



Factors shaping the range-size frequency distribution of the endemic fish fauna of the Tropical Eastern Pacific

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ABSTRACT

Aim To assess the effect of habitat fragmentation and isolation in determining the range-size frequency distribution (RFD) of the shorefish fauna endemic to a discrete biogeographical region.

Location The Tropical Eastern Pacific (TEP).

Methods Habitat isolation represents the separation between oceanic islands and the continental shore of the TEP and habitat fragmentation the degree of spatial continuity of habitats (i.e. reefs, soft bottom, nearshore waters) along the continental coast of the TEP. The effects of habitat isolation and fragmentation were quantified by comparing the RFDs of (1) the species found on oceanic islands vs. the continental shore, and (2) species on the continental shore that use different habitat types.

Results The RFD of the entire TEP fauna was bimodal, with peaks at both small- and large-range ends of the spectrum. The small-range peak was due almost entirely to island species and the large-range peak due mainly to species found in both the continental shore and oceanic islands. RFDs varied among species using different habitats on the continental shore: reef-fishes had a right-skewed RFD, soft-bottom species a flat RFD, and coastal-pelagic fishes a left-skewed RFD.

Main conclusions Variation in dispersal capabilities associated with habitat isolation and fragmentation in the TEP appears to be the main mechanism contributing to differences among RFD structure, although variation in tolerances arising from the dynamic regional environment may contribute to some patterns. Because diversity patterns are strongly affected by RFD structure, it is now evident that the insular and continental components of a fauna should be treated separately when analysing such patterns. Furthermore, contrasts in RFD structure among species using different habitats demonstrate that a full understanding of the causes of diversity patterns requires analyses of complete regional faunas in relation to regional geography.

Keywords

Dispersal, geography, habitat fragmentation, habitat usage, isolation, range-size frequency distribution, shorefishes, Tropical Eastern Pacific.

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INTRODUCTION

One of the most important biological attributes of a species is the size of its geographical range. Range size strongly affects and reflects processes of speciation and extinction (reviews by Lawton, 1993; Gaston, 1994, 1996, 2003; Rosenzweig, 1995; Chown, 1997; Gaston & Blackburn, 2000; see also Hawkins *et al.*,

2000; Jablonski & Roy, 2004), may influence the geography of species diversity (Stevens, 1989) and will affect faunal resilience to ongoing global changes in the environment (Gaston, 2003). A readily discernable feature of any taxonomic assemblage is the tremendous variation in the sizes of species ranges. The pattern typical of many assemblages is that most species are restricted to relatively small areas and only a few span very

large areas. This produces a range-size frequency distribution (RFD) that is unimodal and has a strong right skew. This type of pattern has been observed in a wide range of assemblages of extant marine and terrestrial organisms (see reviews by Gaston & Blackburn, 2000; Gaston, 2003). The fact that such right-skewed RFDs also occur in some extinct marine taxa (e.g. Jablonski, 1986; Jablonski & Valentine, 1990; Roy, 1994) suggests that this pattern has been a persistent feature of life (Gaston, 2003). However, determinants of the structure of RFDs are poorly understood and have received significantly less attention than other macroecological patterns (e.g. spatial patterns of species richness, species-body size distributions – see Gaston, 2003). RFD shape must ultimately be a product of processes that control speciation (i.e. addition of species whose range-size depends on the mode of speciation), extinction (i.e. removal of species whose extinction-risk depends on range-size) and range dynamics over the course of a species' existence (see Gaston, 1998, 2003). However, it is far from clear how these processes operate together to produce the structure of an RFD.

This paper aims to assess how habitat fragmentation and isolation within a region can shape RFDs, through its constraining effects on dispersal and, hence, on the geographical extent of species ranges. Our study is based on the marine shorefish fauna endemic to the Tropical Eastern Pacific (TEP). In our analyses isolation represents the separation between the oceanic islands and the thin continental shelf of the TEP, and between the islands themselves, and habitat fragmentation refers to any breaks in the continuity of major habitat types (reefs, soft bottom, the nearshore water mass) along the coastline of the TEP. The effects of these factors were assessed by comparing RFD structure among species found at oceanic islands and/or the continental shore, and among species restricted to each continental habitat type.

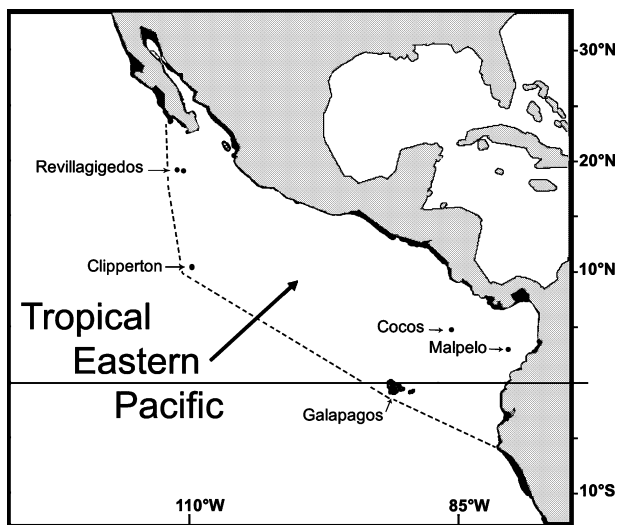


Figure 1 The Tropical Eastern Pacific biogeographical region. The continental-shelf area is shown in black along the coastline.

METHODS

Location

The TEP (Fig. 1) includes the west coast of the Americas between *c.* 32° N and 8° S, plus five isolated oceanic islands and island groups – the Revillagigedo group (400 km from the tip of Baja), Clipperton (1100 km from central Mexico), Cocos (480 km from Costa Rica), Malpelo (400 km from Colombia) and the Galapagos archipelago (1000 km west of Ecuador). All of these islands originated from oceanic volcanoes, and were never connected to the mainland (see Robertson, 2001). Hence their shallow-water shorefish faunas are derived entirely by long-distance dispersal. The continental coastline, which has a very narrow continental shelf, and an uncomplicated form with a roughly longitudinal orientation, provides > 95% of the shallow habitat for the region's shorefishes (Robertson *et al.*, 2004) (Fig. 1). There are only two significant clusters of nearshore islands – one along the coasts of Panama (mainly) and Costa Rica, and the other in the Gulf of California (Mora & Robertson, unpublished data). Within the TEP, rocky shores are common along all but two large sections of coastline that consist entirely of sand and mud, and lack any reefs: a 1000 km section from southern Mexico to El Salvador, and a 370 km section in the south-eastern Gulf of California. These reef-less stretches of shoreline, which are known as the Central American Gap and the Sinaloan Gap, respectively, act as barriers to the distributions of some shallow reef-fishes (Hastings, 2000). In contrast, there are no analogous large barriers in the TEP likely to affect the distributions of either demersal soft-bottom fishes or coastal-pelagic fishes.

Data

Thanks to 150 years of research that culminated in a recent series of regional and subregional guides (e.g. see Allen & Robertson, 1994; Fischer *et al.*, 1995; Grove & Lavenberg, 1997; Thomson *et al.*, 2000), the shorefish fauna of the TEP is now probably as well defined as that of any equivalent tropical region. Latitudinal range-size data used in this paper are taken from a data base of current information (based on 1000+ citations) on the range limits of all known shallow-water shorefishes (those living in <100 m of water) in the TEP (see Robertson & Allen, 2002). That data base includes information on 1195 fishes, among which *c.* 80% of the species that are resident in the TEP are endemic to it. The remainder include species that occur elsewhere in the tropical Pacific, species known in the region only from vagrant individuals, species primarily found in the temperate parts of the eastern Pacific that penetrate the fringes of the TEP, and a handful of species introduced from the Atlantic (e.g. migrants through the Panama Canal). Here we consider only TEP endemics ($n = 827$ species), in order to assess patterns of variation in range-size in a large suite of species that have been subject to the influence of a common set of geographic factors and a common history of exposure to the region's physical environmental regime.

Analyses

We examined the frequency distributions of range sizes among components of the TEP-endemic fauna in three ways: first, we compared species that differ in terms of the extent to which their distributions likely are affected by habitat isolation and have demonstrably different capacities to live in a variety of environments. We considered three groups of species: those restricted entirely to the oceanic islands (hereafter insular species), fishes restricted to the continental shore, and those found on at least one oceanic island as well as the continental shore. Because the oceanic islands of the TEP are well isolated, from each other as well as from the mainland, we predicted that insular species should have small ranges and the most strongly right-skewed RFD. Because species common to both continental shores and oceanic islands have demonstrated both the dispersal power to overcome insular isolation barriers and the capacity to live in a range of environments, we predicted that their ranges should tend to be large and their RFD left-skewed. Finally, we expected that continent-only species would have an RFD intermediate between these two extremes because they are less restricted by habitat discontinuities than are insular species but are less successful than continent + island species at dispersing across oceanic barriers and/or surviving in different environments.

The second analysis is based in all species found on the continent and assesses effects of variation in levels of geographical patchiness of different habitat types, and in adult dispersal potential. Here, we analyse variation in range size among the following assemblages of species: (1) demersal species that are restricted to reef habitats (rock and coral), (2) demersal species restricted to soft-bottom habitats (sand, gravel and mud), and (3) coastal-pelagic species that live in the nearshore water column. It should be noted that coastal-pelagics include both species that have large, vagile adults and live in open water (e.g. scombrids and carangids) and small, less mobile species that live closer inshore, including in estuaries (e.g. atherinids, engraulids, clupeids, some scia-

nids). Species with multiple habitat associations were not included in this analysis. We reasoned that, if the large gaps in the distribution of shallow reef habitats do generally limit the distributions of reef-fishes (cf. Hastings, 2000 for a review), then their ranges should tend to be smaller than those of either demersal soft-bottom or coastal-pelagic species. Further, because adults of many coastal-pelagics are more mobile than those of demersal species, that capacity should add to dispersal capabilities arising from any pelagic larval stage possessed by many members of both groups; hence, coastal-pelagics should have larger ranges than demersal species if dispersal ability is a major determinant of range size.

We tested these predictions as follows: (1) by making statistical comparisons of the structure of the RFDs of the different groups of species, and (2) by comparing the actual RFDs of those groups with a null RFD. In each case a null RFD was derived by randomly selecting a similar number of species to the analysed group from the entire pool of species for the first analysis and from the pool of continentally occurring species for the second analysis. In each case the randomization procedure was repeated 1000 times to generate the 95% confidence limits of the null distribution.

We made one further analysis that takes into account the fact that current knowledge about the biogeography of shorefishes in the tropical Indo-Pacific is based entirely on analyses of reef-fishes (e.g. McAllister *et al.*, 1994; Bellwood & Hughes, 2001; Bellwood & Wainwright, 2002; Hughes *et al.*, 2002; Jones *et al.*, 2002; Roberts *et al.*, 2002; Connolly *et al.*, 2003; Mora *et al.*, 2003). To assess whether TEP reef-fishes represent adequate proxies for the whole fauna we compared the RFDs of the reef and remaining components of the TEP fauna.

RESULTS

The entire endemic fish fauna of the TEP exhibited a right-skewed RFD (Table 1, Fig. 2a,b), as species with the smallest ranges are the largest group. However, there was a second,

Table 1 Statistical descriptors of range-size frequency distributions of the entire endemic fish fauna from the Tropical Eastern Pacific (TEP), and components thereof. The range-size frequency distribution of Indo-Pacific reef-fishes (data from Mora *et al.*, 2003) is included for reference. The skews of all log-transformed distributions were significantly different from the log-normal distribution at $P < 0.05$

	<i>n</i>	Untransformed				Log-transformed			
		Mean	Median	Kurtosis	Skew	Mean	Median	Kurtosis	Skew
Endemic TEP fishes									
Entire fauna	827	18.5	17.0	-1.5	0.1	1.1	1.2	-0.4	-1.0
Continent + islands	277	26.0	30.0	-0.2	-0.9	1.3	1.5	5.3	-2.4
Continent only	452	17.4	15.0	-1.2	0.3	1.1	1.2	0.3	-1.0
Islands only	98	2.5	1.0	11.0	3.1	0.2	0.0	1.1	1.6
Coastal-Pelagic	104	23.9	28.5	-1.0	-0.5	1.3	1.5	3.7	-1.9
Soft-bottom	375	20.7	21.0	-1.3	-0.1	1.2	1.3	0.9	-1.3
Reef	199	17.3	15.0	-1.3	0.2	1.1	1.2	0.3	-1.1
All reef fishes	280	13.0	9.0	-1.0	0.7	0.8	1.0	-1.5	-0.3
Remaining diversity	547	21.4	23.0	-1.3	-0.2	1.2	1.4	1.1	-1.4
Indo-Pacific reef-fishes	1907	24.1	21.0	-1.3	0.4	1.0	1.3	-1.3	-0.6

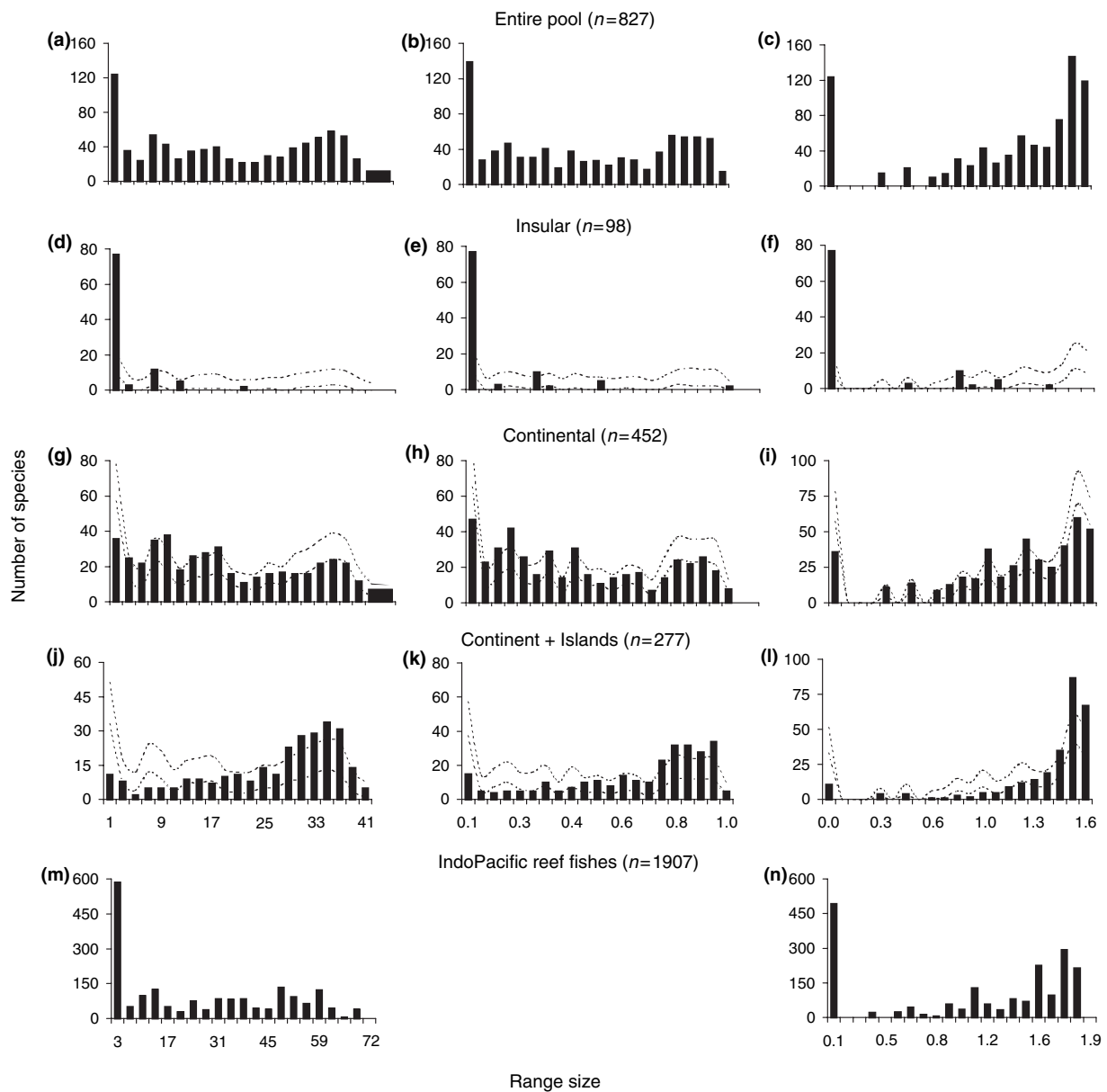


Figure 2 Range-size frequency distributions (RFDs) of the marine fishes endemic to the Tropical Eastern Pacific. The RFDs of the entire fauna and components thereof are shown on untransformed (left panels) and log-transformed (right panels) scales. Dotted lines indicate the 95% confidence limits of a null distribution (see Methods for details). The untransformed and log-transformed latitudinal RFDs of the reef-fish fauna of the Indo-central Pacific (m,n) are added for comparison (data from Mora *et al.*, 2003, with the exclusion of TEP endemics). The RFDs of ranges standardized to domain size are shown for comparison (centre panels; see text). Dotted lines indicate the 95% confidence intervals of a null model (see Methods for details).

smaller and broader mode present towards the large-range end of the distribution (Fig. 2a,b). This bimodality is more evident in the log-transformed RFD (Fig. 2c). There were statistically significant differences in median range-size among insular, continental and continent + island species (Kruskal–Wallis ANOVA, $H = 295.4$, $P < 0.001$). A nonparametric multiple comparison test for unequal sample sizes (Zar, 1996) showed all pairwise comparisons to be significantly different at $P < 0.001$. Insular species had a strongly right-skewed RFD (Fig. 2d–f), the smallest median range-size (Table 1), and

more small-range species and fewer large-range species than expected due to chance (Fig. 2d–f). Continental species had a relatively homogeneous RFD (Fig. 2g–i), an intermediate median range-size (Table 1), and differed from the null model by having fewer smallest-range species and more middling-range species (Fig. 2g–i). Species found on both the continent and oceanic islands had a strongly left-skewed RFD (Fig. 2j–l), the largest median range-size (Table 1), and fewer small-range species and more widely distributed species than expected due to chance (Fig. 2j–l). It should be noted that, while the domain

for continental species is 40° of latitude, that for insular species is only *c.* 20° . Hence insular species cannot have ranges greater than about half the potential maximum range of continental species. To take this difference into account we repeated the analysis described above using relative range sizes (i.e. range-size as a percentage of the domain, which were 40° and 20° , respectively, for continental and insular species). The results and patterns of this comparison of relative range-size were the same as those for the comparison of absolute range-size (see Fig. 2).

Continuously-occurring species with different patterns of habitat usage also exhibited statistically significant differences in median range-size [Kruskal–Wallis ANOVA, $H = 23.7$, $P < 0.001$; all pairwise comparisons (Zar, 1996) were significantly different at $P < 0.002$, except coastal-pelagic vs. soft-bottom, where $P = 0.02$]. Coastal-pelagics had the largest median range-size and reef-fishes the smallest, while soft-bottom species were intermediate in that regard (Table 1). Based on the null models, the coastal-pelagic group had an excess of species with large ranges and a deficit of species with small ranges (Fig. 3a,b); soft-bottom species showed no statistically significant departures from the null distribution (Fig. 3c,d); and reef-fishes included an overabundance of small-range species and reduced numbers of large-range species (Fig. 3e,f).

The median range-size of TEP reef-fishes was distinctly smaller than that of the remainder of the fauna (Mann–Whitney U -test, $Z = 9.18$, $P < 0.0001$) (Table 1). The reef-fish RFD differed from the non-reef fish RFD in having more small-range species and fewer large-range species (Fig. 4a,b vs. c,d). Relative to the entire-fauna pattern, reef-fishes also had an excess of small-range species and a deficit of larger-range species (Fig. 4a,b), and non-reef fishes a deficit

of small-range species and an excess of large-range species (Fig. 4c,d).

DISCUSSION

In many taxonomic assemblages, the frequency distribution of species ranges is right-skewed, because small-range species represent the largest group (reviews by Gaston, 1996, 2003; Gaston & Blackburn, 2000). There are few published examples of RFDs of marine assemblages (reviewed in Gaston, 2003; see McAllister *et al.*, 1994; Roy *et al.*, 1995; Hughes *et al.*, 2002; Jones *et al.*, 2002; Macpherson, 2003). Compared with terrestrial species, marine species tend to have larger ranges and marine RFDs to have less marked skews than terrestrial RFDs (Brown *et al.*, 1996; Jones *et al.*, 2002; Gaston, 2003). This likely reflects the fact that oceans are larger than landmasses and that many marine taxa have highly dispersive larval stages that allow them to spread widely in marine domains. Even so, small-range species represent the most abundant category in both marine and terrestrial assemblages (reviewed in Gaston, 2003; and see McAllister *et al.*, 1994; Roy *et al.*, 1995; Jones *et al.*, 2002; but see Hughes *et al.*, 2002). In the fish fauna endemic to the TEP, the frequency distribution of untransformed range-sizes follows this pattern, with a strong mode at the smallest-range class, although a secondary, broader mode exists towards the large-range end of the distribution. This bimodality is more strongly evident in the log-transformed RFD. In other taxa in which such transformation has been applied, RFDs tend towards an approximately normal distribution (Gaston, 2003), indicating a deficit of both small- and large-range species (Gaston, 2003). Within the TEP fish fauna, however, the log-transformed distribution indicates a paucity of mid-range species and an excess of species with

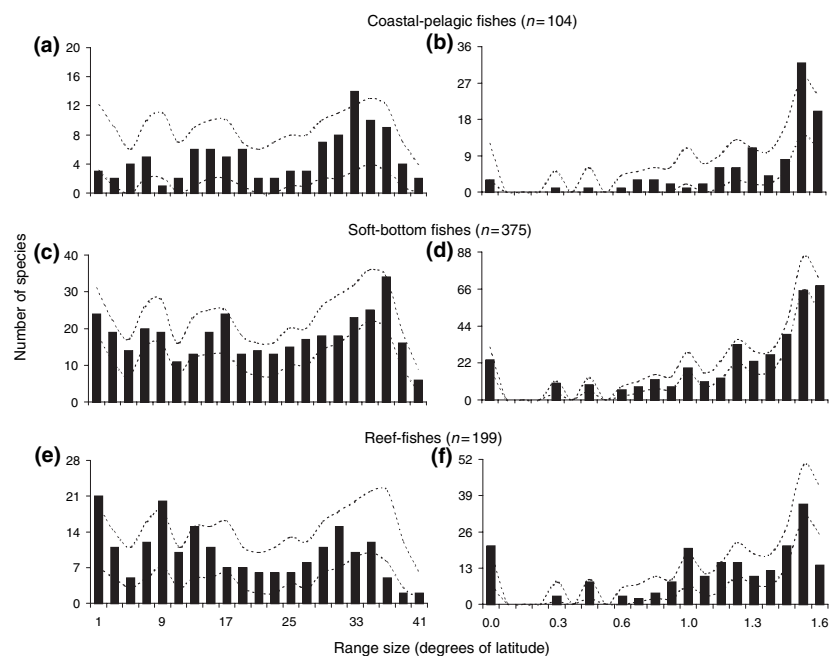


Figure 3 Range-size frequency distributions for fishes using different habitats on the continental shore of the Tropical Eastern Pacific. Left: untransformed patterns; right: log-transformed range sizes. Dotted lines indicate the 95% confidence intervals of a null model (see Methods for details).

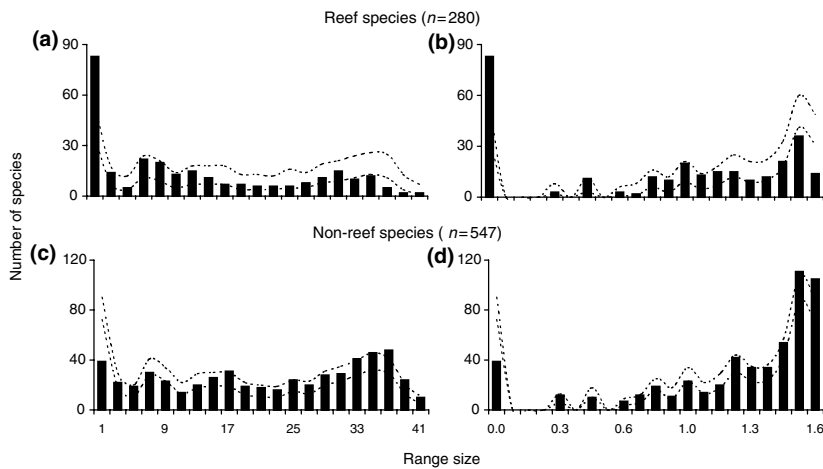


Figure 4 Range-size frequency distributions of the reef- and non-reef components of the endemic fish fauna of the TEP. Left: untransformed patterns; right: log-transformed range sizes. Dotted lines indicate the 95% confidence intervals of a null model (see Methods for details).

very small and large ranges. Insights into possible reasons for this pattern come from our analysis of different components of that fauna.

We found that the peak of small-range species in the total-fauna RFD is due almost entirely to insular species (12% of the total fauna), while the large-range peak is mainly due to species common to the continental shore and oceanic islands. The few extra mid-range species contributed by the continent-only group were insufficient to offset these small- and large-range peaks. These patterns are consistent with range sizes being regulated by habitat isolation and variation in the dispersal potential of members of the different groups.

Dispersal potential is a key determinant of the geographical extent of species ranges (Gaston, 2003, and see Jones *et al.*, 2002 and references therein for tropical shorefishes). In most demersal marine fishes dispersal is accomplished by the pelagic larval phase, although movements of adults can add to this dispersal in some cases (e.g. Mora *et al.*, 2001). The isolation of the oceanic islands in the TEP strongly limits either form of dispersal, leading to the predominance of very small ranges (equivalent to single islands or island clusters) among insular species. Oceanic islands are also characterized by retentive hydrodynamic processes (Mora & Sale, 2002; Sponaugle *et al.*, 2002), which likely assists in local closure of species life cycles (Robertson, 2001). This can restrict gene flow and lead to the formation of species with small ranges at oceanic islands. However, the existence in the TEP of insular endemics that have populations on multiple islands separated by distances greater than those isolating the islands from the mainland (Robertson & Allen, 2002, and see also Lessios *et al.*, 1999) suggests that differences in insular and continental environments are also involved in the production and maintenance of insular endemics. Regardless of the mechanisms, it is clear that in the TEP, oceanic islands contribute the great majority of the small-range species that produce the right skew in the total-fauna RFD. The extent to which insular species have similar effects on the right-skewed RFDs typical of other marine taxonomic assemblages remains to be determined, as insular and continental components of faunas

typically have not been considered separately in previous analyses.

Species found on both the continental shore and the oceanic islands have much larger ranges than strictly continental species. Two factors may be involved in producing this pattern. Such species have demonstrated a capacity for long-distance dispersal (as shown by their presence at sites separated by large barriers) that strictly continental species may or may not have. In addition, continent + island species have demonstrated a capacity to survive in a broad range of environments, a capacity that strictly continental species may or may not have. Thus species found on both islands and the continent not only may include those best equipped to expand throughout the region but also include those with the broadest tolerances, which allow them to survive in most of the region.

The continent-only RFD has a peak of species stretching across the lower half of the RFD and a deficit of species with the smallest ranges. Different geographical attributes of the TEP coastline may contribute to the generation of this pattern. The TEP coastline contains three large patches of reef habitat isolated by the Central American Gap (1200 km) and the Sinaloan Gap (370 km) (see Hastings, 2000) and two well-separated (by 3000 km) areas that have many islands, long shorelines, large areas of bottom and heterogeneous environments (the Gulf of California and Costa Rica/Panama, Mora & Robertson, unpublished data). Both the reef-patches and the island-rich zones support sets of local endemics (Hastings, 2000; Robertson & Allen, 2002; Mora & Robertson, unpublished data) and contribute to the TEP fauna many species with ranges about the sizes of their domains: 7°, 8° and 19° of latitude for the three reef patches and, 6° and 3° of latitude for the two island-rich zones, respectively [note that one of the island-rich zones (in the Gulf of California) is included within one of the reef patches]. These contributions can account for the broad peak across the lower half of the RFD of continent-only species. The shortfall of continental species with very small ranges can be accounted for by the fact that within these zones and patches there are few major physical barriers that seem likely to limit dispersal strongly and/or fragment species

ranges much more extensively. The only known barrier within one of those reef-patches is the separation of the two sides of the Gulf of California, which has some effect on genetic isolation in species that have very short larval lives (see Riginos & Victor, 2001). Yet species can still disperse along the shore of each side of the longitudinally oriented Gulf. It is also important to note that, due to the TEP's simple geography and narrow continental shelf, eustatic sealevel fluctuations are unlikely to have significantly affected the abundance of barriers in the region since its final isolation by the closure of the central American isthmus (*c.* 2–3 Ma). Hence continental species have not had their ranges repeatedly fragmented in the recent past by intermittently active physical barriers.

The interaction between isolation and dispersal seems to play a major role in determining the RFD structure of the TEP fish fauna. However, environmental tolerances are also known to affect species ranges (Gaston, 2003) and may contribute to the shape of RFDs, especially in an environmentally dynamic region like the TEP. In the TEP, as in other tropical regions, the maximum possible extent of each species occurrence is likely set by their thermal tolerances and strong gradients in temperature at the edges of the region (Jones *et al.*, 2002; Mora & Ospina, 2002; Mora *et al.*, unpublished data). The TEP has perhaps the most dynamic environment of any tropical region, due to an abundance of large seasonal upwelling areas and to frequent, intense and widespread effects of El Niño events (e.g. see Glynn & Ault, 2000). Although the isolation of the TEP also has an effect, stresses of this environmental regime are largely responsible for the depauperate coral fauna and paucity of coral reefs in the region (Glynn & Ault, 2000). These events also produce both local mortality of shorefishes and temporary changes in their ranges (Mora & Ospina, 2001, 2002; Victor *et al.*, 2001). While this regime should have selected for broad environmental tolerances among continental species, and promote large ranges, regional geography evidently has had a stronger effect on range-size, as continental species in general do not have large ranges. Only the group least affected by continental barriers, coastal-pelagics (see below), has a large-range peak in its RFD, suggesting that this group is the one most constrained at the northern and southern boundaries of the TEP by effects of thermal tolerances. Changes in range-size brought about by environmental variation in the TEP also indicate that the environmental regime of this region adds some temporal variation to the structure of RFDs.

RFDs varied among habitat-usage classes of TEP fishes that occur on the continental shore. There was a shift in the mode of the distribution from small ranges in reef-fishes to a uniform distribution in soft-bottom species, to large ranges in coastal-pelagic fishes. Similar habitat-related variation in RFD structure has been reported for benthic vs. pelagic invertebrates and fishes from both sides of the Atlantic Ocean (Macpherson, 2003). In the present case, we suggest that these differences arise through a combination of declining effects of large-scale habitat fragmentation and increasing dispersal ability along this hierarchy. Reef-fishes are those most strongly affected by habitat fragmentation. At the other extreme, the

nearshore waters used by coastal-pelagics are continuous throughout the region and those fishes often have more mobile adults with better dispersal capabilities than adults of the other two groups. Soft-bottom fishes are more sedentary than many coastal-pelagics, but have habitat that is more continuously distributed throughout the TEP than is that of reef-fishes. Taken together these patterns support the view that both life-history characteristics associated with dispersal-potential and habitat fragmentation can act as important determinants of range-size and the structure of the RFD of the continental component of a regional fauna.

Variation in range-size can have strong effects on the large-scale geography of species diversity (Colwell & Lees, 2000; Jetz & Rahbek, 2002, as well as the design of conservation strategies (Rodrigues *et al.*, 2004). Here, we found strong differences in the RFDs displayed by the oceanic and continental components of the endemic fauna of a well-defined biogeographical region. From this we suggest that these two components should be analysed separately when addressing questions about the determinants of large-scale diversity patterns, and that macroecological models and conservation strategies based on combinations of insular and continental components of regional faunas may need to be reassessed.

Analyses of the biogeography of tropical Indo-Pacific fishes usually take a big-picture approach with coral reef fishes (e.g. Briggs, 1974; McAllister *et al.*, 1994; Bellwood & Hughes, 2001; Hughes *et al.*, 2002; Jones *et al.*, 2002; Roberts *et al.*, 2002; Connolly *et al.*, 2003; Mora *et al.*, 2003). They deal with causes of geographical patterns of diversity by focusing on mechanisms that affect the integration of the reef-fish fauna over that enormous span and that have produced the global peak of diversity in the Indo-Australian area at the junction of the two oceans. Those mechanisms include effects of habitat area (Bellwood & Hughes, 2001), of geostrophic flow of ocean currents on directionality in range expansion (Connolly *et al.*, 2003), and of dispersal capabilities on range expansion towards the margins of the Indo-Pacific (Mora *et al.*, 2003). In such studies the TEP is viewed as a biologically marginal area within the Indo-Pacific whose unusual faunal characteristics (small size, high level of endemism, atypical reef-fish structure) derive from its great isolation from the Indo-central Pacific (IcP), by the world's widest deepwater marine barrier, for as much as 65 Myr (e.g. Bellwood & Hughes, 2001; Connolly *et al.*, 2003; Mora *et al.*, 2003). However, the TEP is more than just a biogeographically unusual part of an integrated Indo-Pacific. Until relatively recently (*c.* 3 Ma) it had longstanding connections with the western Atlantic, and the TEP shorefish and reef-fish faunas have much stronger affinities with the west Atlantic than with the IcP (e.g. Rosenblatt, 1967; Briggs, 1974; Robertson, 1998; Robertson *et al.*, 2004). Nevertheless, despite the fact that it represents an unusual situation within the context of the entire Indo-Pacific, the TEP provides some important general lessons for analyses of patterns of diversity throughout the remainder of that area. Those concern effects

of regional variation in faunal composition and regional variation in domain geography.

First, reef-fishes constitute only 34% of the endemic TEP fauna, and the geography of their diversity is not representative of that of the entire regional fauna. Reef-fish diversity reaches a global peak in the Indo-Australian area, but non-reef fish diversity is also likely to be high there due to the abundance and variety of continental habitats. In contrast, the fauna of the oceanic islands of the central parts of the Pacific and Indian Oceans undoubtedly consists almost entirely of reef-fishes. How overall faunal composition varies across the IcP and how that influences the regional geography of diversity remains to be determined.

Secondly, the geography of the TEP domain (its thin, uncomplicated coastline and few oceanic islands) has a primary role in determining the structure of the whole-fauna RFD. That the molluscs in the eastern Pacific have a similar RFD (Roy *et al.*, 1995) to that of TEP shorefishes is consistent with such domain characteristics having general effects on RFD structure. That the coastal fishes on the west side of the Atlantic had an RFD with a much stronger right-skew than that of the coastal fishes on the east side (Macpherson, 2003) can also be linked to interregional differences in geography: while the west coast of Africa has a relatively simple geography, with a narrow continental shelf and few islands, the east coast of the Americas is much more complex, with an abundance of both continental shelf and islands in the Greater Caribbean area. Further, the Greater Caribbean has significant eustatically variable barriers to dispersal that have affected range fragmentation (e.g. see Colin, 1975).

Such variation in shorefish RFD structure and geography indicates that there is a need for regional-scale analyses in the tropical IcP to account for its great heterogeneity in domain geography. The central Pacific, with the largest latitudinal span of the IcP, consists of scattered oceanic reefs, with no continental boundaries. The Indo-Australasian area includes an abundance of continental and insular habitats in the geographically most complex part of the globe, has continental boundaries on both northern and southern edges, and has the smallest latitudinal span in the IcP. The central Indian Ocean is similar to the central Pacific, but with the addition of a northern continental boundary. The geography of the western boundary of the IcP (east Africa) resembles that of the TEP. While the Indo-Australian area has an abundance of eustatically variable dispersal barriers, such barriers likely have been much less influential elsewhere in the IcP. While the IcP contains many widespread species (Hughes *et al.*, 2002) it also exhibits substantial faunal subdivision (e.g. Bellwood & Wainwright, 2002; Connolly *et al.*, 2003). Analyses throughout the IcP at equivalent scales to that performed here could provide significant insights into causes of the geographical patterning of shorefish diversity that are likely to be obscured by analyses at the scale of the entire Indo-Pacific, in which the Indo-Australian centre of diversity has a statistically overwhelming effect.

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