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REPORT

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Do coral-reef fish faunas have a distinctive taxonomic structure?

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Abstract Do the highly diverse fish faunas that associate with coral reefs have distinguishing taxonomic and ecological characteristics, as proposed by Choat and Bellwood (1991) and Bellwood (1996)? Does a 50 my old (Eocene) fossil fish fauna from Italy represent a coral-reef fish assemblage that provides unique information about the evolution of such assemblages, as claimed by Bellwood (1996)?

I compared the structure of the reef fish faunas of adjacent tropical regions rich and poor in coral reefs, in both America and Polynesia, and found that they exhibit no substantive differences in relative species richness among families of typical "coral-reef" fishes. While coral-rich regions have larger reef fish faunas, a variety of factors probably contribute to such differences. Thus coral-reef fish faunas may lack a distinctive taxonomic structure. A similar comparative approach would be useful for assessing whether assemblages of fishes on coral reefs have distinctive ecological characteristics.

Based on patterns of habitat use by modern tropical shorefishes, the Italian Eocene fauna includes few definite reef fishes, and may well consist primarily of non-reef fishes preserved in a non-reef habitat. Until we know more about the environment in which those fossils were preserved, that fauna can contribute little to understanding how coral reef fish *assemblages* have evolved.

Key words Reef fish · Assemblage structure · Fossil assemblage

Introduction

Coral reefs epitomize high taxonomic biodiversity, and assemblages of fishes that associate with such reefs are among the most speciose known (e.g., Choat and Bellwood 1991; Paxton 1995). There are obvious, strong contrasts in the species richness and taxonomic structure of fish assemblages on coral reefs and temperate rocky shores. There also is a general concordance in geographic gradients of species richness among fishes, corals and other coral reef biota, including latitudinal and longitudinal declines in diversity away from an Indo-Philippine "center" in the Indo-Pacific (e.g., Springer 1982; Myers 1991a; Veron 1995). This combination of factors has led to a commonly held assumption: the development and maintenance of diversity among coral reef fish assemblages has depended on the diversity of resources produced on those reefs, and those assemblages have major, distinctive taxonomic and ecological characteristics.

Choat and Bellwood (1991) made the first comprehensive attempt at defining potentially diagnostic characteristics of coral reef fish assemblages. They presented a set of taxonomic and ecological characteristics that they proposed distinguish those assemblages from other types of marine fish assemblages. Those taxonomic characteristics include dominance by perciform fishes in general, and by three major perciform taxa in particular, chaetodontoids (butterfly and angelfishes), acanthuroids (surgeonfishes and moorish idols), and labroids (pomacentrids, wrasses and parrotfishes). Bellwood (1996) further developed this idea of taxonomic distinctiveness by proposing a "consensus" list of 10 families of fishes that are widely distributed, speciose and abundant on coral reefs throughout the tropics, and whose combined presence captures the essence of any coral-reef fish assemblage. He did so while examining the structure of the largest, best preserved aggregation of Eocene fish fossils from a ~50 million year old deposit at Monte Bolca in Italy. Bellwood (1996) asserted that that fauna represents the earliest known coral reef fish assemblage (see also Choat and Bellwood 1991). He based that assertion on two lines of evidence: (1) a significant number of

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families that are well represented in both numbers of species and individuals on modern coral reefs also occur in the Bolca fauna. (2) Coral reefs were widely distributed when the Bolca fishes were alive, and Bolca was at the center of the Tethys Sea and would have contained many cosmopolitan taxa. As Bellwood (1996) pointed out about that fauna: "If indeed this is a coral reef fish assemblage, then the Bolca fishes will be of paramount importance in our understanding of the evolution of coral reef fishes..." because they represent by far the largest and best preserved fossil fauna discovered to date.

This study has two aims: (1) to examine the idea that fish faunas living on modern coral reefs have major distinguishing taxonomic characteristics, and (2) to assess the assertion that the Bolca fauna represents a coral reef fish assemblage.

Methods

Here I consider reef fishes to be species that live on consolidated substrata that form coral and inorganic reefs. Coral reefs are reefs on which corals and benthic organisms such as coralline algae produce the physical structure of the reef at both large and small scales, construct the full range of habitat features used by reef fishes, and directly and indirectly provide other benthic resources for them. In contrast, on inorganic reefs, such as rocky shores, the inorganic bedrock provides large- and small-scale physical structure that fishes use as habitat features, although some smaller-scale habitat features are also produced organically, by organisms such as barnacles, algae, and, sometimes, corals, present as a thin veneer over the bedrock.

If coral reefs have been crucial for the evolutionary diversification of perciforms and species-rich families of fishes that characteristically occur on coral reefs, then it follows that those taxa should have more reef-dwelling species, in both absolute and relative terms, in regions dominated almost entirely by coral reefs than in tropical regions that have few coral reefs and are dominated largely by inorganic reefs. I examined that prediction by comparing patterns of species richness among Bellwood's (1996) consensus families in the reef fish faunas of similar sized, adjacent tropical regions very rich and very poor in coral reefs. Such pairwise comparisons allow some degree of control for longer-term effects of history on faunal structure, although they certainly do not eliminate history's shorter-term effects. For example, while two of the regions compared here, the eastern Pacific and northwest Atlantic, have had very different histories since the rise of the central American isthmus, 3.5 my ago (Coates et al. 1992; Veron 1995), they had a common history for a long period before that event. That shared history was very different from the long-term history of the Polynesian sites considered here.

The pairs of regions I compared are in (1) Polynesia: the Society Islands (16°–18°S), a group of high volcanic islands in which coral reefs are the dominant (sole?) reef type, and the Marquesas Islands (7°–10°S), a group of high volcanic islands in which coral reefs are small and restricted to bays, on only a small percentage of the coastline; and (2) America: the tropical north-west Atlantic (9°–27°N), in which coral reefs are abundant, and the tropical eastern Pacific (2°S–23°N), in which coral reefs are rare. Wells (1988a, b) provides a summary of the abundance of coral reefs in those four areas. From Guzman and Cortes' (1993) review of the status of reef development in the tropical Eastern Pacific it seems likely that there are <25 km^2 of structural coral reefs, and only one wave-breaking coral reef (the 3.7 km^2 reef of Clipperton Atoll) in that entire region. It is unclear whether there are any wave-breaking coral reefs in the Marquesas.

For conciseness here I refer to those areas as regions, although, as defined by other authors (e.g., Briggs 1974; Veron 1995), they include zoogeographic regions, provinces and parts of provinces. Those pairs of areas were chosen because their fish faunas have been well defined, and they span the range of conditions in terms of the relative abundances of coral and inorganic reefs.

In the first four of the five comparisons of taxonomic structure made later (and in Tables 1–4) I included only reef fishes that live in <70 m of water (the lower limit of hermatypic coral growth) in the American faunas. I excluded pelagic species, deep-dwelling species, and those that live in soft bottoms, seagrass beds and estuaries. Although all species in the source lists (see Table 1) were included in the Polynesian and Great Barrier Reef faunas, those lists contain few potentially non-reef species. The Eastern Pacific fauna includes a significant number of transpacific shorefishes, i.e., species that also occur in Oceania and, in some, cases, elsewhere in the Indo-Pacific (see Robertson and Allen 1996). About one third of those transpacific species, including many in two consensus families (Chaetodontidae and Acanthuridae) have been found so rarely in the Eastern Pacific that they probably are vagrants that recruited there from Oceania. To avoid undue influence by such vagrants on the structure of the Eastern Pacific fauna I excluded all of them from all analyses.

Results and discussion

Are there more species of reef fishes in coral-rich regions?

As would be expected if coral reefs have promoted diversification, the total number of reef fishes is greater in the coral-rich region of each pair, although the difference is much greater ($\sim$70%) in Polynesia than America ($\sim$12%) (Table 1). However, while differences in the abundances of coral reefs may have contributed to these differences in regional fauna size, other factors undoubtedly are involved. First, the fish fauna of the coral-rich region of each pair has been more effectively sampled than the fauna of the coral-poor region, particularly in Polynesia. Thus the sizes of reef fish faunas in adjacent regions are likely to be more similar than the existing data indicate. Second, the coral-poor Marquesas are more isolated than the coral-rich Societies from sources of additions to their faunas: they are not only considerably further than the Societies from species-rich Western Pacific sources of such additions, but are also upcurrent from all adjacent tropical sources (see Gorshkov 1976). The Tuamotu Archipelago (13°–23°S, coral reefs only) lies between (and is much larger than) the Societies and Marquesas. The Tuamotus' known reef-teleost fauna is $\sim$17% larger than that of the Marquesas, but $\sim$30% smaller than that of the Societies (see Randall 1985). Thus location per se has a strong influence on the size of regional fish faunas within French Polynesia. Third, the coral-rich tropical Western Atlantic has a larger area of reef habitat than does the Eastern Pacific, and a much greater abundance of offshore islands and reefs. The Western Atlantic also has an abundance of near-reef seagrass beds (virtually absent from the Eastern

Table 1 Percent of reef fish faunas represented by species in different taxa of bony fishes in tropical regions in which coral reefs range from virtually the only reef type (+CR), to being uncommon (−CR)

Taxon[a]	America N-West Atlantic (+CR)	Eastern Pacific (−CR)	Polynesia Society Islands (+CR)	Marquesas Islands (−CR)	Australia Great Barrier Reef (+CR)
Muraenidae	2.7	5.9	7.5	7.5	3.0
Holocentridae[b]	2.3	1.5	3.5	4.2	2.5
Syngnathidae	2.3	1.3	2.2	1.3	1.2
Scorpaenidae	2.0	0.8	3.5	2.6	2.2
Serranidae	12.6	9.7	7.3	5.2	7.7
Cirrhitidae	0.2	0.8	1.3	2.0	1.1
Apogonidae	2.9	1.5	4.0	3.6	4.9
Carangidae	2.7	3.1	2.9	3.6	5.0
Lutjanidae	2.7	2.6	2.1	2.0	2.4
Haemulidae	4.1	2.9	0.2	0	1.0
Mullidae	0.9	0.5	2.1	3.6	1.3
Chaetodontidae	1.6	1.0	5.0	4.6	4.3
Pomacanthidae	1.6	1.0	2.1	0.7	2.4
Pomacentridae	3.4	4.9	6.4	6.5	10.4
Labridae	3.2	5.1	9.8	11.7	10.6
Scaridae	2.3	1.5	3.7	1.6	2.7
Blenniidae	2.0	2.6	4.2	4.9	5.0
Other Blennioids	18.0	21.8	0.4	0.7	0.6
Gobiidae	16.2	10.7	8.5	8.1	6.2
Acanthuridae	0.7	1.8	6.0	7.8	3.7
Tetraodontiforms	5.1	4.4	6.8	6.8	6.4
Other families	10.3	14.6	10.5	11.0	15.4
Total perciforms	81.1	80.1	72.5	74.1	82.4
Total Number of species	444	392	519	307	1002

[a] Taxa: other Blennioids = Tripterygiidae, Labrisomidae, Chaenopsidae. Tetraodontiforms = Balistidae, Monacanthidae, Ostraciidae, Tetraodontidae and Diodontidae. Other families (with few or no species in Polynesia and/or America) = Synodontidae, Ophidiidae, Bythidae, Antenariidae, Gobiesocidae, Aulostomidae, Caracanthidae, Pseudochromidae, Plesiopidae, Kuhliidae, Priacanthidae, Malacanthidae, Caesionidae, Lobotidae, Sparidae, Lethrinidae, Nemipteridae, Sciaenidae, Kyphosidae, Ephippididae, Mugilidae, Sphyraenidae, Pinguipididae, Callionymidae, Microdesmidae, Siganidae, Bothidae

[b] "Consensus" families of Bellwood (1996) are italicized

Sources: Randall (1983, 1985), Randall et al. (1990), Robins et al. (1986), Allen and Robertson (1994), Fischer (1978), Fischer et al. (1995), D Hoese, E Murdy and P Hastings, personal communication

Table 2 Relative abundances of different taxa of fishes in the reef-fish faunas of three regions in the Americas

Taxon[a]	Percent of regional fauna represented by each taxon		
	Tropical eastern Pacific	Temperate eastern Pacific[b]	Tropical north-west Atlantic
Hexagrammidae and Cottoids	0	24.6	0
Scorpaenidae	0.8	16.7	2.0
Miscellaneous	32.9	17.4	32.5
Zooarcoids	0	11.6	0
Blennioids	24.4	8.7	20.0
Embiotocidae	0.3	6.5	0
Tetraodontiforms	4.4	3.6	5.1
Serranidae	9.7	3.6	12.6
Gobiidae	10.6	2.9	16.2
Labroids	6.6	2.2	5.5
Pomacentridae	4.9	1.4	3.4
Muraenidae	5.9	0.7	2.7
Total perciforms	80.1	55.8	81.1
Total number of species	392	138	444

[a] Miscellaneous = other families listed in Table 1 that individually contribute little to the temperate eastern Pacific fauna

[b] California to Alaska; data on fish fauna from Eschmeyer et al. 1983

Table 3 Levels of similarity (Czeckanowski Indices, see Bloom 1981) in taxonomic structure of entire reef fish faunas of different regions (percent of fauna/family for all families listed in Tables 1, 2)

A Similarities between American regions, and between them and Central and Western Pacific regions

	Tropical northwest Atlantic	Temperate East Pacific	Great Barrier Reef	Society Islands
Tropical East Pacific	0.77	0.38	0.58	0.63
Tropical northwest Atlantic	–	0.34	0.57	0.58

B Similarities between Central and Western Pacific regions

	Societies	Tuamotus	Great Barrier Reef
Marquesas	0.88	0.87	0.78
Societies	–	0.86	0.81

Table 4 Concordance of patterns of relative species richness among Bellwood's (1996) consensus families in the reef-fish faunas of five regions: the tropical northwest Atlantic (TWA), the tropical Eastern Pacific (TEP), the Society Islands (SOC), the Marquesas Islands (MAR) and the Great Barrier Reef (GBR). Data from Table 1

	Wilcoxon paired sample test probabilities			
	TWA	TEP	SOC	MAR
TEP	0.799	–	–	–
SOC	0.005	0.007	–	–
MAR	0.009	0.005	0.202	–
GBR	0.005	0.005	0.799	0.878

Pacific), which represent an important ancillary habitat for many Western Atlantic reef fishes (e.g. Parrish 1989). Thus the Western Atlantic has a greater overall habitat diversity than the Eastern Pacific, a diversity that is due to various factors in addition to the abundance of coral reefs. Fourth, the paucity of coral reefs in the Eastern Pacific evidently is due to increased environmental seasonality and stress that produced coral extinctions following the rise of the central American isthmus (e.g. Veron 1995). Those environmental changes, and the loss of a coral fauna that largely survives in the tropical Western Atlantic, may have had some, albeit much smaller, negative effect on the size of the Eastern Pacific's reef fish fauna. However, any such declines were offset to some extent by enhanced recruitment of reef fishes from Oceania, due to greatly increased eastward current flow from that area (see Grigg and Hey 1992; Veron 1995). Consequently, environmental stress and the influx of fishes from other regions may have influenced the reef fish fauna of the Eastern Pacific more than that of the Western Atlantic. Thus sampling effort, location, overall habitat diversity and history contribute significantly to differences in the known size of the regional fish faunas considered here.

Do some families of reef fishes occur only in coral-rich regions?

All but two of 48 families of reef-living teleosts in Polynesia occur at both the Societies and Marquesas (Table 1). The two exceptions (Bythitidae and Haemulidae) each have a single representative at the Societies. All but two of 45 families of reef teleosts in the Americas (Table 1) occur in both the Eastern Pacific and Western Atlantic. The two exceptions (Kuhliidae, Pacific only, and Pempheridae, Atlantic only) are not speciose families on reefs anywhere. Thus, there are no reef fish families that are taxonomically significant in either of the two coral-rich regions but absent from neighboring coral-poor regions.

Are reef-living perciform fishes relatively more speciose in coral-rich regions?

Perciforms constitute virtually the same percentages of the reef-living teleost faunas of neighboring coral-rich and coral-poor regions in both Polynesia and America (Table 1). In contrast, those fishes represent a substantially smaller component of the reef fish fauna of the temperate Eastern Pacific, for example, than of the fish faunas of both the immediately adjacent tropical Eastern Pacific, and the other tropical regions considered here (Tables 1, 2).

Do patterns of species richness among families of typical coral-reef fishes differ in regions rich and poor in coral reefs?

Levels of similarity in overall taxonomic structure (species richness/family) of regional fish faunas are fairly high between the American regions and between the

Polynesian regions (Table 3A, B). In contrast, there are marked differences in overall structure of reef fish faunas in contiguous tropical and temperate areas dominated by inorganic reefs (e.g., the tropical Eastern Pacific versus the temperate Northeastern Pacific, Table 3A). Levels of similarity in overall taxonomic structure between adjacent coral-rich and coral-poor tropical regions in both America and Polynesia are close to those between (a) adjacent coral-rich areas (the Societies versus the Marquesas and versus the Tuamotus, Table 3B), and (b) high- and low-diversity coral-rich areas in the Pacific (the Societies versus the Great Barrier Reef, Table 3B). However, similarities in taxonomic structure are substantially higher between the two American regions than they are between either of those regions and regions in the Central and West Pacific (Tables 1, 3).

Bellwood's (1996) consensus families, which include seven of the 10 most speciose reef fish families found in the central and western Pacific (Table 1, and see Myers 1991), do not consistently contribute more to the reef fish fauna of the coral-rich region than the coral-poor region in either Polynesia or America (Tables 1, 4). This lack of a consistent difference persists if the 10 most speciose families of reef fishes are used in the analyses rather than the consensus families (i.e., the holocentrids, mullids and scarids are replaced by the muraenids, serranids and gobiids, see Table 1, and Myers 1991) (Wilcoxon paired sample tests: Tropical Eastern Pacific versus Western Atlantic $P = 0.878$, Societies versus Marquesas $P = 0.594$). Only three consensus families are relatively more speciose in the reef fish faunas of both coral-rich regions, while five others show the reverse pattern. Families with lower relative species richness in both coral-rich regions include the pomacentrids and labrids, two of the three most speciose families occurring on coral reefs, worldwide. Further, even among the consensus families in which there are relatively more species at both coral-rich sites (Apogonidae, Chaetodontidae and Scaridae) the differences are not large in relation to the size of other within-family, between-site differences (Table 1). In contrast to similarities in the patterns of relative species richness of consensus families between adjacent regions rich and poor in coral reefs, there are marked differences in those patterns between the American regions and both the Polynesian regions and the Great Barrier Reef (Tables 1, 4).

It could be argued that the inter-regional comparisons made are inadequate for at least two reasons: (1) Polynesia and America are marginal, low-diversity sites situated far from the Indo-Philippine center of diversity, and high-diversity faunas have more characteristic taxonomic structure. (2) Coral-poor regions are not coral-free and many residents in such regions are coral-dependent (i.e., species that feed primarily on or live solely with live coral at some stage of their life cycles) and rely on corals living away from coral reefs.

There are no real indications that either situation is the case. First, perciforms constitute very similar percentages of the reef fish faunas of both American regions and of the Great Barrier Reef, a high-diversity region (Table 1) close to the Indo-Philippine center of diversity. Perciforms form a somewhat ($<10\%$) smaller percentage of both Polynesian reef fish faunas than of the Great Barrier Reef reef fish fauna, but also less than both American faunas (Table 1). Further, there are no consistent differences in relative richness patterns among consensus families between the low-diversity Polynesian regions and the Great Barrier Reef (Tables 1, 3). However, there is a substantial difference in the patterns of relative richness among the consensus families in the American sites versus those from Polynesia and the Great Barrier Reef: consensus families represent $<25\%$ of each American fauna but $\sim 50\%$ of each Polynesian fauna and the fauna of the Great Barrier Reef (Tables 1, 4). Reef fish faunas in coral-poor regions are not pallid reflections of the faunas of coral-rich regions, with consensus families in coral-poor areas being represented simply by subsets of species from neighboring coral-rich regions. In the Eastern Pacific, each consensus family includes two or more endemic species, and four of them (Apogonidae, Mullidae, Pomacentridae and Blenniidae) are represented entirely by endemics (see Allen and Robertson 1994; Fischer et al. 1995). Randall (1985) estimated an overall level of endemism of $\sim 10\%$ in the Marquesas, where endemics are known from at least several of the consensus families. Thus consensus families seem to be as able as other families to maintain themselves over geologic time as important endemic components of the faunas of coral-poor regions.

Second, probably only two coral-dependent fishes (*Cantherhines dumerilii* and *Arothron meleagris*) are resident in the tropical Eastern Pacific. Besides those, the only Eastern Pacific residents that are found only on coral reefs are those endemic to Clipperton Island However, there are no indications that those Clipperton endemics rely on types of resources found only on coral reefs (Allen and Robertson, 1997). Thus, coral-dependent species make a trivial contribution to the Eastern Pacific reef fish fauna. There is insufficient information on the ecology of reef fishes in the Marquesas to allow any detailed assessment of the level of coral dependency by that region's resident fish fauna, although, based on their diets, a few species recorded from there are probably coral-dependent.

Do families of typical reef fishes have relatively more reef-living species in coral-rich regions?

The two American regions are the only ones with sufficient information on the structure of their shorefish faunas and their general ecology to allow examination of this question. Comparison of the structures of those

Table 5 Percentages of species of different taxa of shorefishes that live in reef versus non-reef[a] habitats in the tropical Americas

Taxon	Percent of species living on reefs in	
	Eastern Pacific	North Western Atlantic
Holocentridae	100	100
Apogonidae	100	87
Carangidae	34	39
Mullidae	50	25
Chaetodontidae	100	100
Pomacentridae	100	100
Labridae	83	74
Scaridae	100	71
Blenniidae	100	100
Acanthuridae	100	100
All perciforms[b]	69.6	71.9
Total number of species[b]	573	646

[a] Soft bottom, seagrass, and pelagic habitats
[b] Taxa are listed in Table 1

two faunas shows that (1) the percentage of species living on reefs rather than other habitats is lower in the tropical Eastern Pacific than the Western Atlantic for one consensus family, higher in the Eastern Pacific in four consensus families and equal in the remaining five, and (2) the percentage of species of perciforms living on reefs is only marginally lower in the Eastern Pacific (Table 5). Thus, neither perciforms nor families of typical coral-reef fishes have disproportionately large numbers of reef-living species in the American region dominated by coral reefs.

Conclusions about distinctive taxonomic characteristics

This analysis found no marked differences in patterns of species richness among families of typical reef fishes in adjacent regions that differ greatly in terms of the importance of coral reefs as fish habitat. The biologically most significant structural difference in the reef fish faunas of the tropical regions considered here is that the American faunas differ much more from the faunas of Polynesia and of the Great Barrier Reef than they do from each other (Table 3). This pattern of difference indicates that differences in long-term history have stronger effects on the general structure of regional reef fish faunas than does extreme variation in the relative abundances of coral versus inorganic reefs. Similarities in the overall taxonomic structure of the fish faunas of the Eastern Pacific and the Western Atlantic have been recognized before (e.g., Rosenblatt 1967: Thresher 1991). However, putative differences between the richness of those faunas that previously were attributed to the paucity of coral reefs in the Eastern Pacific in fact largely seem to reflect inadequate sampling of that region's fish fauna.

Bony fishes appeared in the fossil record some 220 my ago (Long 1995). Symbiotic scleractinian corals appeared shortly thereafter, although they did not begin to dominate reef ecosystems until ~140 my later (Wood 1995). Grazing by fishes and other benthic herbivores may have fostered the evolution of calcareous algae (Steneck 1983), and promoted the development of coral reefs both by controlling populations of fleshy algae that compete with corals and by facilitating the growth of organisms such as calcareous algae that contribute to reef construction (Wood 1995). Although major groups of fishes found on modern coral reefs appeared at about the time coral reefs became prominent, and coral reefs support the most diverse modern marine fish assemblages, there is no clear evidence that long-term association with coral reefs led to distinctive taxonomic characteristics in coral-reef fish faunas.

If coral-reef fish faunas lack a distinctive taxonomic structure then the question shifts to the distinctiveness of their ecological characteristics (see Choat and Bellwood 1991). Comparison of the ecology of fishes on inorganic and coral reefs within and between regions and across Indo-Pacific gradients in biodiversity will help answer that question. The tropical Eastern Pacific offers unique, major opportunities for such studies, due to a combination of the extreme paucity of coral reef development, a large endemic reef fish fauna with strong relationships to the fauna of the coral-rich Western Atlantic, and a significant component of resident transpacific fishes that live on coral reefs elsewhere in the Pacific.

The Monte Bolca fossil fauna

Is it likely that the Bolca fauna represents a reef-fish assemblage and thus offers significant insights into the evolution of reef fish assemblages? In his assessment of the numerical structure of the Bolca fauna, Bellwood (1996) focused on the abundance of 10 families that are well represented on modern coral reefs and the absence of seven families typical of modern, soft-bottom habitats in the tropics. He attributed differences in the species richness of those 10 coral-reef fish families in the Bolca fauna and modern coral reef faunas to evolutionary diversification at the species/genus level over the last 50 my. However, Bellwood (1996) gave only passing attention to what the overall taxonomic and numerical structure of the Bolca fauna indicated about the extent to which its members were drawn from non-reef habitats. Further, while he asserted that coral reefs were abundant in the Tethys sea when the Bolca fauna was fossilized and that the fauna was linked to a coral reef, neither Bellwood (1996) nor Choat and Bellwood (1991) refer to any direct evidence that a coral reef

existed in the immediate vicinity of the soft sediments in which the fossils were buried.

The precise position of the sediments at Bolca relative to contemporaneous reefs (coral or inorganic) is crucial. The further they were from a reef the less likely it is that the dead fishes represent an unbiased sample of a local reef fish assemblage. If those sediments were more than a few tens of meters from a reef, differences between abundances of certain fish taxa on modern reefs and in the Bolca fauna could simply reflect different propensities to move away from reefs following the universal, widespread stress that is thought to have killed and preserved those fishes in an undisturbed state (an algal bloom?, see Choat and Bellwood 1991), and/or to bloat-and-float after death. For example, while Holocentrids (which are abundant in the Bolca fauna) confine themselves to hard reefs during the day they often move away from reefs to feed at night in surrounding habitats. Most pomacentrids (represented by two individuals in the Bolca fauna) rarely move more than a few meters from a reef, even when they characteristically live at reef/soft-bottom interfaces. The Bolca sediments would have had to have been intimately imbedded within a reef complex to have entombed a numerically representative reef fish assemblage.

Members of the families of Bolca fishes that Bellwood considered as coral reef fishes constitute only ~18% of the identified individuals in that fauna, and half of those individuals were Holocentrids. However, many modern species from Bolca's other main reef fish families (Serranidae, Ephippidiidae, Apogonidae, Gobiidae and Acanthuridae) normally live in non-reef habitats (e.g., Munro 1967; Collette 1983; Robins et al. 1986; Myers 1991; Allen and Robertson 1994; Fischer 1978, Fischer et al. 1995). Further, half the individuals in the Bolca fauna belong to other taxa whose modern representatives either usually or often associate with non-reef marine habitats, as well as estuarine and freshwater habitats. On the strength of the association of its modern representatives with reefs, only one family that made a significant contribution to the Bolca fauna, the Holocentridae, probably is exclusively resident on (coral and inorganic) reefs.

Many fishes found on modern coral reefs make extensive use of soft-bottom habitats adjacent to reefs (e.g., Parrish 1989). Is there assemblage-level information on the occurrence of reef fishes on adjacent soft-bottoms that could provide some perspective for viewing the Bolca fauna? Wantiez (1992) found that reef fishes constituted 40% of the species and 24% of the individuals he collected in trawls on the soft bottom of a large New Caledonian lagoon. His data also show the following: (1) the seven families that were virtually absent at Bolca and that, as Bellwood (1996) pointed out, are characteristic of many modern tropical soft bottom faunas, also were absent from those trawls, although representatives of five of them do occur in that area (M Kulbicki, personal communication). (2) All but one of the reef fish families (Mullidae) that were rare in the Bolca fauna also were rare in the trawl samples. (3) While the four most abundant reef fish families in the Bolca fauna (Holocentridae, Ephippididae, Acanthuridae, and Apogonidae) were absent or rare in the trawls, most of those absences can be attributed either to trawling occurring only during the day (when holocentrids hide on reefs), to non-reef members of a family not occurring in the region (ephippidids), or to small body size reducing susceptibility to trawl capture (apogonids?). Thus the New Caledonian soft-bottom fauna and the Bolca fauna are broadly similar in terms of the relative representation of fish families that regularly associate with reefs, but are not necessarily restricted to them, and much of the difference between those two faunas is attributable to sampling effects, or faunal regionalism.

Viewed in the light of this information, the domination of the Bolca fauna by taxa whose modern representatives usually or often are abundant in habitats other than inorganic or coral reefs indicates that, that fauna may well represent an assemblage of estuarine or lagoonal fishes, with the addition of a few taxa of reef fishes. Without doubt the Bolca fauna does offer a unique opportunity to assess aspects of the evolution of tropical marine shore fishes. However, until we know much more about the Bolca environment when its fishes were fossilized, that fauna can provide little information that is unequivocally useful for analysing how coral reef fish *assemblages* have evolved.

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