Population maintenance among tropical reef fishes: Inferences from small-island endemics

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To what extent do local populations of tropical reef fishes persist through the recruitment of pelagic larvae to their natal reef? Endemics from small, isolated islands can help answer that question by indicating whether special biological attributes are needed for long-term survival under enforced localization in high-risk situations. Taxonomically and biologically, the endemics from seven such islands are broadly representative of their regional faunas. As natal-site recruitment occurs among reef fishes in much less isolated situations, these characteristics of island endemics indicate that a wide range of reef fishes could have persistent self-sustaining local populations. Because small islands regularly support substantial reef fish faunas, regional systems of small reserves could preserve much of the diversity of these fishes.

The great majority of marine organisms, including tropical reef fishes, have pelagic larvae, and the prevailing view is that local populations of such fishes are demographically interlinked by larval dispersal (1–3). It is important to know whether this view is true, not only for understanding the population biology and evolution of these organisms, but also for their management and for reserve design. Two recent field studies demonstrated substantial levels of return of reef fish larvae to their natal source (self-recruitment) in reef systems under low to moderate levels of isolation (4, 5). Because simulations also indicate that self-recruitment likely is common among reef fishes at such levels of isolation (6), it probably occurs much more frequently than previously thought. This article considers whether local populations of reef fishes in general have the potential to persist through self-recruitment. To do so, I examine the general biogeographic and biological characteristics of the shore fishes endemic to seven of the smallest, most isolated islands in the tropics: Easter Island (Polynesia); Clipperton, Cocos, and Malpelo (eastern Pacific); and Ascension, St. Helena, and St. Paul (central Atlantic) (Table 1). Such endemics represent vital indicators of whether special biological qualities are required to survive through evolutionary time in the most localized and risky (14) situations available. If the island endemics lack special attributes and simply constitute a representative cross section of the types of reef fishes available regionally, then such fishes in general should be capable of maintaining persistent, self-sustaining local populations.

Shore fishes that have survived at the seven islands through evolutionary time include not only morphologically distinct endemic species and subspecies but also genetically distinct populations of species that are classed presently as widespread nonendemics. The former represent an average of 14.1% of the seven islands' shore fish faunas (Table 1). All of the three studies published to date (15–17) found populations of the latter type at two of these islands, suggesting that currently recognized levels of morphology-based endemism probably substantitally underestimate the percentage of these island's shore fish faunas that are very long-term residents.

Endemics include members of a fifth of the genera and half the families present in the biogeographic regions containing the seven islands. Differences in family-level species richness among the endemic and regional faunas follow the same general pattern: most endemics belong to the families that are regionally speciose, and none or few belong to regionally species-poor families (Table 2). The prominent exceptions are moray eels (Muraenidae), which are regionally species-rich but lack island endemics. The pelagic larval duration (PLD) of morays is among the longest known for reef fishes (23), and long distance dispersal of moray larvae may reduce the likelihood that island populations remain sufficiently genetically isolated for endemics to develop. Except for this case, the combined endemic fauna is broadly representative, in taxonomic terms, of the combined reef fish fauna of the three regions in which the seven islands occur.

Are the general biological characteristics of endemics representative of their regional faunas? First, the relative abundances of species in various major adult-diet categories do not differ in the endemic and regional faunas (Table 3; $G = 0.38$, not significant; power to detect a small effect >99%). Most endemics, like most species in the regional faunas, are predators, and endemics are not disproportionately represented in any particular level of the food chain. Second, body size of endemics varies considerably (4–60 cm in length; see refs. 7–13). Among terrestrial animals, insular forms tend to be average-sized members of their genera (25). A similar pattern exists among the island endemic fishes: 55.6% of 61 endemics from 40 genera occur in the middle third of their intrageneric size-frequency distribution; 19.0% occur in the upper third; and 25.4% occur in the lower third ($G = 6.81$; $P < 0.01$; the null expectation is equal abundances of the three types). Although these results might indicate that large and small members of a genus tend to be at a disadvantage on such islands, body size is influenced by many variables that are not necessarily related to facilitating island living (25, 26). Because longevity broadly correlates positively with body size among fishes (27), the longevity of endemics likely varies widely among genera but is near average within most genera. This aspect of the biology of island endemics in particular needs further examination, because longevity likely affects vulnerability to extinction resulting from occasional recruitment failures. Although many island endemics have broad depth and habitat ranges, each island maintains one or more endemics that is a habitat specialist (7–13, 20). Like the vast majority of marine fishes, all of the island endemics belong to taxa that produce externally fertilized eggs and have pelagic larvae (1, 28). The ability to maintain self-recruiting island populations might be affected by whether a passively floating planktonic egg or a swimming larva leaves the island at the beginning of the pelagic stage (larval activity might enhance near-island retention); by the duration of that stage (shorter PLDs might facilitate retention); and by the form, size, and swimming capacity of end-stage larvae. The proportions of species that release pelagic larvae (hatched from demersal eggs) vs. planktonic eggs do not differ between the endemic and regional faunas (47.7% and 41.7%; $n = 88$ and 1,234, respectively; $G = 0.65$, not significant; power to detect a small effect >99%). Reflecting their taxonomic diversity, larvae of taxa to which island endemics belong have widely varying forms, end-stage sizes ($\approx$1–10 cm in length) and swimming

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Table 1. Seven islands: Isolation, habitat area, and endemism among their shore fish faunas

		Shallow habitat, km²*		Shorefish fauna	
Island	Isolation, km	Now	Recent range	Endemism, %	Total no. species
Ascension	1,300	39	24–39	25.3[†]	79
Clipperton	950	4	4–11	8.8	102
Cocos	450	14	14–110	7.6[‡]	224
Easter	1,500[§]	72	40–72	22.2	126
Malpelo	350	1.2	1.2–17	3.2[‡]	220
St. Helena	1,300	37	36–110	22.1[†]	86
St. Paul	960	0.2	0.2–2	9.5	42

Data from refs. 7–13.

*Habitat <50 m deep from hydrographic charts (areas include soft bottoms as well as reef); recent range is with sea levels to 100 m below present.

[†]Includes 13 species endemic to both islands.

[‡]Includes two species endemic to both islands.

[§]1,500 km from Ducie Island to the west and 450 km to tiny Sala y Gomez to the east.

capacities, and life histories (28, 29). The literature contains information on the PLDs of genera to which 44 endemics belong (e.g., ref. 1 and references therein); 20 of those species belong to taxa that usually have PLDs ≤1 month, and the remainder belong to taxa with durations of ≈1–3 months. PLDs of insular endemics in the eastern Pacific (including species from Clipperton and Cocos) are not shorter than those of congeners with larger geographic ranges (30). A similar pattern exists among Hawaiian endemic fishes (31) and among reef fishes living at isolated small islands vs. conspecifics in larger, less isolated areas (32, 33). Thus, the capacity to sustain small, very isolated populations seems unrelated to variation in the PLD. In summary, the available evidence indicates that island endemics do not have an unusual set of basic adult and larval characteristics that might be important for long-term maintenance of island populations.

How rich are the faunas of these and other small islands? The shore fish faunas of oceanic islands usually are viewed as being depauperate, in part because of their limited area (e.g., refs. 11, 19, and 23). Area effects could be responsible for the fact that each of the seven islands has fewer reef fishes than the region containing it and the tendency for the larger of those islands to have more endemics (Table 1). However, any such effects cannot

Table 2. Taxonomic characteristics of the endemic reef fish faunas of seven islands vs. those of regional faunas

	Endemic faunas, %	Regional faunas, %	
Family*		Average	Range
Group I			
Gobiidae	12.4	7.0	5.8–8.9
Labridae	12.4	7.0	5.4–10.1
Pomacentridae	9.0	6.0	4.9–6.6
Serranidae	6.7	9.5	7.8–12.3
Scorpaenidae	6.7	3.3	2.3–4.1
Blenniidae	5.6	3.9	3.1–5.2
Tripterygiidae	5.6	1.5	0.4–2.8
Chaetodontidae	4.5	3.1	0.9–5.2
Chaenopsidae	3.4	2.0	0–4.7
Muraenidae	0	6.0	4.2–8.5
Group II		Average	Range in averages
9 Families	2.3 Family⁻¹	1.5 Family⁻¹	0.4–3.1 Family⁻¹
13 Families	1.2 Family⁻¹	0.7 Family⁻¹	0.1–3.1 Family⁻¹
Group III		Average	Range in averages
31 Families	0 Family⁻¹	0.7 Family⁻¹	0.1–3.1 Family⁻¹
Total fauna	88 Species, 66 genera, 31 Families	1,234 Species, 62 Families	341 genera,

Data are from refs. 7–13 and 18–22; www.biobase.org/cloftep/; L. Rocha, personal communication for Brazil; and unpublished observations at all the islands except St. Paul.

*Family groups: Group I, 10 families with the highest average levels of species richness in both the regional faunas and (except for the Muraenids) the endemic fauna; Group II, 9 families (Apogonidae, Bothidae, Callionymidae, Gobiesocidae, Holocentridae, Monacanthidae, Pomacanthidae, Sparidae, and Tetraodontidae) and 13 families (Belonidae, Cirrhitidae, Congridae, Creediidae, Dactyloscopidae, Kuhliidae, Kyphosidae, Mullidae, Ogcocephalidae, Ophichthidae, Paralichthyidae, Scaridae, and Synodontidae) with moderate and low levels of species richness, respectively, in the endemic and regional faunas; Group III, 31 families lacking island endemics and with low levels of species richness in regional faunas.

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Table 3. Relative abundances of fishes with different diets in island endemic and regional faunas

Diet	Species with each diet, %	
	Endemics	Regional faunas
Animals		
Mobile	50.0	52.1
Sessile	12.5	11.3
Zooplankton	18.2	15.4
Sessile algae	12.5	14.0
Sessile algae and animals	6.8	7.0

See Table 2 for sample sizes. Diets based on genus and family characteristics (11, 20, 24).

yet be separated from those of isolation, latitude, island age, and the size of the regional source fauna. Although analyses are lacking, the structure of the species-richness/habitat-area relationship among reef fishes across the island-to-region scale, comparison of the relative richness of the faunas of small islands and much larger parts of the surrounding biogeographic regions can provide an indication of the faunal capacity of small areas and the ability of the members of a regional fish fauna to maintain localized populations. I used comprehensive, island-wide surveys of the abundance and the occurrence of juveniles and of adults of varying sizes at Clipperton [1994 (see ref. 11) and 1998] and Cocos [1997 (see ref. 12)] to estimate which members of an island fauna likely are residents, i.e., have self-sustaining populations rather than being rare strays. Those surveys and data from Malpelo (13) indicate that ≥80% of the species at these islands probably are residents. These isolated islands have oceanic origins; therefore, their shore fish faunas were derived entirely by long-distance dispersal, and these islands are inaccessible to many species with low dispersal capabilities. However, despite this limitation and their low habitat diversity, these three islands, which collectively represent <0.1% of the continental shelf area with reefs in the tropical eastern Pacific (34), support one or more resident populations of 42% of the reef fishes endemic to that biogeographic region. Further, Cocos, Malpelo, and five other small islands affected to varying degrees by low habitat diversity, isolation, and latitude have reef fish faunas that are, on average, approximately two-thirds the size of the faunas of adjacent areas that are two to three orders of magnitude larger (Table 4). To assess the sizes of populations of endemics that can be sustained by small islands, I censused five noncryptic endemics (species readily visible to divers) at Clipperton in 1998 in 110 5-m × 20-m strip transects at various depths around the island.

Those counts indicate that <4 km² of shallow habitat supported between $61 \pm 6.0 \times 10^3$ and $4.3 \pm 0.35 \times 10^6$ adults of different endemics and, hence, that small areas can support large populations of individual species of reef fishes. This ability extends to top predators; nonpelagic (as well as pelagic) sharks historically were abundant around at least three of the seven islands (9, 38) and currently are common at Cocos (ref. 12 and unpublished observations). Thus, moderately small islands regularly support relatively rich reef fish faunas and substantial populations of individual species.

The seven islands differ greatly in the amounts of shallow habitat they provide, amounts that have fluctuated considerably during repeated recent >100-m changes in sea level (ref. 39; Table 1). These islands are scattered across 26° of latitude and have differing temperature, wind, and large-scale water current regimes. Although Ascension, Easter, and St. Helena are dry islands, the remainder are wet. The climates of these islands probably also varied historically. The three eastern Pacific islands are affected directly by environmental stresses that might be expected to cause extinctions: Clipperton by occasional hurricanes and Clipperton, Cocos, and Malpelo by El Niño-related water heating (34). Unlike the situation with corals (34), major environmental disruptions in the tropical eastern Pacific produced by recent El Niños apparently have had only limited permanent effects on reef fishes, including insular endemics (one possible localized extinction; see ref. 40). Despite a history of mass shore fish kills caused by low-temperature stress, Bermuda, an isolated, high-latitude coral reef, maintains a fauna of resident shore fishes that includes five shallow-water endemics and is 63% the size of the fauna of the much larger Bahamas (41). Thus, the risks of localized extinctions posed to reef fishes by recent levels of such stresses seem to be relatively low, and the fish faunas of oceanic islands evidently persist under strongly fluctuating environmental conditions.

The diverse and historically unstable environments of the seven islands, the abundance of shore fishes that are long-term survivors at those islands, the diversity of their endemics and the lack of special general characteristics among them, the large population sizes of endemics, and the relative richness of small-island reef fish faunas together indicate that such fishes in general have good prospects for long-term survival as self-sustaining populations in areas similar in size to the larger among the seven islands considered here. Terrestrial biological reserves that are intended to preserve high levels of diversity are large and interconnected to maintain low-density populations of organisms such as trees, birds, and mammals and to take advantage of the fact that species richness increases with area. Small terrestrial reserves suffer declines in

Table 4. Relative richness of reef fish faunas of small islands vs. those of much larger adjacent areas

Small island	Larger adjacent area	Small island habitat area		Small island fauna, % of larger area fauna
		km²	% of larger adjacent area	
Cocos	Galapagos	≈6*	≈0.9*	79.1
Malpelo	Galapagos	≈0.1*	≪0.1*	71.5
Gorgona	Costa Rica–Ecuador†	14*	<0.1*	57.6
Navassa	Four West Caribbean atolls	≈8	≈0.2	80.0
Rose Atoll	Four Samoan islands	≈7	≈0.7	67.1
Pitcairn	Tuamotu Islands	≈8	<0.1	66.2
Rapa	Tuamotu Islands	<10	<0.1	61.6

*Habitat data are from hydrographic charts and ref. 34. * indicates areas of reef rather than total habitat; remaining areas are of total habitat.

†Continental coastline. Data for faunas: Cocos, Malpelo, and Gorgona are from refs. 11–13, 35, and 36, and www.biobase.org/cloftep/; Navassa (Eastern Caribbean) are from B. Collette (personal communication); Rose Atoll are from A. Green (personal communication); Pitcairn and Rapa (South Pacific) are from refs. 10, 18, and 37.

diversity when they become isolated by degradation of surrounding habitat (42). The presumption that management of reef fishes must be organized at large spatial scales derives from the perception that their populations demographically are widely interlinked by larval dispersal (3). However, if local shore fish populations normally are self-sustaining, the diversity that exists in a small marine reserve established now likely will remain largely intact. A system of small reserves dispersed throughout a biogeographic region to include the geographic ranges of the broadest range of resident species should thus have a good chance of preserving most of that region's diversity of reef fish species, genera, and families for the foreseeable future.

Small reserves cannot provide a solution to resource problems, such as rapidly diminishing fisheries for shore fishes, and thus cannot duplicate important functions of large reserves. However, despite such limitations, small-reserve systems represent an important tool that can be readily incorporated in regional conservation plans for preserving diversity *per se* among reef fishes.

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