



How many species of shore fishes are there in the Tropical Eastern Pacific?

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ABSTRACT

Aim To assess whether the total richness of the shore-fish fauna of a discrete biogeographical region can be predicted, and to estimate how long it is likely to take to enumerate that fauna.

Location The Tropical Eastern Pacific (TEP), an isolated biogeographical region with a high level of endemism (72%) among its modestly rich, known fauna of shore fishes (1222 named + 58 known undescribed shallow-water species).

Methods We used patterns in the long-term dynamics and accumulation curves of descriptions of new species, which began in 1758, correlates of these patterns, and the body size–frequency distributions of various ecological groups of the fauna to (1) try to predict the total richness of that fauna, (2) estimate how many species might be missing and what biological characteristics they might have, and (3) estimate how long their discovery and description will take to complete.

Results Accumulation curves for the entire fauna, for all TEP endemics or for reef and soft-bottom species (77.5% of the fauna) are not approaching asymptotes, and their description rates have remained fairly stable over the past century. However, curves for pelagic and multi-habitat species (22.5% of the fauna) may be nearing asymptotes, perhaps because these species are relatively accessible to collection. These curves clearly indicate that the total TEP fauna is substantially richer than the presently known fauna, but do not allow reliable prediction of its richness. Extrapolations from frequency distributions of the body size of different ecological groups of TEP fishes indicate that the entire fauna is at least 12–15% larger than the currently known fauna.

Main conclusions From recent description trends, undiscovered species will tend to be small, have limited geographic and depth ranges, and live in deeper water. Poorly known, priority areas for taxonomic investigation in the TEP include deeper reef habitats, two isolated island groups, and several continental areas with unusual environments. At current levels of traditional taxonomic activity, the description of known unnamed species will take *c.* 15 years, and assessment of the richness of unknown species, which probably number in the hundreds, will take decades.

Keywords

Body-size variation, depth-range effects, faunal richness, geographic range size, habitat richness, habitat-use effects, shore fishes, species-description dynamics, Tropical Eastern Pacific.

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INTRODUCTION

Despite the recent renewal of debate and speculation (May, 1990; Erwin, 1983, 1991; Gaston, 1991a; Ødegaard, 2000),

biologists seem far from providing an acceptable answer to the basic question of how many species there are on the Earth. Knowledge of the richness and composition of the world's biota is fundamental for both theoretical and practical reasons.

First, such information is essential for understanding the ecological and evolutionary forces determining the structure, dynamics and persistence of the faunas and floras of different biogeographical regions and environments (Brown, 1995; Vermeij, 2001). Second, ongoing habitat degradation, changes in ecosystems arising from over-harvesting and from species invasions (Peterson & Estes, 2001; Steneck & Carlton, 2001), and the increasing risk of species extinction (e.g. Carlton *et al.*, 1999; Brooks *et al.*, 2002) mean that the timely acquisition of such knowledge is vital for the development of conservation priorities and effective management policies (Lubchenco, 1998; Palumbi, 2001).

At present, however, the compositions of most taxa in most biogeographical regions remain very incompletely known, including those of some of the best-known terrestrial vertebrate groups (e.g. mammals; see Patterson, 1994, 2000, 2001). The relative lack of such knowledge is a much larger problem in the Tropics than in temperate areas, because the Tropics comprise large areas of habitat that contain most of the world's species, and yet they have received much less attention. This situation is particularly acute in tropical marine environments, which, owing to their enormous areas and depth range, are much more difficult to sample than are terrestrial environments. While tropical marine birds and mammals are relatively well documented, they represent a tiny fraction of the tropical marine biota; most other marine taxa are still very poorly known. For high-diversity tropical ecosystems, such as coral reefs, only crude estimates of the numbers of species in particular regions are available (e.g. Paulay, 1997; Reaka-Kudla, 1997; Bouchet *et al.*, 2002).

Fishes constitute the largest group of vertebrates, with *c.* 26,000 species described, *c.* 64% of which are marine (see FishBase: <http://www.fishbase.org>; Catalog of Fishes: <http://www.calacademy.org/research/ichthyology/catalog>). Because they are a prominent component of regional marine biotas, and represent important resources for humans, they have received considerable attention from taxonomists. However, nearly two and a half centuries after the first formal descriptions by Linnaeus in 1758, 200–300 new species of fishes continue to be described each year, increasing the currently known fauna by *c.* 1% per year (see Catalog of Fishes: <http://www.calacademy.org/research/ichthyology/catalog>). This is true even in the case of regions with relatively modestly rich faunas, such as the tropical Eastern Pacific (TEP).

Determining whether the richness of a major taxon's regional fauna can readily be predicted is useful for assessing how quickly global biodiversity is likely to be adequately documented. Such documentation involves not only traditional taxonomy but also molecular genetics [see Species 2000 (<http://www.sp2000.org>), Systematics 2000 (Anonymous, 1994), and the Census of Marine Life (<http://www.coml.org/coml.htm>)]. CBOL, the Consortium for the Barcode of Life (<http://www.barcoding.si.edu>), for example, proposes to genetically 'barcode' all species of fishes by about 2010 (see Beardsley, 2005). Here we use a comprehensive data set on the shallow shore-living fishes known from the TEP to examine

the rates, patterns and correlates of morphospecies descriptions by traditional taxonomists over the past *c.* 250 years. We then assess whether this information allows us to predict the total richness of the TEP shore-fish fauna, and how long it is likely to take to name formally the undescribed species currently known to exist there. Finally, we identify poorly sampled habitats and locations in that region that represent high-priority areas for taxonomic research.

METHODS

The study area – the TEP biogeographical region

The TEP marine biogeographical region (Fig. 1) encompasses the continental coast of the Americas from about Bahia Magdalena on the southern Pacific coast of the Baja California Peninsula (Mexico), through the Sea of Cortez and south to Cabo Blanco, on the northern coast of Peru. The points where the cold currents that flow from high to low latitudes (the California current in the north, and Peru coastal current in the south) turn westwards define these northern and southern limits of the region (Briggs, 1974; Glynn & Ault, 2000). The TEP also includes five oceanic islands or archipelagoes: the Revillagigedo Islands, Clipperton Atoll, Cocos Island, Malpelo Island, and the Galapagos Archipelago, which are separated from the mainland by *c.* 350–1000 km of deep ocean. Continental islands occur mainly in the Gulf of California and along the coast of Panama (see Mora & Robertson, 2005a). The western limit of the TEP is defined by the Eastern Pacific Barrier (EPB) – a 5000-km-wide expanse of deep open ocean that separates the westernmost island in the region (Clipperton) from the nearest Central Pacific islands, the Line Islands (Ekman, 1953; Briggs, 1974; Robertson *et al.*, 2004). The EPB has acted as a barrier partly isolating the TEP shore biota from that of the rest of the Indo-Pacific for as long as 65 Myr (Grigg & Hey, 1992). The TEP has also been totally

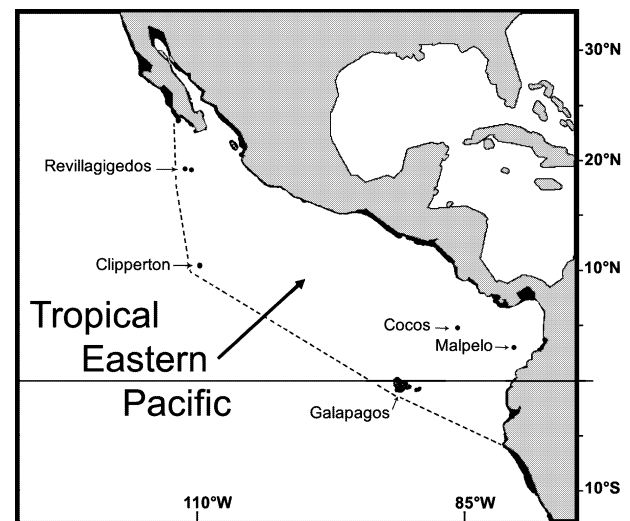


Figure 1 The TEP biogeographical region. The black area along the coastline represents the continental shelf.

isolated from its adjacent sister biogeographical region, the Greater Caribbean, for the *c.* 3 Myr that have elapsed since the final closure of the Isthmus of Panama (Coates & Obando, 1996). As a result of strong isolation by these highly effective barriers, the TEP has the highest level of shore-fish endemism of any region of comparable size: *c.* 72% of all species and *c.* 79% of those resident in the TEP occur only there (Robertson & Allen, 2002).

The great majority (*c.* 96%) of the shallow-water habitat occurs along the continental coastline, which has a very narrow continental shelf (Fig. 1), while the Galapagos Archipelago provides *c.* 95% of the same habitat at the oceanic islands (Robertson *et al.*, 2004). Rocky shores along the coastline are interrupted by two large expanses of sand and mud shorelines – the 370-km-long Sinaloa Gap on the south-east shoreline of the Gulf of California, and the *c.* 1000-km-long Central American Gap, from southern Mexico to northern El Salvador (Glynn & Ault, 2000; Hastings, 2000; Robertson & Allen, 2002). Corals occur throughout much of the TEP. However, the total cover of structural coral reefs in that region is only *c.* 25 km² (Robertson 1998), and such reefs represent a significant source of habitat at only one site within the region – the 4 km² of coral reef that constitutes Clipperton Atoll (Glynn & Ault, 2000).

Data

Information for the analyses presented here comes from a comprehensive data base on the shallow (0–100 m depth) marine shore-fish fauna of the TEP published by Robertson & Allen (2002). This fauna includes species living in brackish shoreline environments as well as those in fully marine habitats. The version of the data base published in 2002 treated 1195 species, and it has since been extended to include 1241 species, 1222 of them currently valid species described in the scientific literature by professional taxonomists. The remaining 19 species are at various stages in the process of being described. Species endemic to the TEP (*n* = 876) are either restricted entirely to the region, or have the bulk (75% or more) of their range within it. Some also occur, typically as vagrants, however, in temperate areas to the north and south of the TEP, or westwards across the EPB. Non-endemics have most of their ranges outside the TEP, and many occur in the TEP only as vagrants. The data base on species characteristics, which includes information that we use here on geographic distributions, depth ranges, habitat associations, and body sizes, is derived from an exhaustive review of the primary taxonomic, zoogeographic and ecological literature (>1000 individual citations from the scientific literature, 524 of which present the species descriptions we refer to here), as well as our own fieldwork throughout much of the region.

Analyses

We used the year of publication of the description of each currently valid species to examine patterns in the rate of

species description over time, and to construct species accumulation curves for the entire described fauna and its various ecological subgroups. Essentially, all these species were described by professional taxonomists or ichthyologists, and there have been virtually no recent descriptions by non-professionals, a practice that has affected the rate of descriptions in other marine groups (e.g. molluscs, Bouchet, 1997). The rate of descriptions of new species in a fauna depends in part on the amount of activity by taxonomists. To provide a crude indication of the dynamics of description in relation to the level of taxonomic activity, we examined how the number of active taxonomists, the number of papers describing species, and the number of species described per taxonomist per year have varied through time. For this, we divided our sample period (1758–2004) into quarter-century intervals, except for the first (1758–1775) and last (1976–2004) intervals, and treated the taxonomist population as all people who authored or coauthored species descriptions during each period.

Our analyses tacitly assume that the description accumulation curve and dynamics of description of currently valid TEP fishes over the past 250 years reflects the actual temporal pattern of species discovery. However, description dynamics can easily be affected by taxonomists splitting or lumping already described species. In particular, a large amount of recent splitting could maintain the upward trajectory of an accumulation curve with little or no actual discovery, while a large amount of recent lumping would have the opposite effect. However, our examination of the literature shows that very little splitting or lumping has taken place with TEP fishes, and that recent (post-1975) reviews of genera that included descriptions of multiple new species relied on new or previously unexamined material relating to poorly known taxa. Hence, we believe that our assumption that the tempo of description reflects that of discovery is correct in the present case.

Species characteristics that are likely to affect the historical pattern of species discovery in any taxon in any environment include abundance, body size, geographic and habitat distributions, and behaviour. Large, widely distributed species that are common, easily observed and occur in a variety of habitats are likely to be discovered earlier than species with the opposite characteristics (Gaston, 1991b; Gaston & Blackburn, 1994; Patterson, 2001; Reed & Boback, 2002; Collen *et al.*, 2004). Hence, we examined species-description accumulation curves for TEP fishes in relation to patterns of variation among species in their geographic and depth ranges, habitat usage and body size. Owing to a lack of data we did not examine the relationship between abundance and description date. Abundance data are completely absent for many species, and abundance measures obtained through different methods (e.g. density estimates obtained by visual censuses of reef fishes vs. numbers of individuals captured by trawling on soft bottoms) cannot be directly compared. As the TEP has a largely uncomplicated and longitudinally oriented continental shoreline, we used the latitudinal range of each species in the eastern Pacific (both in and out of the TEP) as a proxy for its

geographic range. For depth-range characteristics, we considered, for each species, the absolute range, the minimum depth of occurrence, and the midpoint of the depth range. Each species was assigned to either a single primary habitat category [demersal reef, demersal soft bottom (on sand or mud), or pelagic (living in the water column)] or, for fishes using more than one habitat, a multi-habitat category. For size, we used the maximum recorded body length.

Both logistic and von Bertalanffy growth functions can predict an asymptote, which, in the case of well-fitting species description curves, would represent the predicted total fauna size. Hence we examined the fit of species accumulation curves to both functions using the PAST computer program (Hammer *et al.*, 2001). Patterns of covariation between year of description and log-transformed body size, latitudinal range, latitudinal range limits, depth range, and minimum and maximum depths were examined by correlation. Because we found significant correlations between the year of description and all of these variables, we examined the extent to which year of description could be predicted from each variable independently using a multiple (forward step-wise) linear regression analysis. This was carried out for the entire fauna, for TEP endemics, and for species in different habitat-use categories. Habitat-use categories were included as independent binomial variables (1 if the species was present in a given habitat, 0 otherwise) in the analyses of the entire fauna and of TEP endemics.

The comparative analysis of a diverse species assemblage can be confounded by phylogenetic effects. First, apparent patterns may reflect greater trait variation within higher-level than within lower-level taxa. For instance, requiem sharks (Carcharhinidae), which are large-bodied, on average might have been described earlier than gobies (Gobiidae), which are much smaller than sharks, suggesting an effect of body size on time of discovery even if the body-size effect within either family was weak, absent or even opposite. Second, species with a common phylogenetic history tend to exhibit similar trait values and may not be treated as statistically independent data points (Felsenstein, 1985). Methods to deal with these confounding effects of phylogeny, such as phylogenetic-independent contrasts, require a well-supported and nearly complete phylogeny (Harvey & Pagel, 1991), which is not available for TEP fishes. Hence we addressed the first problem by examining relationships within speciose lower-level taxa (within each of 17 families that contain at least 20 species, and each of 12 genera that contain at least 10 species). To reduce the second problem we examined the relationships among variables at the family level across the entire fauna, using family means for both biological characteristics (latitudinal and depth ranges, and body size) and date of description.

Body-size frequency distributions have often been used to examine how many species are expected in different size classes and thus to estimate the full richness of regional or global biotas (e.g. May, 1978, 1988). Although an inverse relationship between body size and number of species in an area was initially predicted (Hutchinson & MacArthur, 1959; May,

1988), some empirical studies have shown that there is a paucity of small species in known faunas (Blackburn & Gaston, 1994; Gaston & Blackburn, 2000). We examined the frequency distribution of maximum body sizes among the members of our fauna and found that it was log-normal (see Results). Based on this property, we then estimated the number of 'yet to be discovered' species from the currently 'unfilled' area under the log-normal curve, using the computer program LOGNORM (Ludwig & Reynolds, 1988). We made two estimates of 'undiscovered' species using different values for the modal size class: (1) the value derived from the log-normal fitting procedure, and (2) the observed value.

The discovery of new species undoubtedly is affected by the intensity of sampling in different habitats at different depths. While the water column and the surface of soft bottoms can be effectively sampled using trawl nets across the entire depth range we consider here, different sampling methods must be used for reefs. Reef habitats are most effectively sampled by SCUBA divers using rotenone or other fish poisons, the only means of effectively sampling the group of small, cryptic species living within the reef matrix (Smith, 1973; Russell *et al.*, 1978; Smith-Vaniz *et al.*, 1999; Ackerman & Bellwood, 2000; Smith *et al.*, 2003). For example, 45% of the fish species collected by Collette *et al.* (2003) at a small Caribbean island were obtained using rotenone. The lower limit of normal SCUBA work for such collecting is about 35 m. Hence we contrasted the body-size distributions of species whose depth-range midpoints were less than or greater than 35 m, to estimate the number of small (< modal size), deep-living species in each habitat-use category that might not have been sampled by faunal surveys carried out to date.

Finally, we also queried 19 professional fish taxonomists who have current or recent experience with all major families belonging to the region's fauna as to how many undescribed TEP species they are aware of in the taxa on which they work; that is, numbers of known species, not guesses of how many there might be. We also used the number of known but undescribed species and the average current annual rate of description of new TEP species to estimate how long taxonomists are likely to take to describe those species alone.

RESULTS

The historical dynamics of species description and structure of species-description accumulation curves

The description accumulation curve of all TEP fishes is somewhat S-shaped (Fig. 2a), reflecting the fact that the rate of description has changed through time (Fig. 2b). Initially there was a slow period from 1758 to about 1832 (an average rate of description of 1.5 new species per year), followed by a rapid phase from 1833 to 1905 (9.5 year⁻¹), and then a slow period again (4.5 year⁻¹; Fig 2a,b). A similar pattern is obtained for the TEP endemics, whose accumulation curve is offset from that of the entire fauna because they began to be described

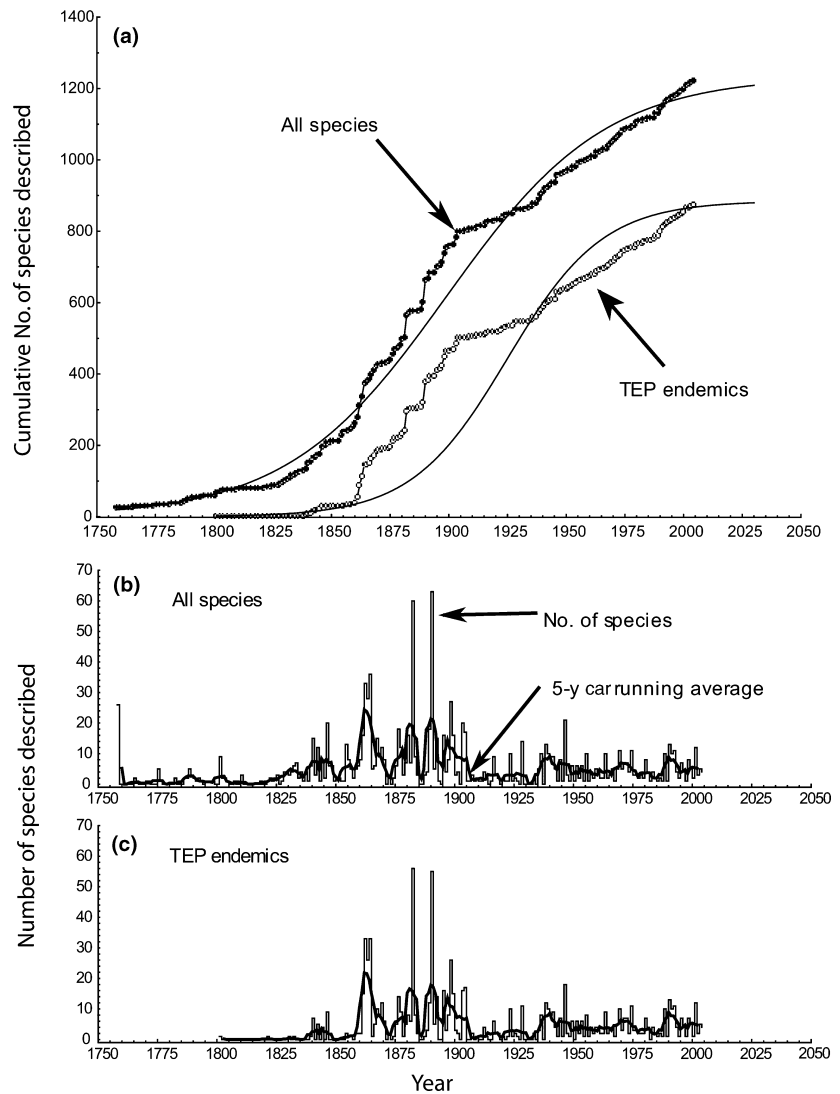


Figure 2 The tempo of species descriptions of members of the TEP shore-fish fauna. (a) Accumulation curves of species descriptions for the total and endemic components with fitted logistic functions. The number of new species described per year with 5-year running means for (b) the entire TEP fish fauna and (c) the TEP endemics.

> 40 years later than the non-endemics (Fig 2a,c). Mean rates of description for regional endemics range from 0.9 species per year during the initial slow phase (1801–61) to 10.2 year⁻¹ during the rapid phase (1862–1905), before settling down to 3.8 year⁻¹ thereafter (Fig. 2c). It is very noticeable that in neither the full set nor the endemics subset has there been a recent decline in the rate of accumulation of species descriptions (Fig. 2). Rather, the rate of descriptions over the past 50 years has continued at the rate maintained over the last century: a mean of 4.6 species per year for the entire set and of 4.3 year⁻¹ for the TEP endemics. For both all-species and the endemics, the slopes of the regression lines of the number of species described per year over that period are positive, but do not differ significantly from 0 (all-species regression: number of species = $-54.9 + 0.030 \text{ year}$, $r = 0.14$, $P = 0.29$; endemics regression: number of species = $-62.3 + 0.034 \text{ year}$, $r = 0.16$, $P = 0.24$).

The level of activity by taxonomists relating to descriptions of TEP shore fishes has varied considerably through time (Fig. 3). Both the number of taxonomists authoring species descriptions

each year (Fig. 3a) and the number of papers that described new species each year (Fig. 3b) have generally increased with time, albeit with a decline between 1901 and 1950. The number of papers describing new species per year and the number of species described per author per year (Fig 3c,d) both peaked in the latter half of the 19th century, probably owing to a burst of discovery activity within a 'virgin' fauna containing an abundance of endemic species. However, the fact that rate of descriptions per author per year has remained fairly stable over the last century indicates that there has been no major decline in return-for-taxonomic-effort over that period.

Species-description accumulation curves differ among species that live in different habitats (Fig. 4a). Descriptions of reef, pelagic and multi-habitat species initially accumulated faster than did those of soft-bottom species. However, after 1860 the rate of description of soft-bottom species exceeded that of species in other habitats. While the rates of description accumulation for pelagic and multi-habitat species have declined over the last century, those of reef and soft-bottom species have not. However, rates of accumulation have remained

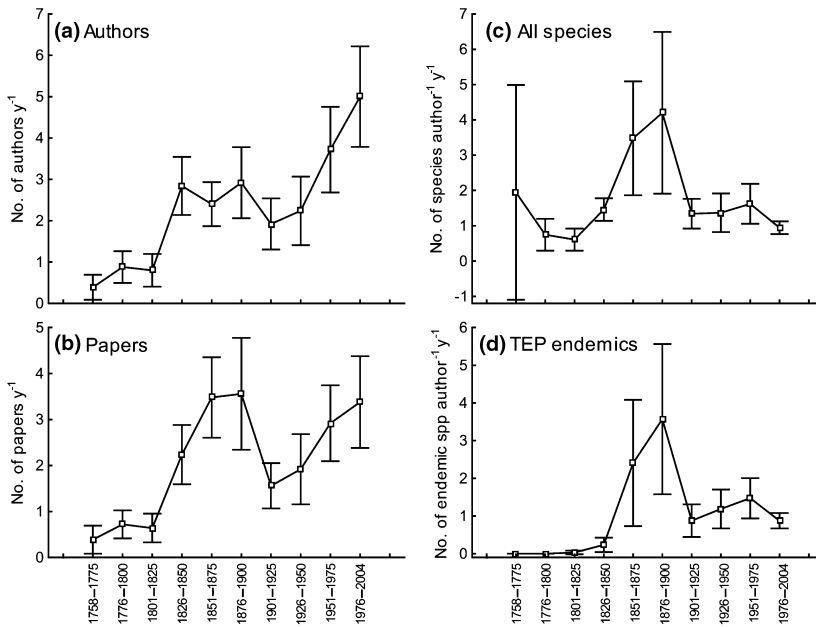


Figure 3 The temporal dynamics of descriptions of new TEP shore fishes. For quarter-century intervals, mean (\pm 95% CI) values are shown for (a) the number of authors involved in species descriptions per year; (b) the number of papers describing species per year; and the number of species described per author per year for (c) all species and (d) TEP endemics. Note that the first and last intervals are slightly shorter and longer, respectively, than a quarter century, and that co-authors count as multiple authors.

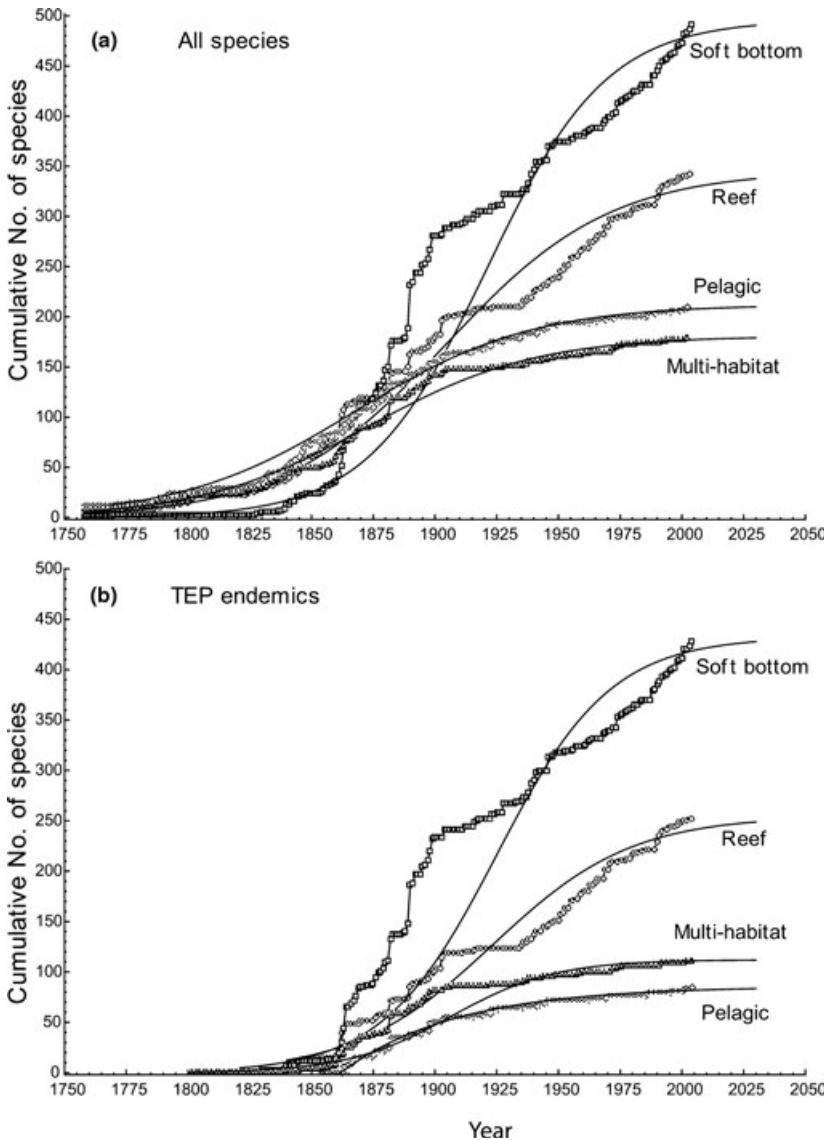


Figure 4 Accumulation curves of descriptions of species in different habitat-use categories of TEP shore-fishes for (a) all species and (b) TEP endemics. Continuous lines show fitted growth functions (logistic functions in all cases except for pelagic TEP endemics, for which a Von Bertalanffy function provided a better fit).

significantly positive in all cases. Patterns of description accumulation among TEP endemics are similar to those of the entire fauna, except that pelagic and multi-habitat species began to be described earlier than reef and soft-bottom species (Fig. 4b). Description accumulation curves for fishes in different habitat categories are better described by a logistic than by a Von Bertalanffy function, except in the case of pelagic species. Although statistical fits of these functions have high and significant coefficients of determination, neither function adequately describes species accumulation curves, except for the Von Bertalanffy growth function in pelagic species (see Fig. 4). Although the recent declines in species accumulation rates of pelagic and multi-habitat species are signs that these groups may be nearing complete inventories, there are no indications that curves of reef and soft-bottom species, which together represent the bulk (77.5%) of the fauna, are approaching asymptotes (Fig. 4). Under the assumption that the fitted functions satisfactorily describe accumulation curves (which clearly they do not – Figs 2 & 4), asymptotes of the endemics curves will not be reached for another 12–19 years (22–24 years for the total fauna) at current levels of taxonomic activity. Based on the current average rate of descriptions, all of the known undescribed species will probably not be formally named for another 12–15 years.

Correlates of species description dynamics

Although the relationship is quite weak, species that have wide latitudinal distributions tend to have been described earlier than those with relatively restricted ranges (Fig. 5a). Average range sizes are *c.* 41° of latitude for species described first vs. *c.* 10° for those described most recently. Furthermore, both the southern and northern limits of the distribution of newly described species moved from higher latitudes towards the Tropics as time progressed, so that most recently described species tend to be those restricted to the central part of the TEP (Fig. 5b), around 12°N (see Mora & Robertson, 2005b).

The tempo of description is related to the depth of occurrence in two ways. First, there is a very weak tendency for species with larger depth ranges to have been described earlier than those with smaller depth ranges: mean absolute depth ranges of species described first vs. those described most recently are *c.* 70 m vs. *c.* 20 m, respectively (Fig. 5c). Second, the upper limit of the depth range of most recently described species tends to be deeper than that of species first described (Fig. 5d). Through time there also has been a continuing decline in the average body size of newly described species (Fig. 5e): those described at the beginning of the present century are, on average, one order of magnitude shorter in length than those described in the 18th

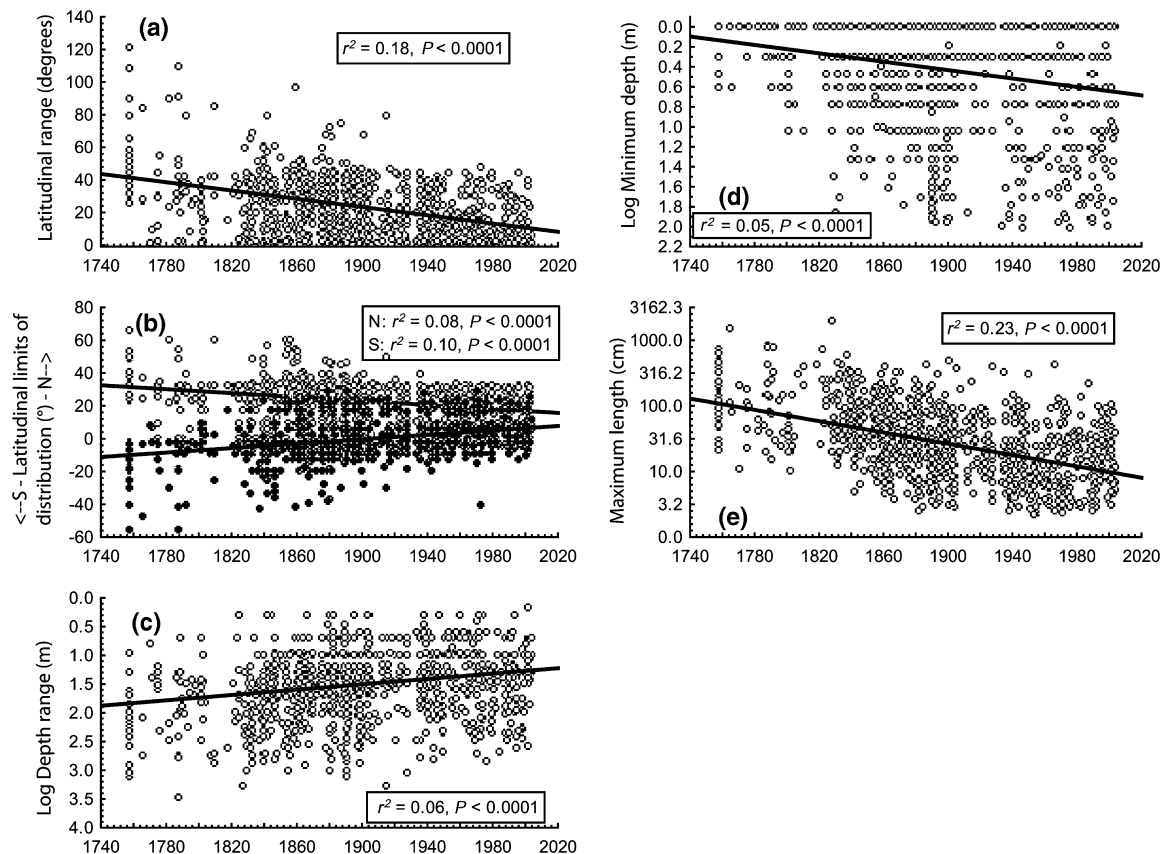


Figure 5 Relationships between date of description of new species in the entire described TEP shore-fish fauna and (a) absolute latitudinal range, (b) northern and southern limits of the latitudinal range, (c) absolute depth range, (d) upper limit of depth range, and (e) maximum body length.

Table 1 Correlations between year of description and body size, latitudinal-range characteristics (northern and southern limits of distribution and absolute range) and depth-range characteristics (maximum and minimum depths and absolute range) for all species ($N = 1222$ in 141 families), TEP endemic species only ($N = 876$), and bony fishes only ($N = 1120$). Correlations for families are based on family mean values for date of description, for body size, and latitudinal and depth ranges

Correlate	Entire fauna							
	Species		Families		TEP endemics		Bony fishes	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Log maximum length	-0.482	< 0.0001	-0.585	< 0.0001	-0.344	< 0.0001	-0.478	< 0.0001
Northern limit of distribution	-0.282	< 0.0001	-0.333	< 0.0001	-0.358	< 0.0001	-0.256	< 0.0001
Southern limit of distribution	0.313	< 0.0001	0.453	< 0.0001	0.343	< 0.0001	0.303	< 0.0001
Latitudinal range	-0.425	< 0.0001	-0.478	< 0.0001	-0.473	< 0.0001	-0.410	< 0.0001
Log minimum depth	0.230	< 0.0001	0.406	< 0.0001	0.168	< 0.0001	0.219	< 0.0001
Log maximum depth	-0.197	< 0.0001	-0.137	0.1050	-0.015	0.6540	-0.160	< 0.0001
Log depth range	-0.236	< 0.0001	-0.161	0.0560	-0.057	0.0930	-0.204	< 0.0001

century. Essentially the same latitudinal-, depth- and body-size-related patterns as shown for the entire fauna in Fig. 5 occur among the TEP endemics and also among the bony fishes (Table 1). The latter results indicate that the entire fauna pattern is generally not dominated by non-endemic species (except for the depth-related pattern, which is weaker in endemics), or by elasmobranchs, which tend to be large, and have broad latitudinal and depth ranges.

Family-level correlations between mean year of description and mean values of body size, and latitudinal- and depth-range characteristics are largely consistent with those found in the species-level analyses. At the family level, all correlations, except those with maximum depth and absolute depth range, were significant and in the same direction as in the species-level results (Table 1). Finally, a number of significant correlations within each of 17 speciose families and within each of 12 genera of TEP teleosts (Table 2) show that the same patterns as found in the entire fauna often

Table 2 Occurrence of statistically significant correlations between year of description and body size, latitudinal-range and depth-range characteristics in 12 genera and 17 families of TEP teleosts.

Correlate	Genera with correlation		Families with correlation		Direction of correlation in		
	% of total		% of total		Genera		Full data set
	No.	%	No.	%			
Maximum length	4	33.3	14	82.4	All -	All -	-
Latitudinal range							
Northern limit	2	16.7	8	47.1	All -	All -	-
Southern limit	1	8.3	1	5.9	+	+	+
Absolute range	5	41.7	8	47.1	All -	All -	-
Depth range							
Minimum depth	6	50.0	4	23.5	All +	2+, 2-	+
Maximum depth	3	25.0	4	23.5	2+, 1-	2+, 2-	-
Absolute range	3	25.0	5	29.4	2+, 1-	2+, 3-	-

occur within lower-level taxa and thus contribute to the overall patterns. Hence, we believe that the results of our species-level entire-fauna analyses are robust, and that the major patterns that emerge in these analyses (Fig. 5 and Tables 1–3) are indicative of recent trends across a range of taxa and can act as predictors, albeit weak ones, of future patterns of discovery.

Inspection of Fig. 5 indicates that most of the correlations discussed above might largely reflect characteristics of species described prior to 1900. Because recent patterns are likely to act as better indicators than longer-term patterns of future trends we re-examined these relationships using descriptions made from 1950 onwards. Body size, the upper limit of depth range and absolute depth range remained significantly correlated with date of description. Thus, most of the long-term patterns reported in Fig. 5 and Table 1 are consistent with recent trends.

A multiple regression model indicates that, for the entire fauna, body size is the most important predictor of the date of description, followed by latitudinal range, and minimum depth of occurrence (Table 3a). The same analysis using family-mean values for these variables confirms this result, although minimum depth appears as the second most important predictor of the mean year of description (results not shown). At the species level, when habitat-use categories were added to the multiple regression model, occurrence on soft bottoms significantly increased (but only by 2.2%) the amount of variance explained, to a total of 34.5%. This effect occurred because soft-bottom and reef species have been described significantly later on average than pelagic and multi-habitat species, with soft-bottom species latest of all. Considering species in each habitat category, body size consistently accounted for the greatest proportion of the variance in the date of description in all habitats except soft bottoms (Table 3a). In the latter case, latitudinal range had a greater effect, although it accounted for a smaller proportion of the variance (c. 14%) than did body size on the other habitats (c. 19–31%). Among the TEP endemics (Table 3b), latitudinal

Table 3 Results of multiple regressions of effects of body size, latitudinal range, depth range and minimum depth of occurrence on year of description of TEP shore fishes

Species group	N	Independent variables					Multi-habitat
		Log max length	Log lat range	Log min depth	Soft bottom	Log depth range	
(a) Entire fauna							
All species	1217	23.05	4.99	3.87	2.18	0.41	
Reef	341	31.46	5.65	3.00			
Soft bottom	487	3.17	13.88	4.30			
Pelagic	210	20.34		1.60			
Multi-habitat	179	18.63	8.03	4.30			
(b) TEP endemics							
All species	871	2.74	22.32	2.63			0.39
Reef	251	6.15	32.50	2.22			
Soft bottom	424	1.19	17.43	4.67			
Pelagic	85	*					
Multi-habitat	111		21.65	2.91			

Percentage of variance in year of description explained by each variable: max length = maximum total length; lat range = absolute latitudinal range; min depth = shallowest depth of occurrence; depth range = absolute depth range. *No independent variable accounted for any significant variation in year of description.

range was the most important predictor of the date of description, both in the entire group and among species using different habitats. Minimum depth was the second most important factor in all cases except in reef fishes, for which body size was the second most important predictor. Together the significant variables explained 24.6–40.9% of the variance in each of the groups of endemics.

Size–frequency distributions and potentially ‘missing’ species

The entire described TEP fish fauna (1222 species) has a log-normal frequency distribution of body sizes (Kolmogorov–Smirnov $D = 0.0319$, $P > 0.15$; Fig. 6a). Numbers of ‘missing’ species indicated by the unfilled areas under the curve range from 7 to 147 species, depending on whether the fit-produced modal value or the observed modal value is used to calculate these areas. Based on our survey of taxonomic experts, we know that there are at least 58 unnamed species (from 34 genera in 19 families) that have been collected in the TEP and await formal description. Adding these undescribed species to the regional sample increases the estimate of undiscovered species to between 10 and 196 species, depending on whether the curve-fitted or the observed modal size value is used.

What types of fishes might the ‘missing’ species be? Depth probably has had an effect on the discovery of different types of species as there has been little sampling below *c.* 35 m by SCUBA divers using ichthyocides, the most efficient method for collecting small fishes that live within the substratum

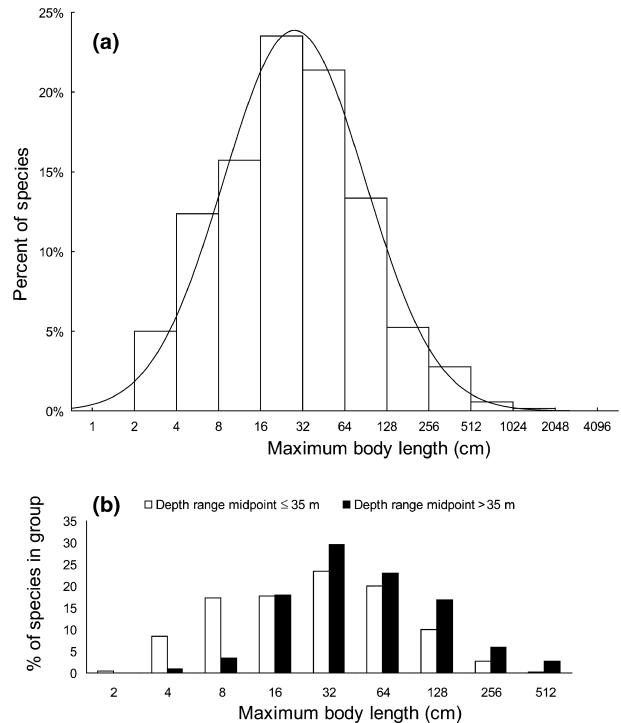


Figure 6 Size–frequency distributions of TEP shore fishes for the entire described fauna ($N = 1222$ species) with fit of log-normal distribution (a) and in relation to depth of occurrence for bony fishes (b).

matrix. The body-size frequency distribution of shallow-living species (those with depth-range midpoints above 35 m) is biased toward smaller sizes, while that of deeper-water species is biased towards larger sizes (Fig. 6b). Not only are shallow species smaller on average than deep species (mean maximum lengths are 21 and 48 cm, respectively, for all species, and 20 and 35 cm, respectively, for bony fishes), but the relative proportions of species in the size classes towards the tails of the distributions differ significantly between the two groups (Kolmogorov–Smirnov two-sample test, $D_{max} = -0.251$, $P < 0.001$ for all species, $D_{max} = -0.254$, $P < 0.001$ for bony fishes). Because body size is positively correlated with most other correlates of date of description (i.e. latitudinal range, depth range and minimum depth), but negatively correlated with date of description, many TEP species yet to be discovered seem likely to be small, have restricted latitudinal and depth ranges, and have a deeper minimum depth of occurrence. As depth range is positively correlated with body size ($r = 0.49$, $P < 0.0001$), most small species found in deep water probably tend not to occur in shallow water. If the proportions of species in the four smallest size classes are approximately equal in species with shallow and deep depth-range midpoints (those with depth-range midpoints above and below 35 m – Fig. 6b), then *c.* 112 species of small bony fishes could be awaiting discovery in TEP waters 35–100 m deep.

Body-size distributions of deep and shallow species also vary among species using different habitats. As with the entire

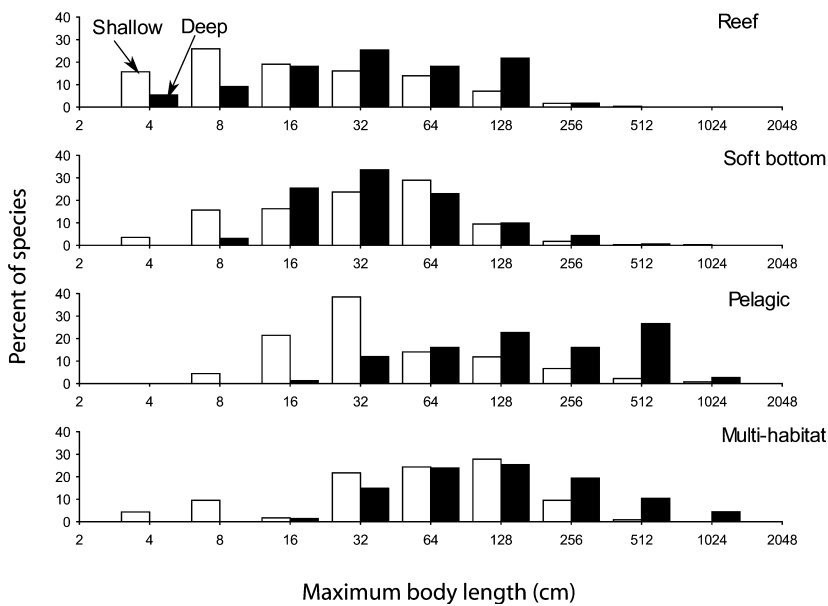


Figure 7 Size–frequency distributions of TEP shore fishes using different habitats in two depth groups (shallow: midpoint of depth range < 35 m; deep: that midpoint > 35 m).

fauna, the distributions of shallow-water species in each habitat are biased towards smaller sizes, while those of deep-water species are biased towards larger sizes (Fig. 7). However, the biases are stronger in pelagic and reef species than in soft-bottom and multi-habitat species. Sampling effects are probably involved in producing some of these differences. For example, trawl nets, which can effectively catch small species on the surface of soft bottoms and in the water column, are not used for sampling reefs. In contrast, the bias towards large pelagic species in deeper water may be real, as pelagic nets should be able readily to catch small pelagic species at depths of 35–100 m, which are relatively shallow for net operations. A deficit of small species on deep reefs and soft bottoms is much more likely to be caused by a sampling effect than is an apparent deficit of large species in shallow water, because the latter are much more amenable to collection than the former. If there are equal proportions of species in the three smallest size classes of deep- and shallow-water species in both reef and soft-bottom fishes, there may be 42 species awaiting discovery in deeper reef habitats and 33 species in deeper soft-bottom habitats.

DISCUSSION

Predicting the total size of the TEP fauna

From the tempo of species descriptions

Neither the species-description accumulation curve for the entire fauna, nor that for the TEP endemics shows a tendency to be approaching an asymptote. Among the four different habitat-use groups, only the curves for pelagic and multi-habitat species appear to be reaching an asymptote, and hence these groups may be almost fully documented. To some extent, differences in the structure of these curves must reflect patterns

of collecting activity. Pelagic species have characteristics that should make them most likely to have been collected: they tend to be large, have broad geographic and depth ranges, and they live in a habitat that makes them relatively accessible to traditional sampling using nets and hooked lines. The curve for multi-habitat species may be approaching an asymptote mainly because usage of more than one habitat increases their accessibility to collection. However, as these two groups represent only 22.5% of the total fauna, the major components of the regional fauna clearly are not approaching full documentation.

Intensive collecting activities by divers using SCUBA, which increased the range of habitats that could be sampled with rotenone, began < 50 years ago. Widespread use of this technique has probably contributed to sustaining the upward trajectory of reef-fish descriptions. Even so, the return for taxonomic effort (the number of species described per author per year) does not appear to have declined recently, indicating that plenty of species remain to be described. Hence, we conclude that the shore-fish fauna of the TEP probably is considerably larger than the currently known fauna, but that species accumulation curves cannot be used to predict the total richness of that fauna. Furthermore, the analysis of accumulation curves suggests that, even if the entire-fauna curve was approaching an asymptote, that fauna would not be fully documented for at least another two decades.

From body-size frequency distributions

Fitting of the log-normal distribution to the size–frequency distribution of the entire fish fauna produced widely varying estimates of the size of the unknown component of that fauna. Using the fit-produced modal value, only 7–10 species are predicted to be currently unknown. Clearly, this is a gross underestimation given recent rates of species discovery, the

lack of levelling-off in species accumulation curves, and the substantially larger number (58) of known undescribed species. However, the use of observed modal values indicates that there may be 147–196 species currently unaccounted for. If so, then the entire fauna could comprise around 1369–1476 species, 12–15% more than are currently known. This seems more reasonable, given the structure of species accumulation curves. Furthermore, these estimates may be conservative because this extrapolation from the log-normal size frequency distribution is to some extent dependent on the size of the known fauna on which estimates are based.

Recently described species tend to be small, to have narrow latitudinal ranges and depth ranges, and to occur in deeper water. Small deep-living species also tend to have narrow latitudinal and depth ranges. In all four habitat categories there is a bias towards larger species in the size–frequency distributions of deeper species compared with shallow species. It seems reasonable that some of that bias could reflect inadequate sampling in deeper water, particularly for reef fishes. If there were proportionately as many small species on deep as on shallow reefs then undiscovered small species on deep reefs alone could increase the currently known fauna of 1280 species by 3.3%. If the same reasoning is applied to soft-bottom species, many of which live buried in the substratum, then undiscovered deep soft-bottom species could represent an additional 2.6% of the known fauna. However, we cannot rule out the possibility that there really are relatively few small undiscovered species in deep habitats. The question of how much of the depth biases in the abundance of small species is the result of a lack of sampling in deep water remains a very open one.

Potential effects of genetic analyses on the determination of faunal richness

The data and analyses presented above all relate to morpho-species. However, most morphospecies in the TEP have relatively large geographic ranges (Mora & Robertson, 2005a), and the assessment of genetic relationships among geographically isolated populations of such species has barely begun. The few such studies done to date have produced a mixture of results. While some provide indications of genetic integration of populations throughout the region (e.g. Bowen *et al.*, 2001; Muss *et al.*, 2001), others indicate the existence of significant genetic breaks among populations along the continental shoreline, not only at the scale of different ends of the region (Lessios *et al.*, 1995; Colborn *et al.*, 2001), but also at the smaller scale of inside vs. outside the Gulf of California (Bernardi *et al.*, 2003; Sandoval-Castillo *et al.*, 2004; Bernardi & Lape, 2005), and at the much smaller scale of different parts of the Gulf of California (Riginos & Victor, 2001). The Sinaloan and Central American Gaps evidently represent significant barriers to the dispersal of shallow-water reef fishes. These barriers have led to the production of geographically isolated species and subspecies, and the subdivision of the continental shoreline of the TEP into three faunal provinces, each of which has its own suite of endemic

species and subspecies (Springer, 1959; Hastings, 2000; Robertson & Allen, 2002). The very limited existing genetic data, when combined with the taxonomic information on allopatric morpho-subspecies, indicate that these barriers could separate a significant number of geographically isolated cryptic species. Each of the oceanic islands and archipelagos has its own endemic shore fishes and, collectively, insular endemics make up about 12% of the TEP endemic shore-fish fauna (Robertson, 2001; Robertson & Allen, 2002). Genetic studies are also needed to assess the extent to which populations of widespread morphospecies living on the isolated oceanic islands represent cryptic local endemics.

Priority areas for future investigations

The most poorly sampled areas in the TEP from the perspective of fish taxonomy include the following.

Deep-reef habitats

Recent collecting in various parts of the central and west Pacific by divers using rebreather apparatus that allows them to sample habitats down to *c.* 125 m has produced an abundance of new deep-living reef fish species (Pyle, 2000). R. Pyle's unpublished data (pers. comm. to D.R.R., 2005) indicate the following patterns concerning the diversity and distributions of deep-reef fishes in these areas. (i) Only about one-third of species living deeper than 45 m also occur in shallow water. (ii) The percentage of species collected that are new (i.e. undescribed) increases with depth, and, at the deepest levels, can reach > 50%. (iii) Deep-reef species may represent 30% of all (i.e. shallow + deep) species at a site. (iv) The geography of diversity differs in deep and shallow species. Notably, the proportion of deep species shared between sites is only about 1/8 of the proportion of shallow species shared between the same sites. This pattern may apply at both small (same island group) and large (different parts of the Pacific) spatial scales. Even if much of this last difference is an artifact of the small number of deep sites so far sampled, the central and west Pacific evidently host a rich fauna of deep-reef fishes.

There has been almost no sampling of reef habitats aimed at small species in the TEP at depths between 40 and 100 m; this group of species is largely inaccessible except through fish-poison collections. The Galapagos Islands represent the only exception. Submarine-based collecting there in the 1990s led to the discovery of 29 new species of deep demersal fishes (J. McCosker, pers. comm. 2005), equivalent to *c.* 13% of the demersal fishes currently known to occur above 100 m depth at these islands. However, the submarine sampling activity was concentrated between 150 and 1000 m, and all the new species were found below 150 m. Among the named reef-only TEP fishes, 67% do not occur below 35 m, and only 2.6% are restricted to depths below that level; in other words, the great majority of the known reef fishes occur only in shallow water, and the known reef-fish fauna includes very few deep species. It is clear from the combination of this information, the results

from submarine collecting in the Galapagos and from rebreather collecting in the central and western Pacific that currently unknown reef fishes living at 40–100 m along the continental shore and at the isolated oceanic islands could represent a substantial component of the TEP reef-fish fauna.

Oceanic Islands

Each of the oceanic islands in the TEP has a significant number of endemic shore fishes (Robertson, 2001; Robertson & Allen, 2002), and the faunas of these islands differ markedly in composition from that of the mainland (Robertson *et al.*, 2004). The least well known of the ocean-island shallow faunas is that of the Revillagigedo group – four islands scattered over 200 km of ocean, 400 km south of the tip of the Baja California Peninsula. Shallow shore fishes have also not been comprehensively collected at the Tres Marias group of islands, located in deep water *c.* 100 km offshore in the southern Gulf of California, although one apparent endemic reef fish is known from them (Robertson & Allen, 2002).

Continental areas

Environmental conditions vary considerably along the continental shoreline of the TEP, with numerous seasonal upwelling systems, and marked differences in mean temperature and average rainfall in different parts (Glynn & Ault, 2000). There are several continental areas where there has been little or no modern collecting of shore fishes, including some with special environmental characteristics that might well be expected to affect the composition of the local shore-fish fauna. These include (1) most of the central and southern coast of Mexico, particularly the large upwelling system in the Gulf of Tehuantepec; (2) the northern coast of Colombia, which receives runoff from a large area with one of the highest rainfalls in the world and has the lowest salinity regime in the TEP; and (3) Ecuador in general and the large estuarine system of the Gulf of Guayaquil in particular. This Gulf is situated at the southern edge of the TEP, where there is a strong gradient in physical conditions in coastal waters.

CONCLUSIONS

Species-description accumulation curves for the entire fauna and its various components indicate that the TEP shore-fish fauna is distinctly richer than the known fauna. However, these curves do not allow prediction of what the total richness of that fauna is likely to be. Based on the shape of the body size–frequency distribution for the entire fauna, and differences in the size–frequency distributions of deep- and shallow-living fishes, we estimate that there may be *c.* 150–200 currently unknown species, which would increase the size of the regional fauna by 12–15%. However, given that the description trajectories of both reef and soft-bottom species, which together represent 77.5% of the known fauna, show no signs

of slowing down, and that there remains a significant number of areas in the TEP where both shallow and deep fishes are not well known, we think that that our estimate is quite conservative. Recent trends indicate that presently unknown species will tend to be small, have limited depth and latitudinal ranges, and live in deeper areas. However, as these trends are weak and collectively leave much variation unexplained, it is likely that the unknown species will include significant numbers of relatively large fishes, fishes that live in shallow water, and fishes that have broad depth ranges and wide latitudinal ranges.

The rate of descriptions has remained at about 4.2 species per year (3.8 year⁻¹ for TEP endemics) over the past century. This represents *c.* 0.3% year⁻¹ of the existing named regional fauna, a relatively low rate compared with the current global total of *c.* 1% year⁻¹ for all currently named fishes (Catalog of Fishes: <http://www.calacademy.org/research/ichthyology/catalog>). At that rate it will take *c.* 15 years to describe the 58 unnamed species that we know exist in the TEP. As it is likely that there are several times as many species remaining to be discovered, and that much sampling will be needed to cover the highest-priority areas in the region, a reasonably complete documentation of this regional fauna will probably take several decades at current levels of research activity. Neither the rate of discovery and description of morphospecies of shore fishes in the TEP nor the lack of genetic data relating to the richness of additional cryptic diversity bodes well for the rapid documentation of the size of that regional fauna. At current rates of activity, documentation by traditional taxonomy alone is likely to take several decades. Problems and time frames relating to the documentation of the TEP shore-fish fauna, which probably represents only *c.* 5% of the global marine shore-fish fauna, are probably representative of the situation in most parts of the Tropics.

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