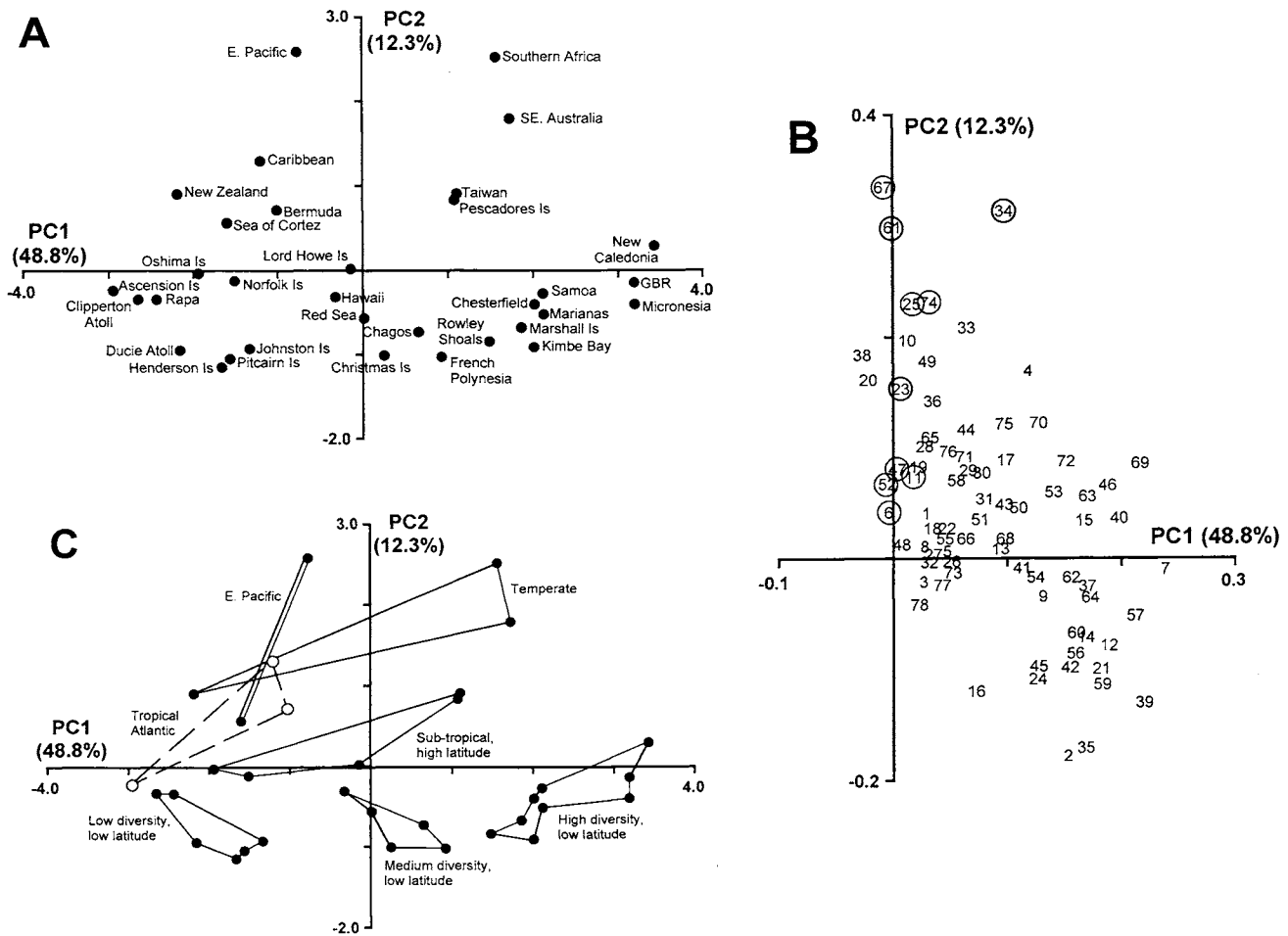


FIGURE 2 Principal Component Analysis of reef and nonreef sites. (A) Plot of sites on the first two axes. (B) Family-vectors, with families as listed below (temperate families are encircled). (C) Plot of sites on the first two axes with tropical, subtropical, and temperate sites delineated. Solid dots and solid lines indicate Indo-Pacific sites; open dots and dashed lines indicate Atlantic sites. Families: 1, Acanthoclinidae; 2, Acanthuridae; 3, Albulidae; 4, Antennariidae; 5, Aplodactylidae; 6, Aploacinidae; 7, Apogonidae; 8, Aulostomidae; 9, Balistidae; 10, Batrachoididae; 11, Berycidae; 12, Blenniidae; 13, Bythitidae; 14, Caesionidae; 15, Callionymidae; 16, Caracanthidae; 17, Carapidae; 18, Centriscidae; 19, Centropomidae; 20, Chaenopsidae; 21, Chaetodontidae; 22, Chandidae; 23, Cheilodactylidae; 24, Cirrhitidae; 25, Clinidae; 26, Creediidae; 27, Dactylopteridae; 28, Diodontidae; 29, Echeinidae; 30, Eleotridae; 31, Ehippidae; 32, Fistulariidae; 33, Gobiesocidae; 34, Haemulidae; 35, Holocentridae; 36, Kyphosidae; 37, Labridae; 38, Labrisomidae; 39, Lethrinidae; 40, Lutjanidae; 41, Malacanthidae; 42, Microdesmidae; 43, Monacanthidae; 44, Mugilidae; 45, Mullidae; 46, Nemipteridae; 47, Odacidae; 48, Ogcocephalidae; 49, Opistognathidae; 50, Ostraciidae; 51, Pempheridae; 52, Pentacerotidae; 53, Pinguipedidae; 54, Plesiopidae; 55, Plotosidae; 56, Pomacanthidae; 57, Pomacentridae; 58, Priacanthidae; 59, Pseudochromidae; 60, Scaridae; 61, Sciaenidae; 62, Scorpaenidae; 63, Serranidae; 64, Siganidae; 65, Sillaginidae; 66, Solenostomidae; 67, Sparidae; 68, Sphyranidae; 69, Syngnathidae; 70, Synodontidae; 71, Teraponidae; 72, Tetraodontidae; 73, Trichonotidae; 74, Triglidae; 75, Tripterygiidae; 76, Uranoscopidae; 77, Xenisthmidae; 78, Zanclidae.

vs. low-latitude low-diversity assemblages in the Indo-Pacific. As one moves away from the center of diversity in the Indo-Australian Archipelago, total species diversity decreases steadily with changes in both latitude and longitude. In both cases, characteristic reef fish families remain consistently well represented, whereas less

speciose families are progressively lost. However, the latitudinal and longitudinal changes are not the same; high-latitude sites have a marked temperate influence.

This temperate influence is even clearer in the tropical Atlantic and tropical East Pacific sites. These sites are united by the presence of endemic families

(Chaenopsidae, Labrisomidae), the absence of several speciose Indo-Pacific families (e.g., Lethrinidae, Nemipteridae, Siganidae), and an increase in the diversity of other families (Haemulidae), including some with a strong representation in temperate waters (e.g., Sparidae, Monacanthidae). This similarity probably reflects a common history of the two areas prior to the closure of the Isthmus of Panama and a shared period of faunal loss (see Sections IV and V). The analyses suggest that the Caribbean, despite being a low-latitude tropical region with strong coral reef development, has a reef fish fauna that is more similar to those of high latitude or temperate Indo-Pacific sites than to tropical Indo-Pacific sites. The Caribbean reef fish fauna has a distinct temperate component.

The similarity between the patterns described in reef fishes and corals are striking (Bellwood and Hughes, 2001). The two groups have markedly different life histories, approaching the extremes seen in marine benthic faunas. If the biogeographic patterns seen in fish and corals reflect a common mechanism, then the processes may be operating at the regional or ecosystem level and at large temporal scales. If this is the case, then one may expect to see congruent patterns in other benthic marine taxa.

III. The Origins of Reef Fishes

A. Major Lineages

Fishes and corals both have a long tenure in the fossil record. However, at what point in the past did events begin to have a direct bearing on the ecology and distribution patterns of modern reef fish taxa? Devonian fish certainly have a legacy that passes through to modern times, but when did the history of modern reef fishes begin? The answer, it seems, is that these groups were already in place by the early Tertiary [50 million years (Ma) ago], with origins spreading back to at least the late Cretaceous (70 Ma), and possibly even to the early Cretaceous (100–130 Ma).

Most reef fish families have been placed in the order Perciformes. This order contains approximately 9293 species, and represents about 63% of all marine fish species (Nelson, 1994). The order encompasses about 75% of the fish species found on coral reefs (Randall *et al.*, 1990), including all of the characteristic reef fish families (Fig. 1). Unfortunately this order is probably paraphyletic (Johnson and Patterson, 1993). However, the Perciformes along with the Scorpaeniformes, Pleuronectiformes, and Tetraodontiformes may form a monophyletic group, the Percomorpha (*sensu* Johnson and Patterson, 1993).

Estimates of the ages of major fish groups are based on fossils or inferences from cladograms and biogeographic patterns. Fossil evidence ranges from isolated fragments, predominantly otoliths, to complete, fully articulated skeletons. Age estimates based on otoliths are consistently older than those based on complete skeletons (cf. Patterson, 1993), possibly reflecting the abundance of otoliths in the fossil record and the fact that otoliths do not require the exceptional conditions necessary for preservation of the complete fish skeleton. Identifying a fish taxon based on otoliths can be difficult because they have a limited range of characters, often of unknown phylogenetic significance. Furthermore, fossil otoliths are often worn, and considerable subjectivity may arise in character-state designations. The taxonomic utility of otoliths also varies widely between taxa (Nolf, 1985). In contrast, complete skeletons often permit fossil taxa to be incorporated into existing cladograms, providing estimates of the minimum age of specific lineages along with a great deal of information on changes in functional capabilities through time. However, complete fossil skeletons of reef fishes are rare and minimum ages based on complete skeletons are likely to underestimate the actual age of the group.

The biogeographic patterns of reef fishes observed today are the result of a long and complex history, which has probably involved a number of vicariance, dispersal, and extinction events (Fig. 3). When trying to disentangle this convoluted history, fossils provide a unique series of reference points. The utility of fossils in the study of phylogeny and biogeography has been critically appraised by Patterson (1981) and Humphreys and Parenti (1986). Fossils provide neither ancestors nor absolute ages of taxa. However, accurately dated fossils, when combined with phylogenies, can provide the minimum age of a lineage, its sister group, and all of the more basal lineages. Given this age one may be able to identify the vicariance events (i.e., environmental changes leading to the separation of populations) that were associated with the origin and subsequent diversification of lineages. Fossils also pinpoint a taxon in a location at a given time. This is particularly valuable when this location lies outside the geographic range of living forms.

The earliest record of the Perciformes is based on otoliths from the late Cretaceous (Cenomanian, 97.0–90.4 Ma) (Patterson, 1993), with the first full skeleton, *Nardoichthys*, being recorded from the upper Campanian/lower Maastrichtian (c. 74 Ma) of southern Italy (Sorbini and Bannikov, 1991). Of the remaining percomorph groups the oldest fossil, to date, is a tetraodontid *Plectocretacicus* (Sorbini, 1979) from the late

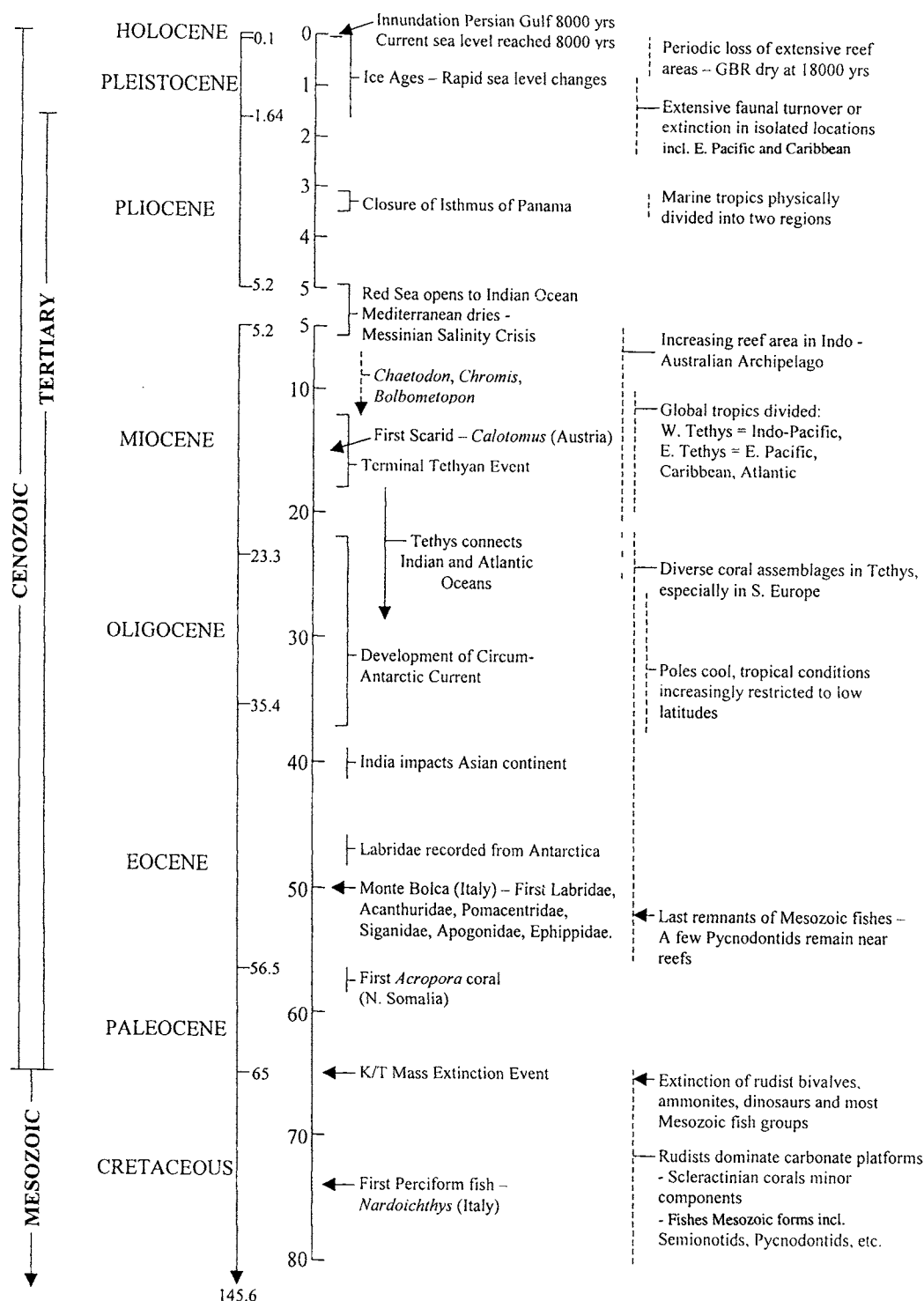


FIGURE 3 Major events in the history of fishes on coral reefs, showing the relationship between the appearance or loss of fish groups, changes in the status of coral reefs, and major biogeographic events. Earliest records of fish groups refer to identifications based on complete skeletal remains. Ages given in Ma. See text for details.

Cretaceous (Cenomanian, 97.0–90.4 Ma). The Pleuronectiformes and Scorpaeniformes are first recorded from otoliths in the Eocene (Ypresian, 56.5–50 Ma), with whole skeletons first recorded in the Lutetian (50 Ma) and Langhian (14.4 Ma), respectively (Patterson, 1993; Schultz, 1993). The oldest records of most of the characteristic reef fish families are equivocal or based on otoliths. The oldest records of the Acanthuridae, Labridae, and Pomacentridae (and the Zaclidae, Siganidae, Ehippididae, and Sparidae) based on skeletal material are Eocene (50 Ma) (Bellwood, 1996a) (Fig. 3).

The second line of evidence that may provide some indication of the age of reef fish lineages is historical biogeography, incorporating geological, biogeographic, and phylogenetic evidence. Of all perciform groups the clearest pattern of historical division is seen in the freshwater cichlids (a group that may be closely allied to the marine Pomacentridae). Today, cichlids are found in rivers and lakes throughout South America, Africa, Madagascar, and the southern extremity of the Indian subcontinent. All of these land masses are Gondwanan fragments. The break up of Gondwana extended over a period of about 80 Ma from an initial separation about 135 Ma to the final separation of South America and Africa in the North Atlantic at about 84 Ma (Lundberg, 1993). The presence of cichlids on all three continents (Africa, South America, and Asia) presents a dilemma. Either they were associated with the land masses prior to separation, cichlid origins being at least 100 Ma, or cichlids maintained contact between land masses through extensive marine connections. Lundberg (1993), in a thorough review of African–South American fish relationships, favored the latter option. This interpretation is consistent with the fossil record. The oldest cichlid fossils are from the Eocene of Africa, at about 46 Ma (Murray, 2001). This date is consistent with the oldest record of the other labroids, the Pomacentridae and Labridae, at 50 Ma (Bellwood and Sorbini, 1996). At 100 Ma the origins of the Cichlidae, based on a biogeographic model, would predate the earliest fossil of the family and that of any other extant perciform family by over 40 Ma.

Although there are brackish or fully marine dwelling cichlids on all occupied continents, Cenozoic trans-Atlantic dispersal seems unlikely given the clear regionalization seen in the major cichlid clades (cf. Stiassny, 1991). A much older origin for the Cichlidae and therefore the Perciformes must remain a possibility, with the Cichlidae being widespread across Gondwana prior to fragmentation. This would require the origin of the group to be in the order of 100 Ma. Comparable early origins have been proposed based on

biogeographic evidence for congrogadins (Pseudochromidae) (Winterbottom, 1986) and teraponids (Vari, 1978). Recent biogeographic interpretations based on molecular phylogenies are consistent with these early origins. In both the Cichlidae and the aplocheiloid cyprinodontiforms the molecular phylogenies strongly suggest that the distributions of taxa within the two respective groups are the result of Gondwanan fragmentation (Murphy and Collier, 1997; Farias et al., 1999). If this were the case, then the cladogram of Streelman and Karl (1997) would suggest that several reef fish lineages (labrids, pomacentrids, acanthurids, and pomacanthids) were already established prior to Gondwanan fragmentation (i.e., over 125 Ma). The biogeographic model therefore suggests that major reef fish lineages may have early Cretaceous origins.

It is almost axiomatic that the only surprise that the fossil record holds, in terms of the age of taxa, is that taxa are older than previously thought. Care must be taken, therefore, in ascribing minimum ages. Phylogenies and biogeographic patterns present interesting possibilities, otoliths provide tentative oldest recorded minimum ages, whereas the most conservative estimates are based on whole specimens. The discrepancy between historical biogeography (perciform origins 100–125 Ma) and the fossil record (74–100 Ma) is yet to be resolved. Molecular techniques that shed light on older relationships appear to be a particularly promising source of new information (cf. Streelman and Karl, 1997).

B. Reef Fish Families

So far we have examined the origins of the major lineages. In terms of the fossil record, this represents a handful of specimens in three or four species covering the whole of the Percomorpha. What about the families and genera of fishes found on reefs today? How did the diversity of fishes seen on modern reefs arise? Was it the steady accumulation of more and more complex forms, a progressive series of faunal replacements with major periods of diversification and loss, as in terrestrial mammal faunas?

Some of the answers to these questions lie in the exceptional fossil fishes collected from Monte Bolca in the foothills of the Italian Alps. Here, Eocene marine deposits have yielded a large quantity of fossil fishes of excellent preservation quality (Fig. 4). The fossil deposits of Monte Bolca have yielded over 250 species in 82 families. These specimens include the first representatives of almost all fish families found on coral reefs today (Patterson, 1993; Bellwood, 1996a). In terms of reef fish families, the Bolca fish fauna is relatively

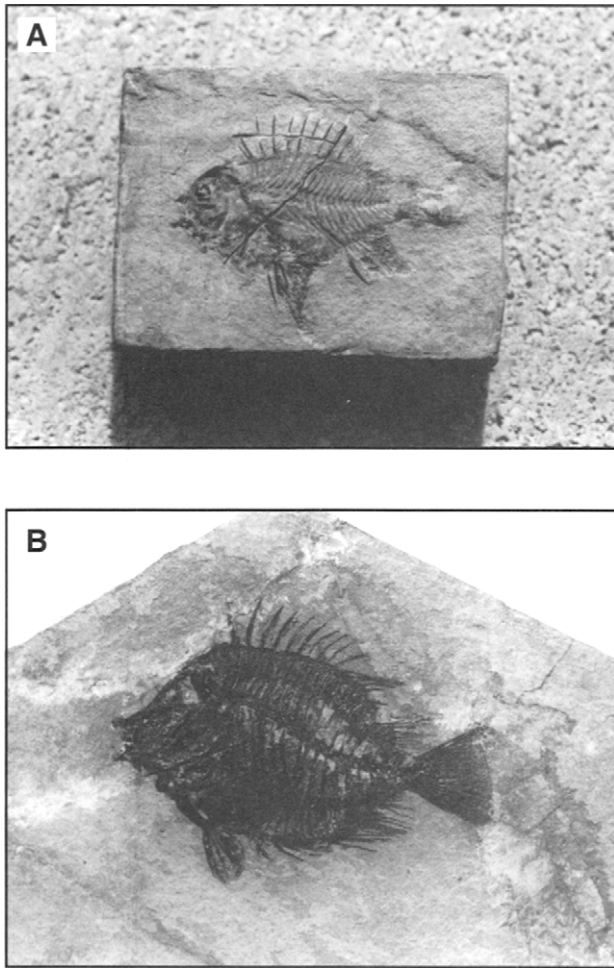


FIGURE 4 (A) *Palaeopomacentrus orphae* Bellwood & Sorbini, a fossil pomacentrid from the Eocene (50 Ma) deposits of Monte Bolca, Italy; 29.5 mm standard length. This is the first of two pomacentrid species recovered from these deposits. (B) *Lehmanichthys lessiniensis* Blot & Tyler, a fossil acanthurid from Monte Bolca; 71 mm standard length. Acanthurids were particularly well represented in Monte Bolca, with over 10 genera recorded. Reprinted with permission from Museo Civico di Storia Naturale, Verona, Italy.

complete. Thus, by the late lower Eocene (50 Ma), almost all modern reef fish families are present in a single biogeographic location. Furthermore, the benthic component of this fauna is dominated by perciform fishes. This may not appear surprising; however, only 15 Ma earlier the Perciformes is represented in the fossil record by only a few specimens of one species. Bolca also marks a period of transition, with the last remnants of ancient Mesozoic forms (i.e., pycnodontids) persisting along with modern reef fish families.

In this chapter families are frequently used to examine historical patterns. It should be noted, however, that

this does not imply equivalent status to these groups (families, genera, and, to a lesser extent, species are relatively arbitrary groupings). Families are often identified by traits that are evident in fossils, providing a common taxonomic basis for comparing living and ancient assemblages (Bellwood, 1996a). Given the paucity of information on relationships among taxa, families have no stronger status than any other taxonomic level—they merely represent major lineages with sufficiently distinct body plans to suggest monophyly. The status of almost all family groupings is in need of reappraisal.

In addition to the strong links between Bolca and modern reef fish assemblages in terms of fish families, several extant perciform genera have also been recorded from the deposits, including *Acropoma*, *Pristigenys*, *Mene*, *Scatophagus*, and *Seriola* (Blot, 1980). The latter may be regarded as a member of a “characteristic” reef fish family (Carangidae), although it is a more open-water genus. Besides this example, the oldest records of extant “reef fish” genera appear to be in the Miocene with *Chaetodon* (Arambourg, 1927), *Chromis* (Bellwood and Sorbini, 1996), and *Bolbometopon* and *Calotomus* (Bellwood and Schultz, 1991).

The morphology of species in reef fish families recovered from Monte Bolca is almost indistinguishable from that of living representatives. These were not “primitive” precursors of modern forms. Their structural features and implied functional and ecological characteristics are comparable to those of modern reef fishes. Indeed, the level of preservation is such that in some cases pigment patterns can be seen, with striking similarities to living forms. A juvenile *Scatophagus* from Bolca has pigment bands on the body that are almost identical to those found on living forms, and the two earliest pomacentrids, *Palaeopomacentrus orphae* and *Lorenzichthys olihan*, both have an ocellus on the dorsal fin comparable to those seen on juvenile pomacentrids today (Bellwood, 1999; Bellwood and Sorbini, 1996). On a dive along the coast of the Tethys Sea in the Bolca region 50 million years ago one would see a fish fauna little different from that in the tropics today. Most reef fish families would be represented, complete with “modern” morphological attributes. Modern underwater fish identification sheets would suffice to identify many of the fish families.

Bolca marks the starting point in the known evolution of most reef fish families. Their presence in one location 50 million years ago highlights the stability of the taxonomic and morphological characteristics of tropical benthic marine fish faunas throughout the Cenozoic. This suggests that the broad similarities in the familial composition of modern reef fish faunas may

reflect an old shared history rather than recent colonization, and that familial differences between reef regions may be explained by subsequent events. It is this post-Eocene history in which the differences between major reef regions probably arose.

IV. Barriers and Vicariance Events in the Evolution and Biogeography of Reef Fishes

Throughout the Cretaceous the Tethys Sea was the dominant tropical marine seaway. During most of this period, there was widespread reef construction. These reefs were dominated by rudist bivalves, although hermatypic corals and algae were present (Kauffman and Fagerstrom, 1993). Scleractinian corals were a minor structural component (Kauffman and Sohl, 1974; Wood, 1999). Toward the end of the Upper Cretaceous the rudist reefs disappeared, to be replaced sometime later by scleractinian coral reefs. By the Eocene, some 20 Ma after the loss of the rudists, the Tethys Sea had an essentially modern tropical fauna. Reefs were dominated by scleractinian corals, and modern reef fish

families were abundant in the vicinity. From these reef fishes we can trace a continuous history through to those fishes living on reefs today.

Throughout their history the tropical seas in which we find reef fishes have been repeatedly divided, with each fragment having a different history through to the present. In some areas, the occupants were completely eliminated; in other areas they prospered, their individual fates being dependent on a complex series of interacting factors, including geographic location, regional connectivity, size, bathymetry, and the timing of the separation.

Barriers separating marine populations vary widely, from complete physical barriers such as land bridges, to partial barriers resulting from distance, currents, or ecology. The barriers may be permanent or intermittent. In several areas barriers can be clearly identified, but in other areas barriers are only inferred, being marked by faunal breaks with no clear geological or biological explanation (Fig. 5). Barriers have been widely implicated in the regional increase in reef fish species, through vicariance (Woodland, 1983; McManus, 1985; Springer, 1988; but see Springer and Williams, 1990), with isolation followed by perturbation being a common theme.

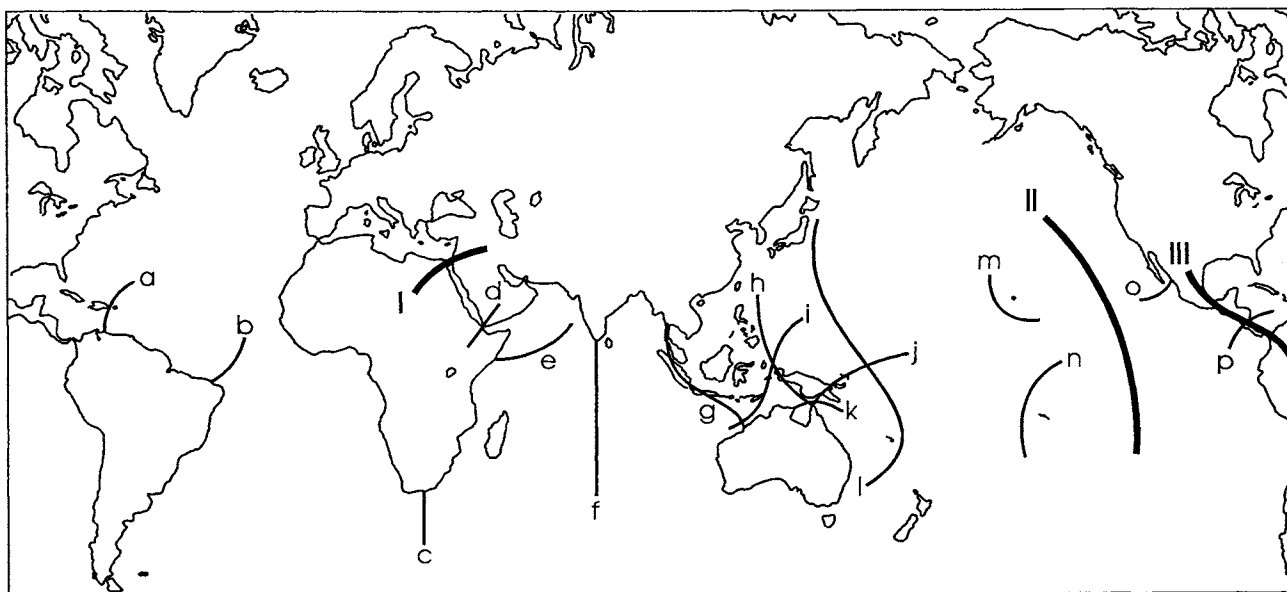


FIGURE 5 Faunal boundaries and proposed locations of vicariance events affecting reef fish taxa (modified after Blum, 1989; with kind permission from Kluwer Academic Publishers). (I) Terminal Tethyan Event (Red Sea land bridge) 12–18 Ma. (II) East Pacific Barrier 0–65 Ma. (III) Isthmus of Panama 3.1–3.5 Ma. Letters denote specific references to reef fishes: a, Hastings and Springer (1994); b and c, Blum (1989); d, Springer and Williams (1994); e, Blum (1989) and Springer and Williams (1994); f, Winterbottom (1986), Springer (1988) Blum (1989), and Springer and Williams (1994); g, h, and i, Indo-Australian Archipelago (see text); j and k, Springer (1988) and Blum (1989); l, Springer (1982); m and n, Blum (1989); o and p, Hastings and Springer (1994) and Lessios *et al.* (1995).

The evolution of modern reef fish families has been largely confined to the past 90 Ma. For most of this period the Tethys was the dominant tropical sea. It provided a broad marine seaway connecting the Atlantic and Indian oceans until the Miocene. This connectivity was reflected by a considerable degree of faunal overlap, with numerous cosmopolitan species (Adams and Ager, 1967; Dilley 1973). Within the Tethys, however, regional faunal differentiation has been recorded during almost every major time period. The evidence suggests that this is the result of a series of temporally distinct vicariance events dividing successive populations, often in the same location. The major events that have shaped tropical marine fish faunas are outlined below, with a summary in Fig. 3.

A. Cooling at High Latitudes

During the late Cretaceous and early Cenozoic there was the potential for extensive connectivity between the oceans, both longitudinally and latitudinally. Latitudinal temperature gradients were not as strong as today. In the Eocene, for example, Antarctica had a temperate climate and a fish fauna that included families that may be found on coral reefs today [e.g., Labridae (Long, 1992); Oplegnathidae (Cione *et al.*, 1994)]. The complete separation of Gondwanan fragments, with the opening of the Australian–Antarctic seaway and the Drake Passage between Antarctica and South America, permitted the formation of the circum-Antarctic current. This effectively isolated Antarctica and was associated with the formation of a steep thermal gradient between the tropics and the South Pole (Veevers and Ettrien, 1988). By 37 Ma, at the end of the Eocene, the circum-Antarctic current was in place and the poles had permanent ice sheets. With increased separation of the continents, the circum-Antarctic current progressively increased in magnitude and the water cooled further. It is likely that this effectively locked in the tropics, preventing significant movement of tropical forms between the oceans at high latitudes. Tropical interoceanic connectivity was probably largely restricted to the Tethys and it is here where further division is seen.

B. The Terminal Tethyan Event

The terminal Tethyan event (TTE) has been regarded as one of the most important events in marine biogeography. Contact between the African and Eurasian continental plates raised a land bridge in the Middle East. This marked the end of a tropical marine connection between the Indian and Atlantic oceans, and the end of the Tethys Sea. Estimates of the timing of the

TTE vary, although the final closure is usually placed between 12 and 18 Ma (Adams *et al.*, 1983; Rögl and Steininger, 1983). The TTE has been associated with the division between Caribbean and Indo-Pacific sister taxa (e.g., Blum, 1989). Estimates of the impact of the TTE on marine faunas vary. The TTE provides a firm minimum age for a split in Tethyan populations. However, this is a minimum age. Much earlier divergences are possible and, in many cases, probable. By the Miocene, the Tethys had been reduced to a narrow channel with seas in peripheral basins (Paratethys). Connectivity between the western (Atlantic) province and the eastern (Indian Ocean) province was probably minimal. The TTE probably represented only the final stage of a progressive division between these two provinces. Fossil evidence suggests that the TTE may have been important for dividing some coral and echinoid species, but most genera were separated prior to the TTE (Rosen and Smith, 1988). Major divisions between Atlantic and Indo-Pacific taxa are likely to reflect an earlier separation. In terms of reef fish, the TTE may have been of limited significance. It provides a minimum age for the possible divergence of some lineages, but there is considerable evidence to suggest that for genera, at least, most divisions occurred prior to the TTE.

C. Tethyan Provinciality Prior to the TTE

For reef fishes, the clearest picture of the relative importance of the TTE is provided by the parrot fishes, for which we have a fully resolved cladogram of genera and a clear, albeit limited, fossil record (Bellwood, 1994). (*Note:* Although the parrot fishes are currently placed in the Scaridae, they almost certainly represent a derived clade within the Labridae.) Today, the scarids are represented by four genera in the remnants of the west Tethys (including *Nicholsina* and *Cryptotomus*), and seven genera in the Indo-Pacific (including *Calotomus*). Separation of these taxa prior to the TTE is strongly suggested by the topology of the cladogram of the family (Fig. 6A), the resultant area cladogram (Fig. 6B), and the record of a fossil *Calotomus* in mid-Miocene deposits (14 Ma) in Austria at about the time of the TTE (Bellwood and Schultz, 1991). Together, these data suggest that the two west Tethyan genera, *Nicholsina* and *Cryptotomus*, and the east Tethyan *Calotomus* are all at least 14 Ma old and were established in their respective provinces prior to the TTE.

The distribution of the remaining scarid genera, with *Sparisoma* restricted to the Caribbean and

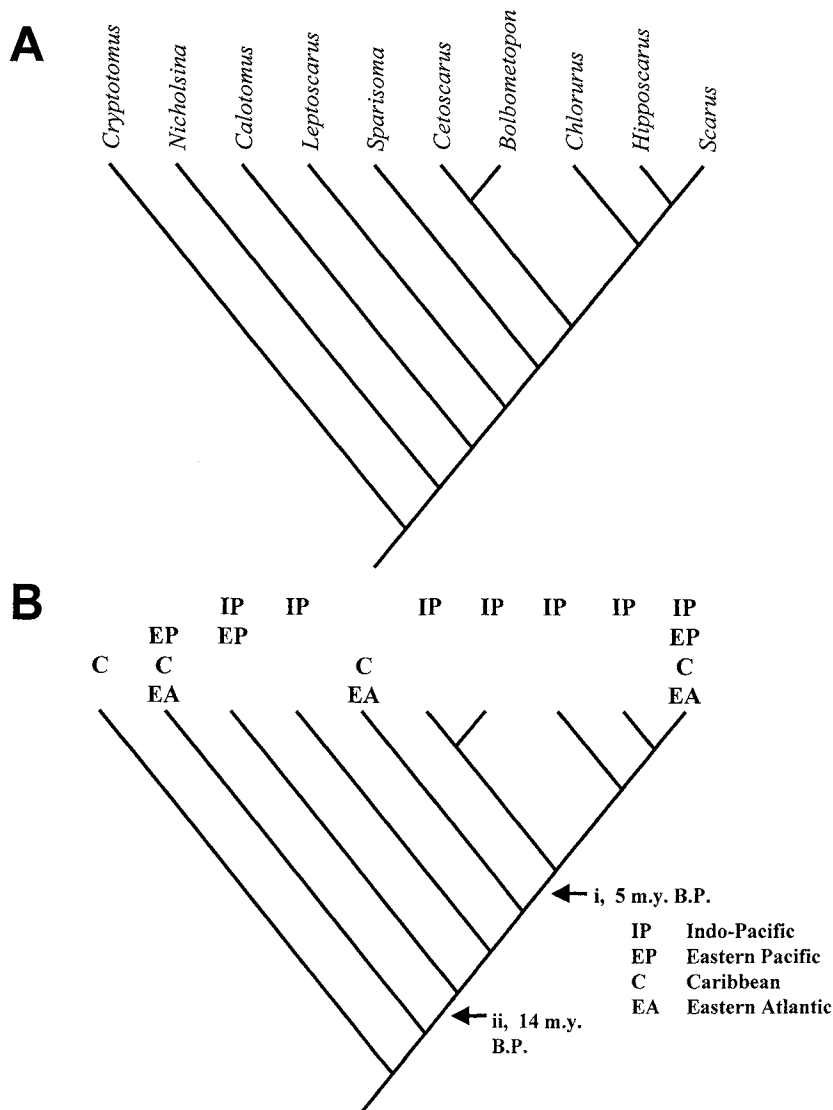


FIGURE 6 (A) Cladogram of scarid genera. (B) Area-cladogram of scarids; i and ii indicate the minimum age (million years before present) of divergence based on fossil evidence (with permission after Bellwood, 1994).

Leptoscarus, *Bolbometopon*, *Cetoscarus*, *Chlorurus*, and *Hipposcarus* restricted to the Indo-Pacific, suggests that these lineages may also have been present and regionally segregated prior to the TTE. The alternative explanation of mutual reciprocal extinctions is less parsimonious. Thus, in this family at least, although it appears that the major faunal divisions fall on either side of the location of the TTE in the Middle East, the actual division may have predated the final closure of the Tethys Sea. Comparable pre-TTE provinciality has been suggested based on fossil data for corals and echinoids (Rosen and Smith, 1988).

Given that these faunal divisions may predate the TTE, are there any clear indications of the principal vicariance events associated with these divisions? Unfortunately, the fossil record for marine taxa does not,

at present, permit detailed resolution of the various vicariance events in the Middle East region. Adams (1981) has raised the possibility of a land bridge in the Middle East region of the Tethys during both the Paleocene and Oligocene. It is also possible that shallow seas in the Middle East region would have provided an effective barrier to marine dispersal for some time prior to the formation of a land bridge, by restricting current flow and increasing susceptibility to rapid salinity changes and periodic habitat loss. Furthermore, given the loss of Mediterranean taxa during the Messinian salinity crisis (5–6 Ma), observations based on living taxa may not be able to resolve the relationships between Tethyan fragments beyond comparisons between the tropical Atlantic (Caribbean) and Indo-Pacific. At this level of resolution one cannot

separate TTE events from divergences as far back as the Cretaceous (see below). At this point, the only consistent indication is that some coral reef fish genera were probably present, with some regional differentiation, prior to the TTE. After the Messinian crisis the Mediterranean probably no longer represented a Tethyan relict, but rather an offshoot of the post-Pliocene Atlantic (but see Jaume and Boxshall, 1996). An alternative explanation for a Tethyan division is provided for ostracids (Tetraodontiformes) by Klassen (1995), who suggests that the two ostracine lineages were separated by raised landmasses between the Americas in the late Cretaceous (100–80 Ma).

Extant reef fish genera common to both the Atlantic and Indo-Pacific oceans may be the result of either a widespread pre-TTE distribution or subsequent dispersal. There is evidence supporting both hypotheses. Several reef fish genera have fossil records from the Miocene, with some extending back to the Eocene (Section III), indicating pre-TTE origins. In two examples (*Naso* and *Oplegnathus*), fossil evidence suggests that these taxa were present in both the Atlantic and Indo-Pacific prior to the TTE (Section II). However, post-TTE origins in the Indo-Pacific with subsequent dispersal into the Caribbean prior to the closure of the Isthmus of Panama have been suggested for two reef fish genera, *Scarus* (Bellwood, 1994) and *Bodianus* (Gomon, 1997). Detailed species-level phylogenies will be required to evaluate the relative contribution of post-TTE dispersal to the Caribbean fish fauna.

D. Cretaceous Provinciality: Division from the Beginning

During the Cretaceous and early Cenozoic there was pantropical marine connectivity through the Tethys seaway (Barron and Peterson, 1989). However, this connectivity did not preclude biogeographic differentiation between regions. Although tropical marine faunas of the Lower Cretaceous were relatively cosmopolitan, in the Upper Cretaceous the Caribbean and Mediterranean became increasingly distinct (Hallam, 1973). Coates (1973), for example, records the first signs of the Caribbean region as a distinct marine biogeographic province in the Aptian–Albian (97–124.5 Ma), with the appearance of endemic genera of corals, rudists, and nonrudist bivalves. The Caribbean remains distinct throughout the remainder of the Cretaceous, with the greatest degree of endemism in all three taxa during the Cretaceous being recorded in the Maastrichtian (65–74 Ma). A similar pattern is reported in the larger foraminifera (Dilley, 1973). The proposed vicariance event, which resulted

in this initial separation of the Caribbean and Mediterranean regions of the Tethys, is the spreading of the Atlantic ridge system and the expansion of the proto-Atlantic. Restriction of water movement between the Americas would have reinforced the extent of isolation by reducing trans-Pacific colonization (cf. Klassen, 1995). Thus, when we look at the origins of reef fishes, the major lineages probably arose in a system marked by some degree of provinciality and in which the principal barriers were already in place and were becoming increasingly effective, i.e., the spreading Atlantic and narrowing Tethyan seaway.

E. Isthmus of Panama

The Pliocene raising of the Isthmus of Panama (IOP) marks the final closure of the tropical seas into two discrete regions. Estimates of the timing of this division vary from 1.8 (Keller *et al.*, 1989) to 3.5 Ma (Coates *et al.*, 1992), with recent estimates of the first complete closure of the IOP around 3.5–3.1 Ma (Coates and Obando, 1996). For fish, the observed impact is predominantly at the species level. There remain about a dozen species of shore fish that span the isthmus with little or no morphological differentiation, and several closely related species pairs. Reef fish examples include mullids (Stepien *et al.*, 1994) and blennies (Hastings, 1990). Along with the divisions on either side of the IOP, there is also consistent evidence of divisions along the East Pacific coast. In one group of pomacentrids, this north–south division appears to predate the final closure of the isthmus, with evidence of a more recent link between the southern East Pacific and the Caribbean than between northern and southern East Pacific forms (Lessios *et al.*, 1995). In contrast, Hastings and Springer (1994) suggest that, for some blennioid fishes, comparable East Pacific divisions occurred after the closure of the IOP.

Within the Caribbean, there is a suggestion of a broad division of the region into northern and southern biogeographic provinces. There are several reef fish species pairs with broadly overlapping northeast–southwest distributions, e.g., *Pomacanthus arcuatus*/*P. paru*, *Holacanthus bermudensis*/*H. ciliaris*, and *Centropyge argi*/*C. aurantonotus*. Hastings and Springer (1994) suggest that there is more overlap in the distributions of Caribbean species than in closely related species in the East Pacific, possibly reflecting more discrete patches of suitable habitat in the latter region. A north–south division within the Caribbean with further subdivisions has been suggested by Domeier (1994) based on *Hypoplectrus*, a reef-associated serranid. A comparable division into north–south faunal

provinces has been proposed for Pliocene mollusc faunas (Petuch, 1982; Vermeij and Petuch, 1986), although the northern province was restricted to the Florida region. A more distinct division between the Caribbean and southwest Atlantic fish assemblages has been described (Rosa and Moura, 1997; Floeter and Gasparini, 2000), with several sister species occurring on either side of the mouth of the Amazon. Although there is some evidence of continuity of benthic marine faunas (Moura *et al.*, 1999), the river appears to present a significant barrier for marine species.

The direct impact of the IOP may have been of limited significance for reef fish taxa. The East Pacific barrier appears to have been a relatively effective barrier and would have limited the effect of the IOP in the Pacific to the isolation of populations along the East Pacific coastline. Here, the greatest effect was probably mediated through the combined effects of isolation and subsequent faunal loss [as in other taxa; cf. J. B. C. Jackson *et al.*, (1993)]. The IOP prevented recolonization of the East Pacific by Caribbean taxa. The IOP marks the latest land bridge in this region. However, there may have been earlier land connections in this location in the Paleogene 30–60 Ma (White, 1986) and Cretaceous 100–80 Ma (Smith *et al.*, 1981). Klassen (1995) cites the latter event as an alternative explanation for an east–west Tethyan division in ostracids (Tetraodontiformes).

The IOP stands as a good example of the nature of land barriers. Although studied in considerable detail, the final date of closure remains uncertain. It appears that the isthmus was completely closed around 3.5–3.1 Ma, with a possible breakdown and marine passage between 2.4 and 2.0 Ma (Coates and Obando, 1996; Cronin and Dowsett, 1996). Furthermore, there is increasing evidence that the shallow waters formed by the rising isthmus represented a significant ecological barrier between Caribbean and Pacific marine systems, with the possibility of speciation on either side of the isthmus since the late Miocene (Jackson *et al.*, 1996; Vermeij, 1997).

F. Gondwanan Fragmentation

Gondwanan fragmentation is widely believed to have been one of the major geological events that has influenced the distribution patterns of plants and animals on the world's continents. In marine systems, it may also have had a direct impact on the temperate marine faunas of the southern continents, with clear links between the temperate fishes of South Africa, South America, and Australia. Although these continents all possess numerous regional endemics, they also

share a number of fish taxa that may reflect Gondwanan associations. These taxa include the Aplodactylidae, Latridae, Congiopodidae, and genera or species in the Cheilodactylidae, Labridae, Sciaenidae, and Sparidae (Wilson and Allen, 1987). The relative importance of vicariance associated with Gondwanan fragmentation and dispersal via the west wind drift remains to be determined, but Gondwanan fragmentation appears to have been a significant factor in the biogeography of temperate fish taxa (cf. Wilson and Allen, 1987).

Evidence of an impact of Gondwanan fragmentation on reef fishes is limited, although three studies are noteworthy. Vari (1978) and Winterbottom (1986) identified Gondwanan fragmentation as the most likely explanation for the observed distribution patterns in teraponids and conragadids, respectively, and Springer (1988) identified the northern movement of India and its collision with Eurasia at about 40 Ma as a major vicariance event dividing the common ancestor of two species groups of reef-associated blennies (*Ecsenius*). Chao (1986) even suggested a late Jurassic origin for the Sciaenidae, with associated Gondwanan links. The main problem with the Gondwanan vicariance scenario, as noted by Winterbottom (1986), Springer (1988), and Briggs (1989), is that the inferred events require that the common ancestral species be extremely old, from about 40–100 Ma, which clearly conflicts with the fossil record (see Section III above).

An alternative explanation for some apparent Gondwanan links is provided by Woodland (1986), who proposed a founder-principle scenario to explain the observed patterns of siganids, with colonization of Australia from Asia as the continent moved into the tropics. In this scenario, the date of colonization is more “reasonable” given that tropical conditions were reestablished in northern Australia by about 15 Ma (Davies, 1988). It may be noteworthy in this context that significant reef growth in the Indo-Australian Archipelago was not recorded until the Miocene (Wilson and Rosen, 1998). Molecular data may help to resolve this dilemma, because the two scenarios have markedly different inferred ages for species divisions and different divergence patterns.

G. East Pacific Barrier

Today, the East Pacific Barrier (Ekman, 1953; Briggs, 1961) separates the Indo-Pacific and East Pacific faunas by an expanse of deep open ocean approximately 5000 km wide. The East Pacific Barrier has almost certainly been in effect since the early Miocene and probably throughout the Cenozoic (Rosen and Smith, 1988). As such, it acted with the Terminal

Tethyan Event to effectively divide the world's tropical seas in two and, after the closure of the Isthmus of Panama, to isolate the East Pacific tropical fauna.

It has been suggested that during most of the Cretaceous, passage of shallow-water benthos across the Pacific was restricted by wide expanses of water similar to the East Pacific Barrier with the exception of a short period during the Campanian/Maastrichtian (83–65 Ma), when a series of volcanic “stepping-stones” is proposed to explain the apparent spread of shallow-water taxa from the Caribbean to the West Pacific (Skelton, 1988). One of the fish groups that may have crossed the Pacific from east to west is the Embiotocidae, which has 20 species off California and three off Japan. However, as livebearers with no pelagic stage, the Embiotocidae are poor candidates for oceanic dispersal across island chains, and movement around the Pacific rim remains a more likely option. Furthermore, as noted above, any Cretaceous connections would require the taxa to be considerably older than the fossil record would suggest.

The East Pacific Barrier is one of the few widely accepted barriers that does not require a “hard” physical separation of marine populations, e.g., land bridges. An interesting issue that arises from the consideration of such “soft” barriers is the reliance on interpretations based on present-day bathymetry and ocean currents. There is increasing evidence that past ocean circulation

patterns were markedly different from today and that even on relatively recent time scales they could have a marked impact on gene flow. In both reef bivalves (Benzie and Williams, 1997) and fishes (Doherty *et al.*, 1995), genetic studies of West Pacific populations have identified barriers that are not apparent based on existing patterns of marine connectivity. Understanding the role of past currents in shaping patterns of connectivity between reef systems is a difficult but significant goal in historical biogeography.

H. Indo-Australian Archipelago: Center of Origin or a Refuge?

One of the most enduring representations in texts of marine biogeography is the “bullseye” pattern of species/generic diversity, with the center of diversity in the Indo-Australian Archipelago (IAA) and a decline in numbers as one moves latitudinally or longitudinally into the Indian Ocean or across the Pacific (Fig. 7). This pattern is found in numerous marine groups, from corals and echinoids to reef fishes. That such patterns are repeated in numerous marine taxa suggests that there may be a general explanation, although a unifying explanation has remained elusive. Explaining these plots has been the focus of numerous works (Wallace, 1997). These revolve around three basic models that describe the center as (1) the center of origin, (2) a region

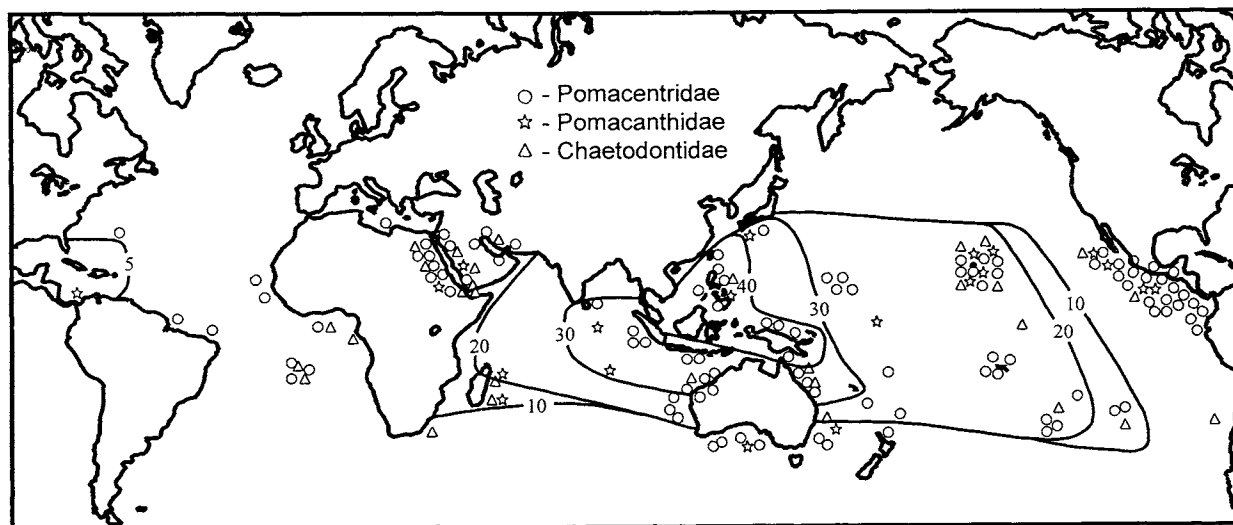


FIGURE 7 Patterns of species richness and endemism in three reef fish families (Chaetodontidae, Pomacanthidae, Pomacentridae). Lines indicate the pattern of species richness in the Chaetodontidae; the patterns for the other two families were comparable. Positions of endemics (open symbols) are approximate and refer only to those species recorded from a single locality [based on data from Allen (1979, 1991)]. Using values for the Chaetodontidae and Pomacanthidae, respectively, the most conspicuous centers of endemism are the Red Sea (28%, 46%), Hawaii (60%, 20%), and East Pacific (100%, 75%).

of overlap, or (3) a refuge. Many early explanations were based on center-of-origin theories, which assume that the center of diversity is also the center of origin, with each species dispersing from this center by its own means. This has been a particularly well-favored explanation, apparently supported by the clear propensity for marine taxa to disperse during their pelagic larval stage. It has been applied to reef fish on several occasions (Allen, 1975; McManus, 1985; Myers, 1989).

Center-of-origin theories, like many others, are often based on the unique features of the area: extensive shallow-water geological complexity, and contacts with two major biogeographic regions. Shallow basins may promote speciation within the region at low sea levels (McManus, 1985; Springer and Williams, 1994), with the area acting as a true center of origin. Alternatively, the extensive shallow habitats may reduce faunal losses, e.g. as a result of habitat reduction during sea level changes (cf. Potts, 1985; Myers, 1989; Paulay, 1996), thus acting as a refuge (Rosen, 1984; Wilson and Rosen 1998) or centre of accumulation (Palumbi, 1997; Bellwood and Hughes, 2001). The tectonic complexity of the area and its position between two major biogeographic realms also increase the number of potential sources of new taxa (a region of overlap). Thus, as Parenti (1991) notes, "a continent is part of the biogeographic regions of all the oceans it contacts." The same applies to archipelagos.

The high diversity in the region may also be due, at least in part, to faunal overlap. The area includes several representatives that are otherwise restricted to the Indian Ocean or West Pacific biogeographic regions. Woodland (1983) described the region as a "zone of overlap" for siganids. This pattern of overlap is consistent with the data of Donaldson (1986) and Blum (1989) for cirrhitids and chaetodontids, respectively. It also appears to hold true for some corals (Wallace, 1997), although for both fish and corals, the total species numbers in the IAA is boosted by a number of regional endemics (but see Bellwood and Hughes, 2001).

Despite the different scenarios proposed to explain the high species richness, most workers seem to agree on the underlying mechanism: vicariance at various sites in or around the Indo-Australian Archipelago during Pleistocene sea level changes leading to speciation. Examples of reef fish taxa displaying apparent patterns of vicariance in this region include *Myripristis* spp. (Greenfield, 1968), *Amphiprion* (Allen, 1972), *Siganus* spp. (Woodland, 1983), *Congragadus subductens* subpopulations (Winterbottom *et al.*, 1984), *Chaetodon* spp. (Blum, 1989), and several blenny species groups

(Springer, 1988; Springer and Williams, 1994). Randall (1998) lists further examples from 15 fish families that may include geminate species pairs. In all these examples, the inferred age of the species or their immediate common ancestors is less than 2 Ma. Such recent species divisions are supported by molecular analyses (McMillan and Palumbi, 1995).

However, there may be other factors involved. The same "bullseye" center of diversity pattern is seen in genera as well as species. This raises the question: Are the factors underlying generic and species diversity patterns similar? One line of evidence suggests that they are, but that it is the role of the IAA as a refuge, not its role as a location for vicariance events, that is common to both species and genera. Of the 31 chaetodontid genera, subgenera, and species groups considered by Blum (1989), most have both Indian Ocean and Pacific Ocean representatives (27 of 31). The remaining four groups, *Amphichaetodon*, *Chelmonops*, *Johnranda*, and a *Hemitaurichthys* species subgroup, are all peripheral Pacific Ocean endemics with sister taxa in the Indian Ocean. There are no endemic chaetodontid genera in the Indo-Australian Archipelago.

For chaetodontid species, the relatively high diversity in the IAA appears to be largely a result of (1) overlap of species from adjacent biogeographic regions and (2) low species richness (= loss of species?) in peripheral locations. For genera, there is no evidence of overlap by adjacent groups (although extensive dispersal may mask earlier divisions). For genera and the nonpaired species (only 8 of the 49 chaetodontids in the IAA are species pairs), the role of the IAA as a refuge may be the most important consideration (Bellwood and Hughes, 2001). Sea level changes may split populations and foster speciation, but for genera the most important effect may be the loss of peripheral species, the overall effect being one of range reduction rather than vicariance.

Although the IAA has been regarded as a key location for Plio-Pleistocene vicariance, much earlier vicariance events are also possible. Woodland (1986) identified divisions either side of Wallace's line in several marine taxa, including two genera of ovoviparous reef sharks (family Hemiscyllidae). While most authors propose Plio-Pleistocene vicariance events for such divisions, Woodland (1986) notes that divisions could date back to the early Miocene, 20–25 Ma, coinciding with the northern movement of Australia. He also points out that these alternatives (Pleistocene sea level changes and movement of Australia) are not mutually exclusive. Furthermore, Springer and Williams (1994) discuss the possibilities of earlier divisions in the IAA ca. 8–16 Ma as a result of Indonesian region tectonic activity that changed surface circulation patterns

in the Indian and Pacific oceans. Modern geological evidence has highlighted the tectonic complexity of this area (R. Hall, 1998) and its potential role in the development of Neogene reefal systems (Wilson and Rosen, 1998). Overall, the IAA is clearly an important location for marine vicariance events; however, the timing, cause, nature, and significance of these events remain to be determined.

If one examines endemics as potential indicators of speciation events there is a strongly congruent pattern within the Chaetodontidae, Pomacanthidae, and Pomacentridae. In all three families the endemics are largely peripheral, all laying outside the center of diversity, with the Red Sea, Hawaii, and the East Pacific being conspicuous centers of endemism (Fig. 7). A similar pattern has been described in the siganid subgenus *Lo* (Woodland, 1986), and in two gastropod groups, Cypraeidae (Kay, 1990) and *Conus* (Kohn, 1985). The mechanism, however, is unclear. Peripheral areas may be marked by relatively high rates of origination vs. extinction. Alternatively, species in peripheral areas may be more likely to remain isolated and thus recorded as endemics (peripheral relicts are considered unlikely). In the IAA endemics may appear to be lost as a result of rapid range extension. Apparent endemism based on presence/absence data can also result from limited sampling and recent descriptions. Given the data currently available it is not possible to resolve these alternatives, although fossil evidence in other taxa with short generation times [e.g., *Conus* (Kohn, 1985); *Cyprea* (Kay, 1990)] lends some support to the suggestion of extensive peripheral speciation in reef-associated taxa (but see Palumbi *et al.*, 1997).

It should be noted that there is a high probability of all the above factors working in concert, the IAA being both a source of vicariance (a center of origin and center of overlap) and a refuge (a center of accumulation), with the more peripheral areas being marked by endemism and extensive faunal loss. In such considerations it is critical to distinguish theories concerning the origins of species from those concerned with the maintenance of species. The two may not necessarily occur in the same location. For reef fishes, a resolution of the relative importance of these factors in explaining high diversity in the IAA remains elusive. However, with a more detailed description of species distributions, robust species-level cladograms, and molecular data, this issue is likely to be resolved. One of the immediate challenges is the selection of appropriate taxonomic units. So far, most barriers have been identified based on the distribution patterns of species pairs, with most species identified based on color patterns.

In fishes, color patterns may not reflect genetic separation (McMillan and Palumbi, 1995), although they may change rapidly and provide a basis for maintenance of discrete morphs (cf. Domeier, 1994). The problem of separating discrete species or subspecies is even greater in corals (cf. Willis *et al.*, 1997). For reef fish, at least, a resolution may be possible.

I. Conclusions

As more data become available it is becoming increasingly clear that congruent divisions in distribution patterns may not reflect a single vicariance event. Congruent patterns at different taxonomic levels in several key locations suggest that either (1) different taxa were affected at different times or (2) a single event affected taxa in markedly different ways. At present these alternatives cannot be resolved. Biogeography based on analyses of distribution patterns, even with cladograms, can only identify the possible location(s) and sequence of vicariance events. Congruence emphasizes the relative importance of locations. However, given the possibility of several temporally separate vicariance events in several key locations, another set of information is needed to provide details of the timing of events. Geology provides the timing of some events but their biological significance can only be inferred. The two most promising sources of information are the fossil record and molecular data. Fossil data are excellent because they provide information on both the minimum age and past locations of taxa. However, fossils are unavailable for many reef taxa. Molecular data are not restricted in this respect and may provide useful age estimates. Indeed, phylogeographic hypotheses and a knowledge of inter- and intraspecific relationships promise to yield invaluable information on historical patterns of connectivity and the origins of lineages. The combination of fossil evidence, molecular systematics, and vicariance biogeography (cf. Reid *et al.*, 1996; Bernardi *et al.*, 2000) offers an exciting avenue for future research in reef fish biology.

For reef fishes, we are beginning to identify the location of major vicariance events. The challenge is to decipher the timing and nature of these events. It is becoming increasingly apparent that there is a need to critically reevaluate the nature of marine barriers. In the past a great deal of work has revolved around hard barriers, e.g., land bridges, where there is a clear physical separation of populations. However, marine taxa appear to respond to a wide range of soft barriers. Of these, the East Pacific Barrier is well documented. Similar barriers probably operate at smaller scales. Even

around hard barriers, such as the Isthmus of Panama and the Terminal Tethyan Event, there is increasing evidence of ecological barriers to marine taxa prior to land bridge formation. Perhaps the best example of the importance of soft barriers is Springer's (1982) classic study of Pacific plate biogeography. Here, fish and non-fish taxa appear to be closely linked to a specific continental plate. The nature of the barrier is unclear. Why do so many taxa with widespread or oceanic distributions and planktotrophic larvae not cross the plate margins? It is as if there is an invisible barrier in mid-ocean. Indeed, given the recent advances in our understanding of the biology of fish larvae, we may be able to begin to understand the nature of such barriers (see Chapters 6 to 9). As with the pioneering work of Leon Croizat (Croizat *et al.*, 1974), it may be the simplest of patterns that provides the foundation for a quantum leap in our understanding of the nature of barriers in marine biogeography.

V. Postvicariance Survival Patterns: Fate after Isolation

In the previous section, barriers that isolated regional fish faunas were identified. The subsequent fate of these faunas, however, may vary widely depending on the component taxa and regional characteristics. The extent and nature of subsequent diversification or loss may have a profound effect on the composition, ecology, and functional attributes of surviving faunas. In reef fishes, the available evidence does not permit detailed analyses of the fate of faunas in various regions. However, based on the data in Section II the most marked difference between reef fish faunas is seen between the Caribbean-eastern Pacific and the Indo-Pacific regions, the remnants of the east and west Tethyan provinces. In the following sections, therefore, we restrict comparisons to these two major biogeographical realms.

Today, Caribbean reefs support only about 22% of the number of fish species found on Indo-Pacific reefs and about 80% of the families. The data in Section II suggested that the difference between these areas is primarily a result of a lack of taxa in the Caribbean, in that there is little evidence of faunal replacement. With the exception of the Chaenopsidae, Labrisomidae, and Inermiidae, Caribbean reefs merely possess a subset of the families found in the Indo-Pacific. There are two possible scenarios: the missing taxa were either never present, or they were present but have been subsequently lost. The best way to evaluate these alternatives

TABLE 1 Species Richness of Extant Perciform Reef Fish Families Recorded from Monte Bolca, Italy, and Recent Biogeographic Distributions

Family	Species at Bolca	Occurrence in biogeographic region	
		Atlantic	Indo-Pacific
Acanthuridae	13	X	X
Apogonidae	2	X	X
Blenniidae	1	X	X
Carangidae	4	X	X
Centropomidae	2	X	X
Enoplosidae	1		X
Ephippidae	2	X	X
Gobiidae	1	X	X
Haemulidae	1	X	X
Labridae	2	X	X
Monodactylidae	1		X
Mullidae	1	X	X
Pomacentridae	2	X	X
Scatophagidae	1		X
Scombridae	5	X	X
Serranidae	2	X	X
Siganidae	2		X
Sparidae	10	X	X
Sphyraenidae	1	X	X
Zanclidae	1		X

is to examine the fossil record. Of all extant perciform families represented in Monte Bolca (see section IIIB.), most occur today in both the Caribbean and the Indo-Pacific (Table 1). However, although all 20 are represented today in the Indo-Pacific, only 15 are recorded from the Caribbean. There are no families recorded in Monte Bolca that are found solely in the Caribbean. The Caribbean today appears to possess only a portion of an old and possibly widespread fish fauna, which was largely retained in the Indo-Pacific. The proximity of Bolca to the Atlantic (5000 km upstream, along a coastline) would suggest that the missing families were present in at least the East Atlantic.

Given that the Caribbean has been faunistically distinct since the Cretaceous (Section III), there remains the possibility that these families were never present in the Caribbean. Unfortunately, the fossil record of fishes in this region during the Cenozoic is poor, and direct evidence for the loss of fish taxa in the Caribbean is sparse. There are only two records that support the suggestion that the region is characterized by loss rather than absence. An Eocene (?) acanthurid fossil from Antigua, West Indies (previously identified as *Naso*) has been placed in the genus *Eonaso*, as an extinct putative

sister taxon to *Naso* (Tyler, 1997). Today, no member of the *Naso-Eonaso* lineage remains in the Atlantic. Similarly, the Oplegnathidae (Cione *et al.*, 1994) has been recorded from the Miocene of both North America and Europe. Today, this family is found only in the Indo-Pacific.

Faunal loss in the Caribbean and East Pacific has been recorded in numerous other marine taxa (Vermeij and Petuch, 1986; J.B.C. Jackson *et al.*, 1993; Edinger and Risk, 1994), with a major period of faunal turnover in the Plio-Pleistocene (Jackson *et al.*, 1996). There is a strong likelihood that this period also marked a period of change in fish faunas. These studies have identified a number of factors that may have been implicated in the differential loss of taxa from the East Pacific and tropical Atlantic including changes in turbidity, productivity, temperature, and circulation patterns. Cooling of the oceans during the Plio-Pleistocene, in particular, has been closely linked with regional losses (e.g., Stanley, 1984; Jackson, 1994), although temperature alone appears unlikely to explain the observed faunal loss (Jackson *et al.*, 1996). This applies equally well to reef fish families. Their presence in subtropical waters (Section II) suggests that they would be relatively insensitive to temperature changes. Furthermore, shallow reefs persisted in the Caribbean throughout the Neogene (Johnson *et al.*, 1995; Budd *et al.*, 1996).

There are several factors associated with low sea levels, which may have been detrimental to reefs and fishes on reefs. During low sea levels there would be a marked decrease in the area available for shallow-water taxa. Given that reefs and reef fishes are largely restricted to the top 50 m, a drop in sea levels of 180 m would result in reefs being relocated off continental shelves. Taking the area enclosed by the 0- to 50-m isobath and comparing it to the area enclosed by the 150- to 200-m isobaths, as a proxy for comparable shallow waters during Pleistocene lows, the area of shallow water in the Caribbean was reduced by about 89% (Fig. 8). Paulay (1990) provided a comparable explanation for the loss of bivalves on oceanic islands in the West Pacific but highlighted the role of key regions (e.g., Australia's northwest shelf and Fiji) where a shallow sloping bathymetry would provide refuges for shallow-water taxa during low sea stands. Lower sea levels may decrease not only the area of shallow habitats but also the nature of these habitats, with an increase in the proportion of benthic habitats between 0 and 50 m being restricted to relatively steep escarpments along continental margins. In the Caribbean, this resulted in an estimated change in the mean slope of coastal shallow waters from 1.4 to 10.1 m km⁻¹. Furthermore, there would probably be extensive loss

of shallow banks, lagoons, and sediment aprons that are characteristic of the shallow continental shelves (cf. Potts, 1985; Myers, 1989; Paulay, 1990; Domeier, 1994). The two effects are quite different. The former is just a proportional loss of area; the latter may result in the total loss of a given habitat from a whole region. The former (area changes) alone have been linked with speciation in reef fishes (Domeier, 1994), whereas habitat loss has been identified as a significant factor in the loss of taxa during the Pleistocene in crustacea (Dall, 1991), corals (Potts, 1985), bivalves (Paulay, 1990, 1996), and reef fishes (Myers, 1989).

Restriction of shallow-water habitats to the edge of continental shelves and more exposed locations on isolated land masses may increase the impact of other potential disruptive factors, including cool upwellings, turbidity, hyposalinity, and storm damage. Fleminger (1986) presents evidence for enhanced cool upwelling in the Indo-Australian Archipelago during Pleistocene periods of low sea level, arguing that this cooler water may have acted as a thermal barrier effectively separating stenothermal populations. Furthermore, he suggests that mean wind speeds and upwellings were enhanced during these cool low-water periods. In addition, coastal freshwater runoff and silt loads may be increased, because both are dependent on rainfall and land area (Schopf, 1980). As shallow waters are restricted, the detrimental effect of runoff may be increased because the runoff is concentrated near the narrow reefs along the shelf break rather than being diluted inshore over broad continental shelves. Springer and Willams (1990, 1994) argue that these effects, when combined, may be responsible for the loss of reef fish taxa in the Indo-Australian Archipelago. Edinger and Risk (1994) describe a comparable scenario for coral losses in the Caribbean during the Oligocene-Miocene.

Overall, it appears that shallow-water faunas were subject to a wide range of potential detrimental effects during low sea stands. The Pleistocene sea level changes are the best documented, but similar effects would be expected during any of the Cenozoic marine regressions, including those in the Oligocene and Miocene. For reef fishes, many of these factors have been implicated in the loss of species, but they offer little in terms of an explanation for the loss of families from the whole of the Caribbean, particularly because many families have broad habitat associations (Section II). These broad habitat associations are noteworthy when examining the families that appear to be missing from the Caribbean. Of those taxa that were present in Monte Bolca but are absent

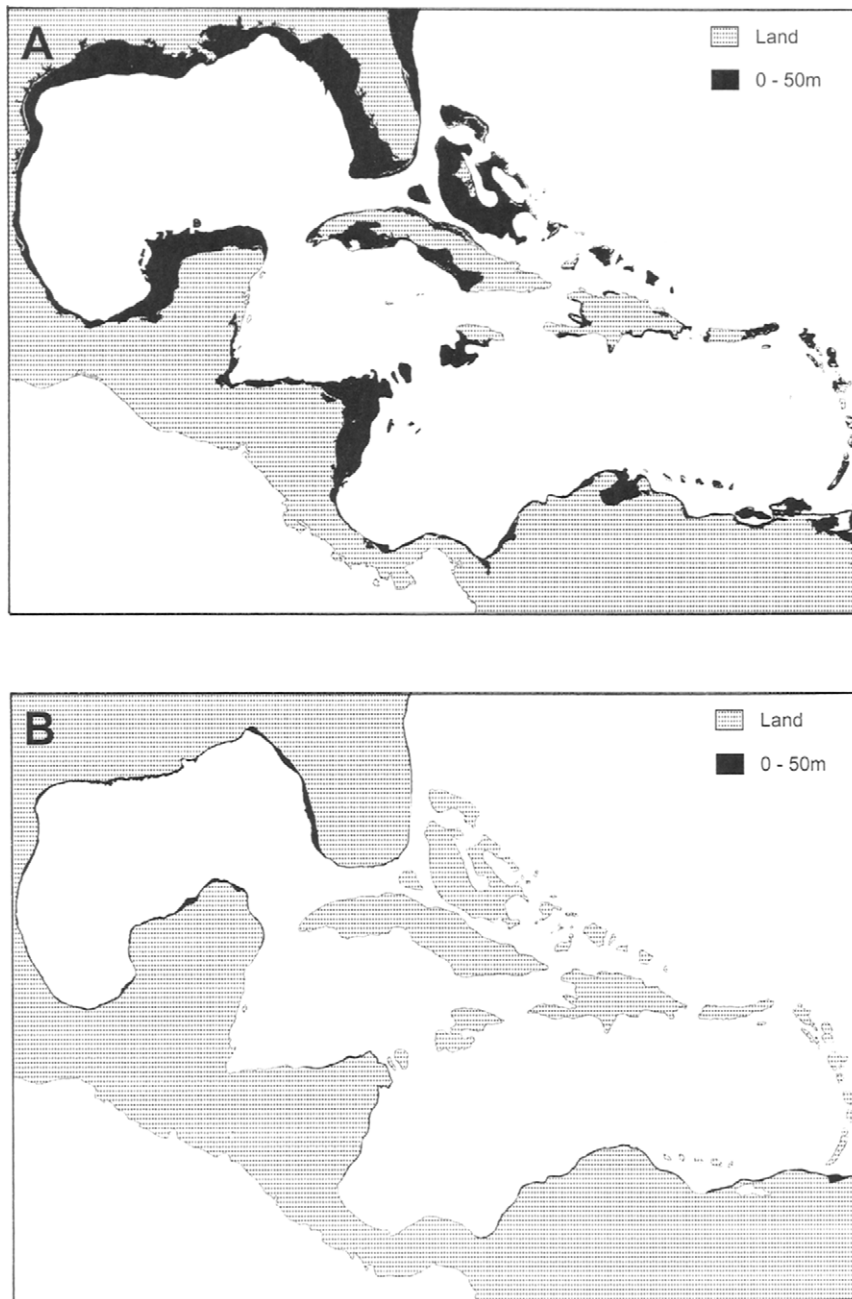


FIGURE 8 Estimated changes in shallow-water habitat availability in the Caribbean. (A) Area of shallow water enclosed by the 0- to 50-m isobaths today. (B) Area enclosed by the 150- to 200-m isobaths (coastal margins indicated only), taken as a proxy for shallow areas during glacial low sea stands, with sea levels 150 m below present. During such low sea stands, the area of coastal shallow-water habitat was only approximately 11% of that in the region today and the mean slope of coastal benthic habitats increased from 1.4 to 10 m km⁻¹.

from the Atlantic today, only two have strong reef associations (Zanclidae, Siganidae), and of these, one (Siganidae) contains several nonreef species. The remaining families are either estuarine (Monodactylidae, Scatophagidae) or temperate coastal forms (Enoplosidae). Furthermore, of the families that are absent from the Caribbean but present in the Indo-Pacific, many have associations with nonreef habitats, including seagrass and soft sediments (Lethrinidae, Nemipteridae) and estuaries (Plotosidae, Teraponidae, Aploactinidae).

Only the Pseudochromidae is strongly reef associated. The absence of these families from the Caribbean strongly suggests that the loss of fish taxa was associated with changes that impacted a wide range of coastal and shallow-water habitats, not just coral reefs. In this context, it is interesting to note that during the Plio-Pleistocene the loss of reef corals was most marked in seagrass communities; diverse coral-rich communities appeared to fare relatively well (Budd *et al.*, 1996).

VI. The History and Nature of the Reef–Fish Relationship

Today, many fish species are intimately associated with coral reefs, and it is on reefs that numerous fish families reach their greatest species diversity and abundance. Documenting diversity patterns and examining the factors responsible for producing and maintaining species diversity are major goals in ecology. In this respect coral reefs offer an exciting challenge, with over 1200 fish species on the Great Barrier Reef alone (Randall *et al.*, 1990) and over 250 species on a single reef (Russell, 1983). Many studies have highlighted the close relationship between fish species and various reef attributes, such as habitat complexity (e.g., McCormick, 1995; Chabernet *et al.*, 1997). However, to what extent can we assume that coral reefs have been the arena in which these reef fishes evolved? Today, coral reefs are sites of high diversity, but do they also represent sites of origin? Given the diversity of fishes on reefs and the long tenure of reefs in the fossil record, it appears logical that the fish probably evolved on reefs. Conditions on the reef all appear to be “favorable,” with numerous niches, abundant food, high productivity, structural complexity, and habitat continuity through time. Yet, as was noted in Section II, few of the characteristic reef fish families are restricted to coral reefs. The focus of this section, therefore, is to examine the nature of this reef–fish relationship in an evolutionary context.

Direct examination of the fossil record offers little assistance in evaluating this relationship (Bellwood, 1998). However, phylogenetic data provide an alternative line of evidence that may give a clearer indication of the history of the reef–fish relationship. Phylogenetic studies provide a basis for examining not only relationships between taxa but also the evolution of various character states. These characters may include behavioral, trophic, and ecological traits, including habitat associations (Brooks and McLennan, 1991; Winterbottom and McLennan, 1993).

There are two possible scenarios:

1. *Coral reefs as the site of origin of reef fish lineages.* Today, coral reefs support a vast array of fish lineages. Coral reefs were present in some form prior to the origins of these lineages. Did they therefore provide the environment within which these fish lineages arose? In the fossil record, modern scleractinian-dominated coral reefs and modern reef fishes first appear and then diversify at approximately the same time. In the early Cenozoic, coral reefs may have filled an ecological vacuum (cf. Boucot, 1983) and provided a habitat within which

basal percomorphs could rapidly diversify. Coral reefs may therefore represent the site of origin and the site for the maintenance of reef fish faunas.

2. *Coral reefs as a benign sanctuary.* Coral reefs may merely provide a habitat capable of supporting a diverse fish fauna. Reefs may have acquired lineages from existing nonreef faunas, acting as a sanctuary for the maintenance of diversity with no specific role in the origins of this diversity.

The relative importance of these two alternatives can be assessed using cladograms, by mapping then optimizing habitat details (*sensu* Winterbottom and McLennan, 1993). If the first scenario (coral reefs as the site of origin of reef fish lineages) is correct, then one would expect to find basal taxa living on reefs and that this is the inferred habitat of the hypothetical ancestral taxon. This would suggest that these lineages have lived on coral reefs from their earliest beginnings. If the second (benign sanctuary) scenario is correct, then the reef dwellers should be derived and the basal taxa and hypothetical ancestral taxon would occupy nonreef habitats. This would suggest that the lineages evolved in nonreef areas followed by a movement onto coral reefs. Furthermore, if fossil data are incorporated into the cladograms, the timing of these inferred events can be estimated.

Cladograms of higher taxa and habitat utilization patterns are available for four reef fish lineages: hypsigenyine labrids, scarids, the Acanthuroidei, and the Chaetodontidae (Fig. 9). Today all of these lineages are closely associated with reefs, and include many of the “characteristic” reef fish families (Fig. 1). Mapping and optimizing the principal habitat utilization patterns of these taxa reveal an interesting pattern, with clear links to nonreef habitats:

1. In the hypsigenyine labrids [Fig. 9A; cladogram from Gomon (1997)], the basal divisions all incorporate temperate or deep-water lineages. It appears that a reef-dwelling mode arose at least twice within this clade, in both of the two main lineages. In one lineage, the reef-dwelling genus *Choerodon* is derived from a lineage that lives in deep (40–240 m), soft-sediment habitats. In the second major lineage, the reef-dwellers *Clepticus* and *Bodianus* both have sister taxa living on temperate rocky coasts. The inferred habitat of the hypothetical ancestor of the Hypsigenyini is equivocal. However, there are strong links with both temperate waters and deep soft-sediment habitats. The age of these hypsigenyine lineages is unknown, although the first record of a putative hypsigenyine labrid is from Monte Bolca (Bellwood, 1990). It is interesting to

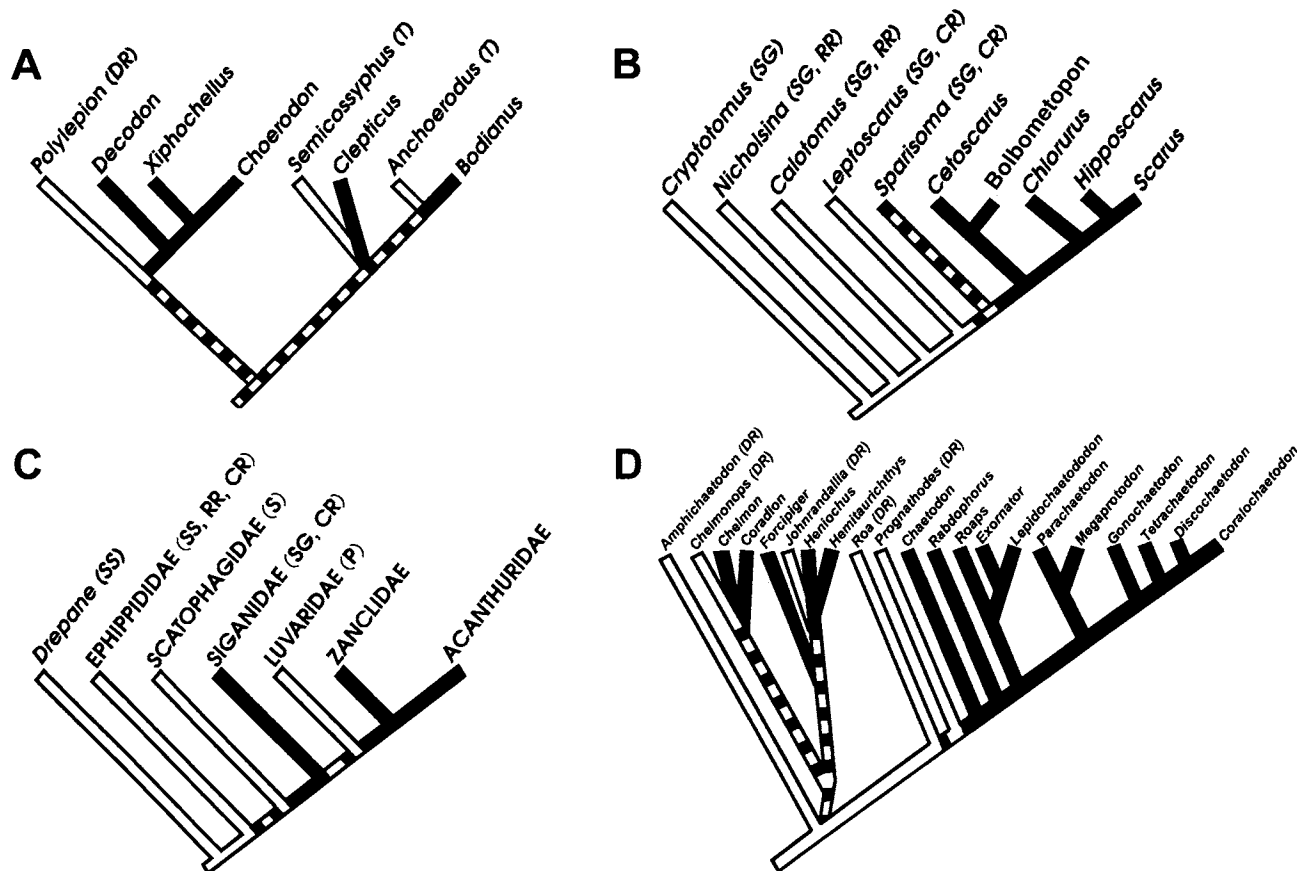


FIGURE 9 Patterns of habitat use in four "reef fish" lineages. (A) Hypsignenyne labrid genera. (B) Scarid genera. (C) Acanthuroidei families and lineages. (D) Chaetodontid species groups. Open bars, nonreef habitats; solid bars, coral reef habitats; dashed bars, equivocal. Abbreviations: T, temperate coastlines; SG, seagrass; RR, rocky reef; CR, coral reef; SS, soft sediments; P, pelagic.

note that a slightly younger Eocene hypsignenyne labrid has been recorded from Antarctica (Long, 1992), at a time when Antarctica had a temperate coastal margin. Furthermore, the Antarctic specimen is similar in structure to extant taxa living on temperate rocky shores.

2. The scarids (Fig. 9B) are a derived clade within the Labridae. Today, they are a conspicuous and abundant component of reef fish assemblages. However, if habitat associations are examined based on a cladogram of the family, there is a clear indication that the lineage lived initially in seagrasses and that the early evolution of the group was predominantly off-reef (Bellwood, 1994). Fossil evidence indicates that the seagrass-dwelling forms are at least 15 Ma old and that the move onto reefs occurred at least 5 million years ago (Bellwood and Schultz, 1991; Bellwood, 1994).

3. In the Acanthuroidei [Fig. 9C; after Tyler *et al.* (1989)] all of the basal taxa (and *Drepane*) have strong associations with coastal soft-substratum nonreef habi-

tats. In the Ehippidae a few species occur on reefs as adults. However, the juveniles of these forms are most frequently reported from estuaries and coastal mangroves (Kuiter, 1996), suggesting that reef dwelling was secondarily derived. The Ehippidae, Scatophagidae, Siganidae, Zanclidae, and Acanthuridae have all been recorded from Monte Bolca (Bellwood, 1996a). This suggests that some of these taxa may have already moved onto reefs by the Eocene (50 Ma).

4. Finally, the Chaetodontidae (Fig. 9D), one of the most conspicuous and brightly colored of all reef fish families, also appears to have nonreef origins. Using the cladogram of chaetodontid genera and subgenera of Ferry-Graham *et al.* (2001b) and the habitat and depth data of Allen (1979), an interesting pattern emerges. The basal taxa live predominantly in deep water (at least 20 m, most below 50 m, maximum 200 m), usually on drop-offs or over rock (cf. Pyle and Chave, 1994). Many of the records are from temperate or marginal

reef areas. Overall, the data suggest that chaetodontids arose as a deep-water lineage, living on rocky substrata and feeding on benthic invertebrates, possibly in a subtropical region. Furthermore, it appears from the cladogram that the chaetodontids may have colonized coral reefs on at least two separate occasions. It is noteworthy that, as in many groups, the coral reef lineages are particularly speciose when compared to nonreef lineages. A coral-reef-dwelling habit may not have been implicated in the origins of reef fish lineages, but it may have played an instrumental role in the diversification of these lineages (e.g., *Chaetodon*, *Scarus*, and *Halichoeres*).

Other families with strong reef associations may also have nonreef origins. The Pomacanthidae, like the Chaetodontidae, have several genera or species groups living in deep water, often over rock on steep slopes or drop-offs (e.g., *Aplomichthys*, *Genicanthus*, and *Centropyge*). Given the provisional phylogeny in Allen (1979) there appears to be the possibility of a basal deep-water, nonreef association. The Holocentridae may also be derived from deep-water taxa. Many beryciform taxa, including "basal" groups, inhabit deep waters (cf. Johnson and Patterson, 1993; Nelson, 1994). In both families, further analyses require a clear resolution of the systematic relationships of the component taxa.

Given the likelihood of nonreef origins for several lineages of fishes that are conspicuous on reefs today, the next question arises: What was the fate of these lineages on the reef? Did they proliferate without further input from nonreef habitats? It is apparent from Section IV that many reef fish species appear to have arisen as a result of vicariance events, and that the increasing diversity may be at least partially the result of repeated cycles of division, speciation, and intermixing. However, relatively few studies of reef fishes have considered the impact of vicariance events on nonreef marine habitats. For reef fishes it may be assumed that major vicariance events isolate both reef and nonreef habitats. However, the possible effect of nonreef habitat utilization patterns may be important. For example, in the Indo-Australian Archipelago, the presence of cool or nonreefal environments may not represent a barrier to the basal taxa of many reef fish lineages. The historical biogeography of coral reef fishes may incorporate habitats other than coral reefs (Bellwood, 1997).

Nonreefal habitats may continue to be a source of new species. The location of endemics in three reef fish families, the Pomacentridae, Pomacanthidae, and Chaetodontidae (Fig. 7), are broadly congruent, with

numerous peripheral endemics, i.e., away from the center of diversity in the Indo-Australian Archipelago (see Section IV). Many of these endemics are in nonreefal habitats. The presence of numerous endemics in peripheral locations, including many marginal or nonreef areas, points to the possibility of a continuing role for nonreef areas in the origins of evolutionary novelty and the generation of fish diversity on coral reefs. Data from a comparable high-diversity system (rain forests) have emphasized the importance of noncore habitats in the generation of diversity (Smith *et al.*, 1997).

These nonreef associations have implications for our view of reef fishes. First, historical links with nonreef habitats may help explain current ecological links with nonreef habitats, e.g., reef fish taxa settling in seagrass beds or mangroves (e.g., Shulman and Ogden, 1987; Bellwood and Choat, 1989; Parrish, 1989). Second, these observations may help to explain the functional, morphological, and ecological characteristics of extant reef fishes, particularly in considering exaptations (*sensu* Gould and Vrba, 1982). For example, the highly modified jaws and pharyngeal apparatus of scarids probably evolved in taxa that fed on seagrasses and seagrass epiphytes. Only later were these structures used by taxa feeding on coral reefs (Bellwood, 1994). Finally, nonreef associations will have a major bearing on biogeographic studies. Distributions of reef fish taxa may not be delineated by coral reefs. The history of reef fishes may depend on the distribution, continuity, and connectivity of habitats other than coral reefs. Nonreef areas may act as refugia for reef fish in both ecological and evolutionary contexts.

VII. Functional Aspects of the Reef-Fish Association

Fishes play a variety of functional roles on coral reefs, with direct involvement in numerous reef processes (i.e., interacting with the movement of energy or material). The role of fishes in reef processes, however, is not dependent solely on the number of species or individuals present, but on the identity of the species and the nature of their functional role. In terms of functional roles, all fishes are not equal. At a functional level the role may transcend taxonomic boundaries, as in the changes associated with the mass mortality of *Diadema* in the Caribbean (Hughes, 1994), where the echinoid may have replaced fishes as the dominant grazer prior to the mass mortality event. In this case the functional role passed from fishes to a single invertebrate species.

When considering the implications of historical factors in the ecology of modern reef fish faunas,

the immediate challenge is in interpreting the available data. The structures of modern reef fish faunas are often described based on species richness or relative abundance (e.g., Williams, 1982; Thresher, 1991), although a few have considered functional categories (e.g., Williams and Hatcher, 1983). There has been a recent surge of interest in the functional group approach, effectively extending the "guild" concept. It permits interactions and patterns to be examined without the need for detailed species-level observations (cf. Hay, 1994; Steneck and Dethier, 1994). This approach offers a means of gathering broad-scale data on community composition and trophic interactions. It may therefore be useful to consider the information base necessary to identify meaningful functional groups among reef fishes and the possible role of history in determining the nature of these groups.

A. Functional Groups on Coral Reefs: Piscine Bioerosion as a Case Study

Bioerosion refers to the removal of material by living organisms. On coral reefs there are numerous taxa that bore or excavate carbonate substrata (Hutchings, 1986). Of these taxa, the parrotfishes (scarids) and the

echinoids are the dominant external bioeroders. Both scarids and echinoids erode the substratum by removing calcareous material as they graze the epilithic algal matrix (sensu Wilson and Bellwood, 1997). Scarids have long been recognized as a distinctive group of bioeroders, with numerous studies documenting their erosional activities (Hutchings, 1986). This designation was based largely on their feeding mode, which often leaves bite marks or scars, and gut contents that invariably include a large proportion of finely ground carbonate. Scarids have been long regarded as a relatively uniform group of grazing or scraping herbivores that erode the substratum during feeding (reviews by Hutchings, 1986; Horn, 1989; Steneck, 1988).

However, based on observations of the functional morphology, ecology, and feeding behavior of scarids, Bellwood and Choat (1990) suggested that only a minority of Indo-Pacific scarid species are significant bioeroders. A comparable pattern is seen in the Caribbean (Bruggemann *et al.*, 1996). Thus, in terms of bioerosion, the functional group of bioeroders is composed of a small number of species not scarids per se (Fig. 10). As species composition and species densities can vary widely among sites, comparisons of total erosion between biogeographic regions are tenuous. Nevertheless,

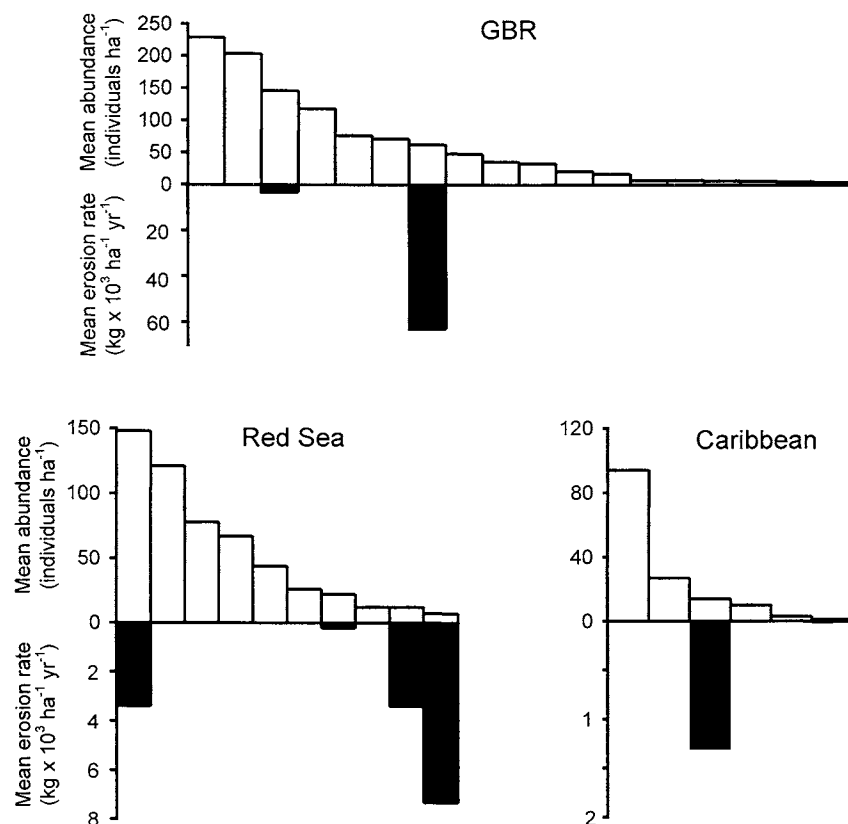


FIGURE 10 Patterns of scarid abundance and respective bioerosion rates at sites in the Indo-Pacific [Red Sea and Great Barrier Reef (GBR)] and Caribbean. [Caribbean values based on Lewis and Wainwright (1985) and Bruggemann *et al.* (1996); GBR values based on Bellwood (1996b); Red Sea values from C. M. Roberts (unpublished data)]. The following species are found in each region, in order of decreasing abundance. GBR: *Scarus rivulatus*, *Chlorurus sordidus*, *S. globiceps*, *S. frenatus*, *S. schlegeli*, *C. microrhinos*, *S. spinus*, *S. niger*, *S. psittacus*, *S. altipinnis*, *S. oviceps*, *S. rubroviolaceus*, *C. bleekeri*, *S. ghobban*, *Cetoscarus bicolor*. Red Sea: *Chlorurus sordidus*, *S. ferrugineus*, *Hipposcarus harid*, *S. niger*, *S. frenatus*, *S. psittacus*, *S. ghobban*, *S. fuscopurpureus*, *Cetoscarus bicolor*, *C. gibbus*. Caribbean: *S. croicensis*, *Sparisoma aurofrenatum*, *Sp. viride*, *Sp. chrysopteron*, *Sp. rubripinne*, *S. vetula*.

two features are noteworthy in the patterns of erosion in the two regions. First, species richness and species densities have little impact on erosion rates because, in both locations, bioerosional activity is restricted to a few, often relatively rare, species. Despite the fact that the Caribbean is characterized by fewer species and genera, the functional abilities of the fish community may be unaffected. In terms of scarid bioerosion, neither the number of species or genera nor even total numbers of individuals can provide a sound basis for estimating erosion rates; this requires estimates of the abundance of eroding species only. Second, there is no overlap in the taxa responsible for erosion in the two regions, with *Sparisoma* in the Caribbean and *Chlorurus*, *Bolbometopon*, and *Cetoscarus* in the Indo-Pacific. This difference appears to be historical (Section IV) and may have direct implications in terms of the nature of erosion in the two regions.

In both the Caribbean and the Indo-Pacific, scarid erosion is dependent on a few species, with local patterns dependent on the abundance, size, and behavior of these key species. In the Indo-Pacific, one of the primary eroders, *Chlorurus microrhinos* (formerly *Chlorurus gibbus*), has very specific feeding patterns, with most erosion being from convex epilithic algal-covered substrata in shallow water, near the reef edge (Bellwood, 1995b). Sediment is preferentially released in deeper water, with fish swimming up to 60 m away from the feeding sites. In one area an estimated 67 kg of sediment was deposited in two small "defecation sites" over a 4-day period (Bellwood, 1995b). Comparable species-specific behavior is seen in *Sparisoma viride*, the primary eroding species in the Caribbean (Bruggemann *et al.*, 1996). In both regions these species are removing material at a rate that is comparable to local calcification rates (Bellwood, 1995a; Bruggemann *et al.*, 1996).

Given that one can identify the principal taxa involved in bioerosion (and the morphological features associated with an excavating feeding mode), one can focus efforts looking at the biology of eroding species. It is thus possible to provide a detailed picture of the role of these species on the reef in terms of erosion, habitat modification, and sediment production (e.g., Bellwood, 1995b, 1996b; Bruggemann *et al.*, 1996). Furthermore, the close relationship between jaw morphology and excavation potential provides a basis for examining the fossil record for evidence of the history of bioerosion by scarids. A Miocene fossil *Bolbometopon* jaw fragment from Sri Lanka (Bellwood and Schultz, 1991), for example, indicates that excavating scarids have been present in the Indo-Pacific for at least 5.2 Ma. The cladogram of genera and current biogeographic

distributions (Section IV), however, suggest that excavating forms may be considerably older.

Using the cladogram and data on feeding mode in scarids it is possible to track the evolution of the various feeding modes. For example, eroders appear to have arisen from seagrass-dwelling browsing forms, Whereas the excavating (eroding) feeding mode arose independently as a result of hypermorphosis in both *Sparisoma* in the Caribbean and its sister taxon, the *Bolbometopon*–*Cetoscarus*–*Chlorurus*–*Hipposcarus*–*Scarus* lineage, in the Indo-Pacific (Bellwood, 1994; Bernardi *et al.*, 2000). Given that the Caribbean and Indo-Pacific probably had different scarid taxa prior to the Neogene, and that the two areas have had markedly different histories, it is striking that scarid erosion in the two systems is so similar, with most erosion restricted to one or two large species. The disparate histories of the Caribbean and Indo-Pacific offer an exciting format for examining broader questions of ecosystem function, assembly rules, trophic networks, and the relationship between species diversity, cladogenesis, trophic diversity, and functional redundancy. Central to these studies is the recognition and definition of appropriate functional groups (see Chapter 2).

B. Functional Groups in the History of Coral Reefs

In the evolution of marine systems major faunal change has often been marked by mass extinction events followed by rapid diversification (Boucot, 1983). The role of biotic interactions in evolution has been the subject of considerable debate. Of all examples, the Mesozoic Marine Revolution (MMR) (Vermeij, 1977) stands out as a clear example of historical changes in the nature of benthic communities that have been explained by changes in ecological interactions. In the MMR, changes in the composition of benthic faunas, and the form of component species, are interpreted as a response to an increase in predation intensity. This change in predation pressure is based on the appearance and diversification of numerous predator groups in the Mesozoic. It has been argued that these changes accounted for the appearance of many antipredator adaptations, including increased external ornamentation in gastropods (Vermeij, 1977), and infaunalization, boring, and cementation in bivalves and other sessile taxa (Stanley, 1977; Harper, 1991; Wood, 1999).

A second ecologically driven revolution may have coincided with the massive radiation in marine fishes during the late Mesozoic and early Cenozoic: a Cenozoic Marine Grazing Revolution. At this time,

the appearance of several herbivorous fish groups may mark the origins of fish-based herbivory on coral reefs, with benthic algae forming a key food source for members of the relatively new and rapidly expanding group, the perciform fishes. Today, perciform fishes dominate modern benthic marine systems. The combination of the MMR and Cenozoic changes has been interpreted as two parts of a long-term trend. Jackson and McKinney (1990) argue that the observed trends (i.e., changes in distribution, prey shape, and infaunalization) can be readily explained as part of a progressive escalation in the defenses employed by prey to counter increasing predation intensity, and an increase in the diversity of forms preying and grazing on the marine benthos.

During the Cenozoic, coral reefs represented a critical arena in which these changes in the nature of trophic interactions may be seen, in that they represent one of the most complex assemblages of marine benthic invertebrates and one of the primary habitats that may be occupied by the rapidly expanding perciform fish faunas. Following a global hiatus of 7–10 Ma in the late Cretaceous–Paleocene, when there was no significant deposition of shallow tropical carbonate platforms (Kauffman and Fagerstrom, 1993), there arose a new and widespread coral reef system that, by the Eocene, appears to have been characterized by the taxa and possibly processes observed on coral reefs today.

The presence of modern reef taxa in the Eocene is readily established by examination of the fossil record. This period marks the first record of most fish families found on modern reefs (Bellwood, 1996a) and many modern scleractinian genera (Veron, 1995). It is harder to determine if processes were similar. However, there are several lines of evidence to suggest that the new reefs of the early Cenozoic were playing by “modern” rules.

Predators capable of excavating or crushing calcareous skeletons have been around since at least the Jurassic. Among the neopterygian fishes, the pycnodonts were a major group of durophages throughout the Mesozoic (Nursall, 1996). However, the Cenozoic appears to mark a major change in the nature of fish-based predation, from the more carnivorous Mesozoic fish faunas, with relatively few durophagous taxa (cf. Viohl, 1990; Maisey, 1994; Tintori, 1995), to Cenozoic faunas with numerous durophagous taxa and a suite of grazing or browsing herbivores. There appears to have been a major shift in the relationship between fishes and benthic substrata, probably including coral reefs. In the Mesozoic, reef–fish interactions were probably indirect, with reefs providing structure and shelter for potential prey. In the Cenozoic, numerous fish groups appeared that were capable

of feeding directly on the reef surface. These fishes probably included epilithic algal grazers and algal browsers, with the presence of families including the Acanthuridae, Siganidae, and Pomacentridae (Bellwood, 1996a; Bellwood and Sorbini, 1996). Today, these fish groups are major determinants of benthic community structures on coral reefs (Steneck, 1988).

On modern reefs, most reef substrata are dominated by corals, coralline algae, and short epilithic algal communities. The maintenance of these groups appears to be dependent on grazing pressure. Removal or reduction of grazing activity may result in an increase in algae and a decline in corals. This scenario has been documented over many scales, from sites over months to reefs over years, with increasing evidence that many components of the benthic community are dependent on intensive grazing pressure (Carpenter, 1986; Hughes, 1994; Steneck, 1997).

C. Grazing through History

Throughout the Phanerozoic there have been shallow-water reef structures with associated grazers. Steneck (1983) documented the changes in the relative intensity of excavating grazing on hard substrata, with a progressive increase in the number of taxa and grazing depth. The most marked change, particularly in excavation depth, was in the late Mesozoic and Cenozoic corresponding with the increase in piscine herbivory. It appears that the “new” Cenozoic reefs were different from their Mesozoic precursors in that the fish fauna contained a diverse array of percomorph fishes that were able to play a key role in shaping benthic communities. Moving onto reefs from other habitats, these fishes would be in position to stamp their impression on evolving coral reefs.

Mesozoic grazers were predominantly invertebrates, which were relatively slow moving and left only shallow scars and minimal structural damage. Only in the late Mesozoic were deep-grazing limpets and urchins recorded. Among the fishes, the pycnodontids are widely regarded as the dominant durophagous group feeding on benthic hard substrata (Viohl, 1990; Maisey, 1991, 1994; Tintori, 1995; Nursall, 1996). At this time there were few, if any, clearly recognizable grazing or browsing fish. Piscine herbivory may date from the Devonian, but there is little evidence to suggest that an herbivorous feeding mode arose prior to the Cenozoic. In the Cenozoic, in addition to the invertebrate grazers, vertebrate grazers appeared in significant numbers with several different fish groups represented (Bellwood, 1996a). These new grazing forms were all characterized by high mobility and in some taxa the

potential for deep scars and significant structural damage. These new herbivores could have radically changed the nature of grazing, combining intensive grazing with the potential for selectivity and mobility.

Marine vertebrate grazing may not have been restricted to fishes. Chelonioid turtles have been recorded since the upper Jurassic (Carroll, 1988), although the origins of herbivory within this group are unclear. Today only two species are predominantly herbivorous, *Chelonia midas* and *Chelonia agassisi*, the former occasionally grazing algae on reefs. The earliest record of the family to which these species belong is in the early Cenozoic (Legler and Georges, 1993). The other major group of vertebrate herbivores, the Sirenians (dugongs and manatees), likewise dates back to the early Cenozoic, with the first records from the Lower Eocene (Carroll, 1988).

The impact of these changes in grazing pressure is hard to assess. The fossil record of tropical fleshy algae is poor. However, several lines of evidence suggest that grazing pressure increased during the late Cretaceous and Cenozoic and that there was an associated change in the structure of benthic communities. This is most clearly seen in the coralline algae and corals. Historically there have been two major groups of coralline algae, the Solenoporaceae (Cambrian–Miocene) and the Corallinaceae (Carboniferous–recent). The two forms differ markedly in their inferred resistance to grazing, with the former being much more susceptible to damage. Steneck (1983) related changes in the relative abundance of the two algal forms to changes in the levels of herbivory, arguing that the decline in solenopores was correlated with the appearance of deep grazing urchins, limpets, and fishes. A comparable decrease in delicate (herbivore-susceptible) branching corallines was recorded in the tropics after the Eocene (Johnson, 1961). The inferred scenario is one of increased herbivory, both in intensity and excavation depth, with a concomitant decrease in the abundance of macrophytes. This results in a system dominated by close-cropped turfs, where decreased competition between algae and corals permits coralline algae and corals to proliferate.

Scleractinian corals have been a significant component of reefs since the mid–late Triassic. From the late Triassic onward, coral assemblages included taxa with large colonies and with a strong probability of a well-established zooxanthellate association (Wood, 1995). Coates and Jackson (1985) argue that the risk of mortality is the primary selective force in shaping the geometry of epibenthic marine invertebrates. In addition, they suggest that the nature and extent of coloniality and module integration are directly related to

this mortality risk. Today reef corals are predominantly multiserial (erect or encrusting) hermatypic (i.e., containing zooxanthellae) with small corallites and high levels of integration (Coates and Jackson, 1985). This growth form confers not only the ability to grow to large sizes and great flexibility in growth morphology, it also compartmentalizes damage, with the ability to regenerate from fragments or to rapidly repair damage (Jackson and Hughes, 1985; Meesters *et al.*, 1994). This growth form is also strongly linked with an association with zooxanthellae (Coates and Jackson, 1985), an association that brings additional benefits to corals with the potential for faster calcification and rapid growth (Barnes and Chalker, 1990). In many respects therefore, modern scleractinian corals possess a suite of traits that may limit the impact of predation. Although driven largely by a decline in one family, an increase in the degree of colony integration during the Cenozoic may be indicative of changes in the nature of mortality risks during this period (Coates and Jackson, 1985; Wood, 1995).

There are several other taxa in which changes in taxonomic composition, distribution, or morphology have been linked to increased predation, bioerosion, or grazing pressure by fishes during the late Mesozoic and Cenozoic. This includes the loss of shallow-water stalked crinoids (Meyer and Macurda, 1977) and articulate brachiopods (Stanley, 1974; Logan, 1977), and morphological changes in bryozoans (Jackson and McKinney, 1990). Changes in the structure of non-calcareous algal assemblages are difficult to determine because there are few well-preserved specimens and numerous unreliable records (Dawson, 1966). Changes in the algal community can only be inferred; however, the patterns seen in corals, calcareous algae, and other benthic taxa suggest that the Cenozoic would be marked by the rise of grazing-resistant, integrated, clonal algae, possibly with burrowing or endolithic components—in all, the characteristics of a modern turf or epilithic algal community.

Today, the structure of the jaws and multidentulate dentition of many acanthurids are closely associated with the browsing or grazing of short, filamentous, epilithic algae (Jones, 1968; Purcell and Bellwood, 1993). The presence in Monte Bolca of several acanthurid genera with comparable dentition (Blot and Tyler, 1990) suggests that these fishes would have been able to graze short-turfing algae. With over eight genera and representing over 4% of the nonclupeid specimens recorded from Monte Bolca (Bellwood, 1996a), these early acanthurids may have been a significant group of epilithic algal grazers. Other potential grazing groups include the Siganidae, and the

Pomacentridae, and, to a lesser extent, the Zancidae, Scatophagidae, and Ephippidae.

Given the evolutionary history of reef fishes and modern scleractinian coral reefs it appears that the appearance and proliferation of modern scleractinian-dominated coral reefs in the late Eocene/Eocene were not the catalyst in the origin and the early diversification of reef fish lineages. These lineages were almost certainly established in nonreefal habitats prior to the widespread appearance of modern coral reefs. However, the converse may not be true: the presence of reef fishes may have been instrumental in the formation of modern coral reefs and their successful invasion of oligotrophic tropical waters. Although the dominant constructional elements of modern reefs—scleractinian corals and coralline algae—have been around since the Triassic, the evolution and development of modern reefs may have been dependent on the presence of modern fish groups, particularly the herbivores.

Most Phanerozoic reefs were calcified algal or soft-substrate heterotrophic communities that were trophically unlike modern coral-algal reefs (Wood, 1993, 1995). An increase in the intensity and nature of grazing and predation provided a dramatically different environment for reef builders in the late Cretaceous and early Cenozoic. Suppression of macroalgae would give corals and grazing-resistant coralline algae a competitive opportunity, and may have underpinned their successful proliferation and invasion of oligotrophic environments. Reefs have been present throughout the Phanerozoic. It is unlikely that reef development *per se* required fishes, but it is likely that the nature of reef development and the composition of benthic communities were shaped by fishes, the result being a system dominated by grazing-resistant algae, leading to modern benthic communities that are strongly influenced by, and possibly dependent on, intensive predation and grazing.

VIII. Discussion and Conclusions

It is clear that knowledge of history can change the way we view living reef fish faunas. The study of marine evolution and biogeography is at an exciting stage. Phylogenetic analyses have provided the stimulus for a reevaluation of historical information and fostered a synergism between disciplines that is increasingly evident in biogeography today. Numerous workers have recognized the extent to which local patterns are dependent on regional factors, which in turn are shaped by historical and biogeographic events (cf. Ricklefs and Schluter, 1993a). The global decline in biodiversity has

highlighted the need to understand the processes operating at regional and large biogeographic scales.

Reef fishes represent one of the most diverse vertebrate assemblages. With a 50-million-year history and biogeographic ranges that can span the entire tropical Indo-Pacific, from Africa to the Gulf of California, they offer a unique insight into the role of history and biogeography in marine systems. The fishes seen on reefs today are the product of a long and complex history, with superimposed patterns of origin and loss extending over at least 50 million years. Indeed, regional fish faunas may have been shaped by events as far back as the Cretaceous. The Indo-Pacific and Caribbean probably share a common faunal history, yet today the species richness in the Caribbean is only about a fifth of that in the Indo-Pacific, with strong temperate influences. The two regions have been shaped by their subsequent period of isolation, with the Caribbean being characterized by a history of decline and loss.

For reef fishes, the inclusion of historical evidence in our analyses has already challenged us to reappraise our understanding of the term “reef fishes” and the nature of interactions between fishes and the reef. Reef fishes defy simple definition, with nonreef habitats playing a critical role in the origin and maintenance of reef fish taxa. Reef fish assemblages appear to be a collection of lucky survivors. Those taxa that survived the vagaries of division and regional extinctions form the basis of Recent reef fish assemblages in major biogeographic realms (e.g., Indo-Pacific, Atlantic, East Pacific). Within these realms subsequent vicariance events may lead to speciation and regional subdivision. However, many fish assemblages appear to be relatively constrained, as marked by the similarity in the familial composition and relative species richness of families in the Red Sea and on the Great Barrier Reef.

Reef fish faunas also represent a collection of ancient body forms. The staggering diversity of species on reefs today, belies this ancient history. Much of this diversity may be only skin deep, with diversity being based largely on differences in color patterns; the body plans have changed little over millions of years. Most families, and their associated structural features, were established 50 Ma ago and some lineages may even extend back into the Cretaceous.

This long and complex history challenges us to look at the way that the fishes and the reef interact. It appears that many fish families do not need reefs. In both evolutionary and ecological terms, coral reefs represent only one of a range of suitable habitats. Reef associations may be largely facultative. In contrast, the presence of fishes appears to have been of critical importance in the evolution of modern coral reefs.

There are four major components in biogeographic studies: (1) the description of patterns, (2) elucidating the origins of the patterns, (3) examining the mechanisms maintaining patterns, and (4) determining the ecological consequences of these patterns. In reef fish studies, progress has been made in all four areas. For reef fishes, our knowledge will continue to grow, not only from the steady accumulation of more fossils and phylogenies, but also from the application of new methods. Fossils continue to provide new data, but further analyses of both form (cf. Foote, 1996) and function (cf. Valkenburgh, 1994; Jernvall *et al.*, 1996) offer promising avenues of investigation in order to expand our understanding of the nature and impact of changes in form through time. Furthermore, the full impact of molecular studies has yet to be felt in our analyses of reef fish biogeography, although the initial results offer exciting insights, with ancient origins for the major lineages and extensive turnover and intermixing, at a species level, in relatively recent times.

Reliable species lists are now available for most major reef areas and interesting patterns are emerging, with the identification of the location of possible vicariance events. These locations are identified largely on discontinuities in the distributions of color morphs or species. However, the nature and timing of these vicariance events remain to be determined. Many other questions remain: What are the primary determinants of species richness on coral reefs and to what extent does congruence between fishes and nonfish reef taxa (e.g. Bellwood and Hughes, 2001) reflect general biogeographic processes? The maintenance of assemblages and biogeographic patterns is still an area of active investigation although regional comparisons of processes maintaining assemblages (cf. Hughes *et al.*, 1999) are limited.

Of all components, the last is arguably the most important: the ecological consequences of historical events and biogeographic patterns. Reef fish assemblages are not uniform. Their differences are the product of both historical and ecological factors. The consequences for management of reef resources are far reaching. How can the Red Sea thrive with only a

quarter of the fish species on the Great Barrier Reef? Do reef fish assemblages follow assembly rules? And to what extent would such rules apply to functional groups? To what extent is ecosystem function shaped by species richness and regional history? At what point will declining species richness compromise ecosystem function? And to what extent is the answer dependent on biogeographic location: are peripheral sites more vulnerable than those close to high-diversity locations? Clearly, we must look beyond species numbers and even biogeographic patterns in species abundances. A knowledge of the functional abilities and role of fishes on reefs appears to hold the key to our understanding of the significance of biodiversity in reef ecosystems.

Preliminary data have identified patterns that will serve as a basis for future research into the nature and significance of biodiversity. Within the Indo-Pacific there are strong gradations in species richness that permit comparisons of faunas of differing diversity within a biogeographic region, whereas comparisons between the Caribbean and Indo-Pacific permit comparisons between regions with markedly different histories. Such analyses will provide a rich source of comparative data to examine the role of history in shaping faunas and the role of species richness in the function of reef ecosystems.

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