

Zoogeography of the shorefish fauna of Clipperton Atoll

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Abstract. One hundred and fifteen species of fishes (14 oceanic, plus 101 shore and nearshore species) are known from Clipperton Island, a small, remote coral atoll in the tropical eastern Pacific (TEP). This fish fauna includes only ~14% of the region's shallow-water species, and also is depauperate relative to the fish faunas of other isolated tropical islands. The island's isolation, small size, reduced habitat diversity, and oceanic environment contribute to this paucity of species.

Fifty-two species at Clipperton can be identified as TEP; these include 37 widespread species, six species shared only with the Revillagigedo Islands [the nearest (950 km) offshore shoals], and eight endemic to Clipperton. Endemics species apparently have a mix of west and east Pacific origins. Sixty-three species are transpacific; they include three new records (of *Naso* surgeonfishes) that may be vagrants recruited >4,000 km from Oceania.

Clipperton is situated at the juncture between the TEP and Oceania. Its fish fauna contains about equal numbers of TEP and transpacific species. This faunal structure reflects the relative influence of surface currents from Oceania and the TEP. Although most of Clipperton's transpacific shorefishes are widespread in eastern Oceania, the Clipperton fauna has specific affinities to the fauna of the Line Islands, which are located within the main east-bound current from Oceania. Clipperton may therefore be a major stepping stone for dispersal between Oceania and the remainder of the TEP. About 50% of the non-oceanic, tropical transpacific fishes occur there, and at least 75% of those species apparently have resident populations at the island.

biogeographical perspective for several reasons. First, the island lies 1,100 km SW of the closest part of the American mainland and 950 km S of the nearest offshore shoal habitat (the Revillagigedo Islands), and is one of the most isolated reefs in tropical seas. Second, coral reefs represent a very small fraction of the shallow hard-bottom habitat in the TEP, and only a handful of the region's fishes can be classed as "coral reef" species (i.e. strongly dependent on corals). Clipperton is the largest reef in the TEP and the only reef whose fish fauna is not influenced by large contiguous areas of non-coralline habitats. This combination of features should strongly influence the structure of its fish fauna. Third, Clipperton may be a significant stepping stone connecting the tropical shore biotas of the eastern and western Pacific, which are separated by the world's largest deep-water barrier, the 4,000–7,000 km wide East Pacific Barrier (EPB) (Ekman 1953, Briggs 1961). Clipperton lies at the northern edge of the east-bound surface current (North Equatorial countercurrent, NECC) from the likely source of recruits in Oceania. Clipperton Atoll is at least 2,000 km closer to Oceania than other TEP sites in the main path of the NECC.

While zoogeographers have had a long-standing interest in the relationship of the shorefish faunas of Oceania and the TEP (Herre 1940, Briggs 1961, Hubbs and Rosenblatt 1961, Rosenblatt 1967, Rosenblatt et al. 1972, Leis 1983, 1984, Brothers and Thresher 1985, Rosenblatt and Waples 1986, Victor 1987, Clarke 1995), the shorefish fauna of Clipperton has not been previously described. In this paper we examine the structure of the fish fauna of the Atoll and discuss its zoogeographic implications.

Introduction

Clipperton Island is a small (4 km diameter) coral atoll at the western edge of the tropical Eastern Pacific (TEP) marine region, at 10°18' N, 109°13' W (see Fig. 1 of Glynn et al., this issue). It is particularly interesting from a

Methods

We spent 13 days at Clipperton in April 1994, making intensive observations (including photography of many species) and collections (using spears and rotenone) of fishes, between the shore and 60 m. Details of collection methods and an annotated species list will be presented elsewhere (Allen and Robertson in preparation). The discussion below is based on data collected in April, 1994, other

Table 1. The fishes of Clipperton island: habitat, geographic distributions and population status

Family	Species	Habitat	Range	Population status	
Carcharhinidae	<i>Carcharhinus albimarginatus</i>	I, O-P	IP-EP	R	
	<i>C. falciformis</i>	O-P	CT	—	
	<i>C. galapagensis</i>	I, O-P	CT	R	
	<i>C. limbatus</i>	I, O-P	CT	?	
Sphyrnidae	<i>Sphyrna lewini</i>	I, O-P	CT	?	
Muraenidae	<i>Anarchias galapagensis</i>	B	EP	R	
	<i>Echidna nebulosa</i>	B	IP-EP	R	
	<i>Echidna nocturna</i>	B	EP	?	
	<i>Enchelychore octaviana</i>	B	EP	?	
	<i>Enchelynassa canina</i>	B	WP-EP	R	
	<i>Gymnomuraena zebra</i>	B	IP-EP	?	
	<i>Gymnothorax buroensis</i>	B	IP-EP	?	
	<i>G. dovii</i>	B	EP	R	
	<i>G. flavimarginatus</i>	B	IP-EP	R	
	<i>G. panamensis</i>	B	EP	R?	
	<i>Siderea picta</i>	B	IP-EP	R	
	<i>Scuticaria tigrina</i>	B	IP-EP	?	
	<i>Uropterygius macrocephalus</i>	B	IP-EP	R	
	<i>U. versutus</i>	B	EP	R	
	Ophichthidae	<i>Apterichthys equatorialis</i>	B	EP	R
		<i>Myrichthys pantostigmus</i>	B	EP(RC)	R
<i>Phaenomonas pinnata</i>		B	EP	?	
Chanidae	<i>Chanos chanos</i>	I-S	IP-EP	V	
Antennariidae	<i>Antennarius cocinneus</i>	B	IP-EP	?	
	<i>A. sanguineus</i>	B	EP	R	
	<i>Antennatus strigatus</i>	B	EP	R	
Belonidae	<i>Tylosurus acus melanotus</i>	I, O-P	IP-EP	—	
Exocoetidae	<i>Cheilopogon heterurus hubbsi</i>	O-P	EP	—	
	<i>C. spilonopterus</i>	O-P	IP-EP	—	
	<i>Fodiator acutus rostratus</i>	O-P	EP	—	
	<i>Euleptorhamphus viridis</i>	O-P	IP-EP	—	
Hemirhamphidae	<i>Oxyporhamphus micropterus</i>	O-P	CT	—	
	<i>Myripristis berndti</i>	D	IP-EP	R	
	<i>M. clarionensis</i>	D	EP(RC)	R	
	<i>M. gildi</i>	D	EP(CE)	R	
	<i>Plectrypops lima</i>	D	IP-EP	?	
	<i>Sargocentron suborbitalis</i>	D	EP	R	
	<i>Aulostomus chinensis</i>	D	IP-EP	R	
Aulostomidae	<i>Fistularia commersonii</i>	I-S	IP-EP	R	
Fistulariidae	<i>Doryhamphus excisus excisus</i>	B	IP-EP	R	
Syngnathidae	<i>Pontinus vaughani</i>	B	EP(RC)	V	
Scorpaenidae	<i>Scorpaenodes xyris</i>	B	EP	R	
	<i>Dermatolepis dermatolepis</i>	D	EP	R	
Serranidae	<i>Epinephelus labriformis</i>	D	EP	R	
	<i>Paranthias colonus</i>	I-MW	EP	R	
	<i>Pseudogramma axelrodi</i>	B	EP(CE)	R	
	<i>Rypticus bicolor</i>	B	EP	R	
	<i>Kuhlia mugil</i>	I	IP-EP	R?	
Kuhliidae	<i>Apogon atricaudus</i>	D	EP(RC)	R	
Apogonidae	<i>Remora remora</i>	O-P	CT	—	
Echeneidae	<i>Carangoides orthogrammus</i>	I-MW	IP-EP	V	
Carangidae	<i>Caranx caballus</i>	I-MW	EP	V	
	<i>C. lugubris</i>	I-MW	IP-EP	R	
	<i>C. melampygus</i>	I-MW	IP-EP	R	
	<i>C. sexfasciatus</i>	I-MW	IP-EP	R	
	<i>Decapterus macarellus</i>	O,P	CT	—	
	<i>Elegatis bipinnulata</i>	I, O-P	CT	R	
	<i>Naucrates ductor</i>	O-P	CT	—	
	<i>Selar crumenophthalmus</i>	I, O-P	CT	?	
	<i>Seriola rivoliana</i>	O-P	CT	—	
	<i>Trachinotus stilbe</i>	I-MW	EP	R	
	Coryphaenidae	<i>Coryphaena equisetis</i>	O-P	CT	—

Table 1. (continued)

Family	Species	Habitat	Range	Population status	
Lutjanidae	<i>Lutjanus viridis</i>	D	EP	R	
Haemulidae	<i>Orthopristis cantharinus</i>	D	EP	V	
Mullidae	<i>Mulloidichthys dentatus</i>	D	EP	R	
Kyphosidae	<i>Kyphosus analogus</i>	D	EP	R	
	<i>K. elegans</i>	D	EP	R	
	<i>Sectator ocyurus</i>	I-MW	EP	V	
Chaetodontidae	<i>Forcipiger flavissimus</i>	D	IP-EP	R	
	<i>Johnrandallia nigrirrostris</i>	D	EP	R	
Pomacanthidae	<i>Holacanthus clarionensis</i>	D	EP(RC)	V	
	<i>H. limbaughi</i>	D	EP(CE)	R	
Pomacentridae	<i>Chromis alta</i>	D	EP	R	
	<i>Stegastes baldwini</i>	B	EP(CE)	R	
Cirrhitidae	<i>Cirrhitichthys oxycephalus</i>	B	IP-EP	R	
	<i>Cirrhitis rivulatus</i>	B	EP	R	
Mugilidae	<i>Chaenomugil proboscideus</i>	D	EP	V?	
Labridae	<i>Bodianus diplotaenia</i>	D	EP	R	
	<i>Novaculichthys taeniourus</i>	D	IP-EP	R	
	<i>Stethojulis bandanensis</i>	D	WP-EP	R	
	<i>Thalassoma grammaticum</i>	D	EP	R	
	<i>T. purpureum</i>	D	IP-EP	R	
	<i>T. robertsoni</i>	D	EP(CE)	R	
	<i>T. virens</i>	D	EP(RC)	R	
	<i>Xyrichtys wellingtoni</i>	D	EP(CE)	R	
	Scaridae	<i>Scarus rubroviolaceus</i>	D	IP-EP	R
	Blenniidae	<i>Entomacrodus chiostrictus</i>	B	EP	R
<i>Ophioblennius steindachneri clippertonensis</i>		B	EP (CE)	R	
Gobiidae	<i>Bathygobius arundelii</i>	B	EP(CE)	R	
Zanclidae	<i>Zanclus cornutus</i>	D	IP-EP	R	
Acanthuridae	<i>Acanthurus achilles</i>	D	CP-EP	V	
	<i>A. nigricans</i>	D	P-EP	R	
	<i>A. triostegus triostegus</i>	D	IP-EP	R	
	<i>A. xanthopterus</i>	D	IP-EP	?	
	<i>Ctenochaetus marginatus</i>	D	CP-EP	R	
	<i>Naso annulatus</i>	D	IP-EP	V(NR)	
	<i>N. hexacanthus</i>	D	IP-EP	V(NR)	
	<i>N. lituratus</i>	D	IP-EP	V(NR)	
	Sphyracidae	<i>Sphyraena ensis</i>	I-S	EP	V
	Scombridae	<i>Acanthocybium solandri</i>	O-P	CT	—
<i>Euthynnus lineatus</i>		O-P	EP	—	
<i>Thunnus albacares</i>		O-P	CT	—	
Bothidae	<i>Bothus mancus</i>	B	IP-EP	R	
Balistidae	<i>Balistes polylepis</i>	D	EP	V	
	<i>Canthidermis maculatus</i>	I, O-P	CT	—	
	<i>Melichthys niger</i>	D-MW	CT	R	
	<i>Sufflamen verres</i>	D	EP	R	
Monacanthidae	<i>Xanthichthys mento</i>	D-MW	WP-EP	V	
	<i>Aluterus scriptus</i>	D	CT	V	
	<i>Cantherhines dumerilii</i>	D	IP-EP	R	
Ostraciidae	<i>Ostracion meleagris</i>	B	IP-EP	R	
Tetraodontidae	<i>Arothron meleagris</i>	B	IP-EP	R	
	<i>Canthigaster punctatissimus</i>	B	EP	R	
Diodontidae	<i>Diodon holacanthus</i>	D	CT	?	
	<i>D. hystrix</i>	D	CT	V	

Habitat: I = Inshore, O = Oceanic, P = Pelagic, B = Benthic, S = Surface water, D = Demersal, MW = Midwater
 Range: CP = Central Pacific; CT = Circumtropical; EP = Eastern Pacific (CE = Clipperton endemic, RC = only at the Revillagigedo Islands and Clipperton); IP = Indo-Pacific; P = Pacific
 Population status: R = Resident: frequently observed and/or collected, and appeared sufficiently abundant to have a resident popula-

tion; V = Vagrant: rare (<20 individuals recorded during the 1994 expedition), individuals present probably recruited from other distant sites (although they could have been remnants of a local population approaching extinction); NR = New record for the TEP; ? = uncertain population status due to cryptic behavior and/or possible presence in deep habitats

Table 2. Number of fish species at six isolated tropical islands

Island	Site ²	Habitat ³ (km ²)	Isolation (km)	Fish fauna ⁴		
				Total no. species	No. endemics	% Regional fauna
Clipperton	TEP	< 4	950	101	8(7.9%)	~14
Malpelo	TEP	< 2	350	~240	~5(2.0%)	~30
Cocos	TEP	~ 25	450	~230	15(6.5%)	~30
Johnston	HI	~150	800	~240	1(0.4%)	~40
Cocos-Keeling	IO	~110	850	~530	1(0.2%)	~27
Christmas	IO	~ 20	300	~560	1(0.2%)	~29

Sources – 1: This paper, Rubio et al. 1992, WA Bussing personal communication, Randall et al. 1985, Kosaki et al. 1991, Randall et al. 1993, Allen and Smith-Vaniz 1994. 2: TEP = tropical eastern Pacific; HI = Hawaiian Region; IO = Indian Ocean (Indo-Malayan fauna). 3: area to 50 m depth. 4: from nearest shoal habitat

published information (Fischer et al. 1995) and lists of specimens deposited in U.S. museums.

Results and discussion

A depauperate fish fauna

The known Clipperton fish fauna consists of 115 species belonging to 89 genera and 43 families (Table 1). Fourteen of these species (*Carcharhinus falciformis*, three exocoetids, two hemiramphids, three carangids, the remora, the dolphin, and the three scombrids) are found in offshore pelagic habitats but they also occasionally visit reef areas. Three other species (*Tylosurus acus*, *Elegatis bipinnulata*, and *Selar crumenophthalmus*) are epipelagic forms that regularly associate with reefs. Ninety-eight species are mainly restricted to shore habitats or nearby waters. These include 19 midwater forms such as carangids and sharks, nine demersal species that live in and/or feed primarily on unconsolidated bottoms such as sand and rubble (*Apterichthys equatorialis*, *Myrichthys pantostigmus*, *Phaenomonas pinnata* (probably) *Pontinus vaughni*, *Orthopristis cantharinus*, *Mulloidichthys dentatus*, *Novaculichthys taeniourus*, *Xyrichtys wellingtoni*, and *Bothus mancus*), plus 70 benthic species that live in consolidated rocky-reef habitats. Three species we found at Clipperton in 1994 (*Naso annulatus*, *N. hexacanthus*, and *N. lituratus*) are new records for the TEP. Because all three were rare (<20 individuals of each present, all large adults) they may represent vagrants that recently recruited from eastern Oceania across the EPB. Clipperton has eight endemic species and subspecies belonging to seven families: *Myripristis gildi*, *Pseudogramma axelrodi*, *Holacanthus limbaughi*, *Stegastes baldwini*, *Thalassoma robertsoni*, *Xyrichtys wellingtoni*, *Bathygobius arundelii*, and *Ophioblennius steindachneri clippertonensis*.

There are ~825 species (in ~105 families) of shallow-water, nearshore fishes that are largely restricted to or have partial distributions in the tropical eastern Pacific (Allen and Robertson 1994, Fischer et al. 1995). Thus, only ~14% of the region's species and ~40% of its families occur at Clipperton. In contrast, other isolated tropical reefs, including Malpelo and Cocos Islands in the TEP, have much larger fish faunas, and larger percentages of their regional faunas (Table 2).

Several factors may contribute to the paucity of species found at Clipperton:

(1) *Unsampled deep habitat*: Large areas of habitat that include substantial amounts of sand and rubble bottom exist at Clipperton at depths beyond those sampled using conventional SCUBA, at 50–110 m on the “60 m terrace” (see Fig. 3 of Glynn et al., this issue). Shallow-water fishes that are largely restricted to unconsolidated bottoms (sand, mud, rubble, estuaries, beaches) represent ~40% of the TEP's inshore fishes, and are important components of ~1/3 of its families. We estimate that, among the fishes known from Malpelo Island (Rubio et al. 1992), ~20% associate with unconsolidated bottoms; whereas only ~9% of the known Clipperton shore fishes are. Because shorefishes, including those that live in these types of habitats, often have wide depth ranges (e.g. Randall 1985a, Randall et al. 1985, Fischer et al. 1995, Allen and Robertson in preparation), additional shallow-water benthic fishes can be expected to occur on the 60 m terrace at Clipperton.

Sampling effort however probably does not account for much of the apparent paucity of fishes at Clipperton. Groups that generally are abundant elsewhere on Indo-Pacific reefs and in the TEP are poorly represented at Clipperton. For example, only two pomacentrids are present, while the region contains 18 species. Notably, Clipperton is the only tropical Indo-Pacific locality at which a damselfish in the genus *Abudefduf* is not known to occur. Despite the fact that gobies frequently are the most speciose group living in coralline and other rocky habitats, this family is represented by only one species (out of ~70 TEP species). Similarly, four families of blennioid fishes (Blenniidae, Tripterygiidae, Labrisomidae, and Chaenopsidae) that contain ~70 TEP species, and commonly occur on reefs and other rocky habitats, are represented by only two blenniids. Only five of ~40 TEP sharks have been recorded, and Clipperton is the only atoll within the range of the reef shark *Triaenodon obesus* where it is not found.

(2) *Habitat availability*: Habitat availability is likely to effect the size of an isolated reef's fish fauna in several ways. The size of a reef affects whether it can provide sufficient living space for a resident population to persist. Local extinction due to changes in environmental conditions becomes more likely as local population size decreases (MacArthur and Wilson 1967, MacArthur 1972, Kosaki

et al. 1991). Local extinctions of corals have been associated with stress from high water temperatures during El Niño-Southern Oscillation events (ENSOs) in the TEP. Glynn et al. (in press) suggest that such extinctions may have contributed to the small size of the coral fauna (eight species) at Clipperton. The only information on similar effects of ENSOs on fish faunas in the TEP indicates that the extreme 1982–1983 ENSO produced increases in the abundances of tropical species and declines in populations of temperate species in the Galapagos (Grove 1984), where the TEP abruptly ends, and both temperate and tropical species are common. Clipperton is in the center of the TEP and because the ranges of only a few temperate reef fishes extend into the central parts of the TEP, Clipperton likely has always had an essentially tropical fish fauna. Thus ENSOs may not limit the size of the shorefish fauna at Clipperton by producing local extinctions due to stress.

In French Polynesia, overall species diversity of reef fishes is strongly correlated with atoll size, although such a relationship is absent in certain families (Galzin et al. 1994). Clipperton has ~10 km² of habitat less than 200 m depth, and ~3.7 km² shallower than 50 m depth (Fig. 3 of Glynn et al., this issue). Although Clipperton is a very small atoll it is large enough to support eight endemic fishes in a variety of ecological groups. Other small islands in the TEP also support a similar range of endemic fishes (Table 2). Among the non-oceanic fishes, about 75% of the transpacific species and 77% of the TEP species (excluding local endemics) present at Clipperton in 1994 have significant (probably resident) populations. (Table 1). Many shorefishes are small and normally occur at high population densities similar to those of Clipperton endemics. Thus, there does not appear to be any simple relationship between the size of an isolated island or reef and its ability to support a substantial resident fish fauna, including a significant number of endemic species.

There is a strong temporal aspect to the presence of populations of transpacific species of other taxa at other localities in the TEP. Local populations of various benthic organisms appear and disappear over periods of a few years (Glynn et al. this issue, Lessios et al., this issue). It would be useful to revisit the island periodically to reassess the population status of shorefishes that were present in 1994, and determine how much species turnover occurs, the extent to which vagrants of new species arrive from distant sources, and whether they establish resident populations.

The size of an isolated reef might also affect recruitment from other sources to it (MacArthur and Wilson 1967, Kosaki et al. 1991). Although Clipperton is very small, half the known non-oceanic, tropical transpacific shorefishes (52 of ~102 species, Robertson et al., in preparation) have been recorded there. Most of these species recruited in sufficient numbers to be able to establish resident populations. This suggests that island size may have less of a limiting effect on recruitment than generally thought, and/or that the arrival of recruits from distant sources is a common event. While there is very little information on the abundance and distribution of shorefish recruits crossing the EPB (Leis 1984, Victor 1987), Clarke's (1995) data indicate that a considerable

number of reef fish larvae are entrained in currents entering the EPB from eastern Oceania. The terminal pelagic stages of many shorefishes are large and have good sensory and swimming abilities (Leis and Rennis 1983, Leis and Trnski 1989) and some species may disperse as sub-adults or adults associated with drift material (Jokiel 1990). Such recruits may be able to detect and actively move toward Clipperton from quite some distance. Hence, the effective size of Clipperton may be much larger for shorefishes than for other taxa whose recruits have little or no independent motility (e.g. corals, mollusks and sea urchins).

The range of habitats present may also affect the ability of an isolated reef to support various fishes (e.g. Hourigan and Reese 1987, Kosaki et al. 1991, Galzin et al. 1994). Galzin et al. (1994) found that, although there is no relationship between variation in lagoon structure and species diversity of reef fishes in French Polynesian atolls, the lack of a lagoon connected to the open sea is associated with severely reduced diversity. Adults of some shorefishes are strongly associated with lagoonal habitats and a small but significant percentage of an atoll's fish fauna may depend on the presence of a lagoon: ~15% of the shorefishes at Fanning Atoll in the Line Islands (Chave and Eckert, 1974), and ~10% of those at Cocos Keeling Atoll in the Indian Ocean (Allen and Smith-Vaniz 1994) are restricted to the lagoons at those sites. Closure of the Clipperton lagoon occurred late last century, and it now is brackish and lacking in fishes (Allen and Robertson in preparation). Prior to closure, the lagoon would have comprised the atoll's largest area (~7.3 km²) of shallow habitat for shorefishes. Clipperton now lacks not only a marine lagoon, but also many other shallow habitats that occur in the TEP and/or at other atolls: leeward-seaward exposures; shallow, protected sand, rubble and mud bottoms; estuarine and mangrove habitat; and seagrass beds and macroalgal stands. The atoll has very little stable unconsolidated substratum at depths <50 m of water (Glynn et al., this issue, Allen and Robertson in preparation). Thus, reduced habitat diversity appears to contribute substantially to the small size of Clipperton's fish fauna.

Many coral reefs are characterised by high habitat diversity and support diverse fish faunas that include a variety of specialized, coral-dependent species. Clipperton, however, is a simple reef constructed by few coral species (Glynn et al., this issue). It has much lower habitat diversity than other TEP coral/rocky reef areas and the other offshore islands in the region. In fact Clipperton's fish fauna includes only two fishes that are classed as strongly coral dependent- the corallivorous Guineafowl Pufferfish, *Arothron meleagris* (see Guzman and Robertson 1989) and the Coral Hawkfish, *Cirrhitichthys oxycephalus*. None of Clipperton's endemic fishes are coral dependent. They do not feed on corals nor do they live exclusively within corals. Thus the most significant coral reef in the TEP (Glynn et al., this issue) does not have a "coral reef" fish fauna per se.

(3) *Larval life-history characteristics*: The ability of potential recruits to endure long-distance dispersal has a major effect on the distribution of Indo-Pacific fishes. Species with more extended larval durations have wider distributions and are better represented among trans-

pacific fishes than are species with shorter larval lives (Rosenblatt et al. 1972, Brothers and Thresher 1985). Dispersal potential of shorefishes also depends on the habitat preferences of larvae. Larvae of some species tend to remain nearshore, and are less likely to be advected and subject to long distance dispersal than larvae that characteristically live offshore. Such larval habitat preferences evidently have strong effects on the distributions of shorefish, as all transpacific species belong to families that produce offshore larvae (Leis 1984). However, as Leis (1984) has pointed out, some taxa that produce offshore larvae have no known transpacific representatives.

A number of major TEP fish families that are absent from Clipperton have inshore larvae: bythitids, gobioidids, dactyloscopids, chaenopsids, labrisomids and tripterygiids. These families contain ~11% of the TEP's species. In six other fish families that include ~20% of the TEP's species, and that are absent from or poorly represented at Clipperton, some species have either exclusively nearshore larvae or larvae that spend part of their development nearshore (Pomacentridae, Haemulidae, Gobiidae, Gerreidae, Clupeidae, and Engraulidae—Leis 1993, Brogan 1994). Larval habitat preference and larval longevity thus appear to strongly affect the TEP component of the Clipperton fish fauna by affecting dispersal potential. The poor representation at Clipperton of several families that produce offshore larvae seems likely to be related to the lack of suitable adult habitat, because many species in those families are associated with unconsolidated bottoms. Those include the Synodontidae (none of four TEP species present), scorpaenids (one of ~7 TEP species present), serranids (six of ~45 TEP species present), and bothids (none of ~20 TEP species present).

The ability of an isolated site to support a resident population depends on the availability of habitat not only for adults but also for larvae. Large lagoons can be important as nurseries for a great variety of reef fishes, and the distribution of some taxa of shorefishes in Oceania reflects the distribution of such lagoons (Leis 1986). Even small lagoons can be nurseries for a limited range of reef fishes (e.g. some Apogonids, Atherinids, Blenniids, Callionymids, Clupeids, Gobiids, Microdesmids, Pomacentrids—Leis 1993). In addition, differences in environmental seasonality at the origin and final destination of larvae may limit successful second generation recruitment at the new site (Randall et al. 1985). Such effects could limit the establishment at Clipperton of species recruited from the more temperate parts of the TEP, such as the Revillagigedos. Low primary productivity in the waters around Clipperton (Koblentz-Mishke et al. 1970) and the lack of a marine lagoon are probably both important in limiting the diversity of fish fauna by way of their effects on larval survivorship.

(4) *Geographic isolation*: Clipperton is the most isolated (by ~1000 km) emergent site in the TEP (Fig. 2 of Glynn et al., this issue). Besides Clipperton and the Revillagigedos, the other main offshore sites in the TEP are Cocos Island, Malpelo Island, and the Galápagos, which are 2,500 km, 3000 km and 2,100 km, respectively, to the SE of Clipperton. On the western side of the EPB there are four tropical reef areas, scattered between 10° S and 20° N.

The nearest of these in a straight line from Clipperton, is the Marquesas Islands (7°–10° S), 3900 km SW of Clipperton. The Line Islands lie 5,400 km WSW at 1°–7° N. Johnston Island (16° N) and the Hawaiian Islands (18° N) are situated 7,000 km and 5,200 km, respectively, to the NW of Clipperton. Thus, distances between Clipperton and *all* other emergent reefs to both the east and the west are large. However, while Clipperton is physically much closer to the rest of the TEP than to Oceania, it is the pattern of currents that could carry larval recruits from eastern and western sources to the atoll that determines its relative isolation.

Glynn et al., (this issue) summarise published information and provide new data on surface and near-surface currents in the EPB around Clipperton. Clipperton is exposed to surface currents from both Oceania and much of the rest of the TEP, with eastern and western influences predominating at different times of the year. For ~2/3 of the year (May–December) Clipperton is likely to be under the influence of the (NECC), which flows from Oceania across the EPB at about 4°–11° N to Clipperton and to Cocos and the Gulf of Panama. Between January and April, the NECC flow weakens and Clipperton is exposed to flow from both northern and southern inshore parts of the TEP, including the mainland and around the Revillagigedos, Cocos and the Galápagos. Speeds of net westward movement of surface water are about 1/3–1/2 the average speed of net eastward flow by way of the NECC (Wyrki 1965). Increased flow from the NECC especially during ENSO events, which occur at 4–9 y intervals (Glynn et al., this issue) is likely to decrease the relative influence of currents from the east. At present, there are no indications of periodic reversals in this preponderant influence of current from Oceania. Thus Clipperton may be as isolated from the remainder of the TEP as it is from Oceania.

How important is isolation relative to the other factors discussed above in limiting the diversity of Clipperton's fish fauna? Taking into account the number of species of fish at Cocos and Malpelo and their lower isolation and greater habitat diversity, and the abundance of sand/rubble bottom fishes at Malpelo (~20%) and in the TEP as a whole (~40% of the species), it seems reasonable to assume that, given appropriate habitat, no more than 40% of the atoll's fishes would be unconsolidated-bottom species. Hence, as many as 45 species could be "missing" due to low habitat diversity (some of those probably do occur on the 60 m terrace, see above). "Addition" of these "missing" species to the Clipperton fauna would bring it up to ~60% of the number of fish species at either Cocos or Malpelo. If the remaining difference (~90 species) is due to Clipperton's greater isolation, then isolation would be the major factor limiting the richness of the atoll's fish fauna.

Zoogeographic affinities of the Clipperton fish fauna

(1) *Relative abundance of transpacific and TEP species*: The Clipperton fish fauna includes approximately equal numbers of transpacific fishes and species endemic to the TEP (63 versus 52 species, Table 1). About half (23 of

49) of the non-oceanic TEP species belong to families that also have transpacific representatives. There are ~102 shallow-water, tropical transpacific shorefishes (Robertson et al. in preparation). These and ~57 other oceanic transpacific species represent ~16% of the TEP fish fauna. Transpacifics have a strongly disproportionate representation in the non-oceanic component of the Clipperton fish fauna: ~50% of such transpacific species occur at the atoll compared to only ~8% of the species endemic to the TEP (G test for independence, $p < 0.001$). Some of this difference undoubtedly is due to differences in dispersal ability of larvae of species in different families (see above). To control for such effects, the representation at Clipperton of 15 families that contain both TEP endemics and transpacific species was compared (Muraenidae, Antennariidae, Holocentridae, Scorpaenidae, Carangidae, Lutjanidae, Chaetodontidae, Cirrhitidae, Mugilidae, Labridae, Scaridae, Acanthuridae, Bothidae, Balistidae, and Tetraodontidae). The bias towards transpacific species is strongly evident: 52% of 64 transpacific species from those families are present at Clipperton, compared to only 22% of 118 species for the TEP (G test for independence, $p < 0.001$).

It is not possible to test for differences in the proportions of the total shorefish faunas in Oceania and the TEP present at Clipperton. The fauna of the most likely western source of fish recruits, the Line Islands, has not been comprehensively described. Chave and Eckert's (1974) list of 241 species is for Fanning Island only, and the role of the Marquesas Islands as a source is unclear (see below). However, the upper limit to the size of the Line Islands' shorefish fauna can be estimated from numbers of species present at nearby islands. The Marquesas Islands have ~350 species (Randall 1985b). Johnston Island has ~240 species (Randall et al. 1985, Kosaki et al. 1991). The entire Marshall Islands (2,500 km W of the Line Islands and much nearer the center of Indo-Pacific diversity) have ~830 species (Randall and Randall 1987). The Hawaiian region has ~550 species (Randall 1992). Because the Line Islands are small and relatively isolated it is likely that they have a fish fauna about the size of that of the Marquesas, i.e. about half the size of the TEP endemic fauna. If so, and if all transpacific fishes occur at the Line Islands, then the Line Islands' fauna is more strongly represented than the TEP fauna at Clipperton (G test for independence, $p < 0.001$). The Line Islands fish fauna would be under-represented at Clipperton only if it was larger than the TEP fish fauna.

Thus, while Clipperton geographically is part of the TEP, from the perspective of its fish fauna, the island effectively is at least equidistant between that region and Oceania, and probably is closer to Oceania. Zoogeographic affinities of other organisms on Clipperton follow a similar pattern favoring western Pacific elements. About half of the mollusks (Emerson 1994) and echinoderms (Lessios et al., this issue) are transpacific species, while six of eight species of corals at Clipperton are transpacifics (Glynn et al., this issue). The dominance of transpacific elements in the Clipperton faunas reflects the influence of currents from Oceania across the EPB.

(2) *Clipperton as a stepping stone*: At least 30 of the non-oceanic transpacific fishes known from Clipperton

have resident populations there (Table 1). This group represents ~38% of such fishes that appear to have resident populations in the TEP (Robertson et al., in preparation). Thus, Clipperton may be an important stepping stone for gene flow from Oceania to the rest of the TEP. Due to the complexity and seasonal variability in currents within the TEP (Glynn et al., this issue) recruits released from Clipperton could disperse to much of the rest of the TEP. Submerged seamounts to the west and south of Clipperton may have also been important stepping stones for dispersal of shallow water organisms across the EPB during various ice ages, when sea levels were much lower (Grigg and Hey 1992).

Most (77%) the TEP endemic fishes (excluding the local endemics) at Clipperton also appear to have resident populations there. Hence, Clipperton might also act as a bridge between northern and southern populations of species that are separated by the large faunal gap on the mainland coast between Mexico and Honduras (see Springer 1958).

(3) *Eastern Pacific affinities*: Eight demersal shorefishes apparently are endemic to Clipperton (Table 1). Based on the distributions of the probable nearest relatives of these species, one or two of the Clipperton endemics have western Pacific origins while the remainder have eastern Pacific origins (Allen and Robertson, in preparation). Within the TEP, the Clipperton fish fauna has limited affinities to the faunas of both the nearest offshore islands, the Revillagigedos, and the Galapagos. The nearest relative of at least one Clipperton endemic is a subspecies that lives in the Galapagos (Allen and Robertson, in preparation). *Gymnothorax dovii* is restricted to the southern half of the TEP, including the Galapagos. Resident populations of four species occur only at Clipperton and the Revillagigedos. One Revillagigedos endemic occurs at Clipperton as a vagrant. One temperate species (*Pontinus vaughani*) occurs both in the Revillagigedos and at Clipperton (Fischer et al. 1995).

However, most (37) of the TEP fishes found at Clipperton are widely distributed throughout the region, at island and/or continental sites. There is insufficient documentation of the shorefish faunas of the other offshore islands to allow more detailed comparison of sub-regional affinities of the Clipperton fish fauna. Surface water currents are sufficiently complex in the TEP (Wyrki 1965; Glynn et al., this issue) that recruits arriving at Clipperton could have originated just about anywhere within the region, and recruits leaving Clipperton could reach almost anywhere in the region.

(4) *Affinities to sites in oceania*: Most (34 of 48) of the non-oceanic, transpacific species present at Clipperton are widespread in eastern Oceania, and the transpacific component of the Clipperton fish fauna does not appear to be strongly related to the fish fauna of any single Oceania site among the three sites that have been well studied (Table 3). Unfortunately, the fish fauna of the most probable source for dispersal of organisms to the TEP, the Line Islands (see below), is poorly documented. While 26 species of the non-oceanic transpacific fishes known from Clipperton were not recorded by Chave and Eckert (1974) at Fanning Atoll in the Line Islands, many seem likely to be present

Table 3. Occurrence of 48 non-oceanic, transpacific shorefishes from Clipperton Island and tropical sites on the eastern edge of Oceania

Species	Known occurrence			
	Marquesas Islands	Line Islands	Johnston Island	Hawaiian Islands
<i>Carcharhinus albimarginatus</i>	+	?	—	—
<i>Carcharhinus galapagensis</i>	—	?	+?	+
<i>Carcharhinus limbatus</i>	+	?	—	+
<i>Sphyrna lewini</i>	+	?	—	+
<i>Echidna nebulosa</i>	+	?	—	+
<i>Enchelynassa canina</i>	+	?	—	+
<i>Gymnothorax buroensis</i>	—	+	+	+
<i>Gymnothorax zebra</i>	+	?	+	+
<i>Gymnothorax flavimarginatus</i>	—	+	+	+
<i>Siderea picta</i>	+	+	+	+
<i>Uropterygius macrocephalus</i>	+	?	+	+
<i>Scuticaria tigrina</i>	—	?	+	+
<i>Chanos chanos</i>	+	?	—	+
<i>Antennarius coccineus</i>	+	+	+	+
<i>Myripristis berntdi</i> ¹	—	+	+	+
<i>Plectrypops lima</i>	+	?	+	+
<i>Aulostomus chinensis</i>	+	?	+	+
<i>Fistularia commersoni</i>	+	+	+	+
<i>Doryrhamphus excisus excisus</i>	+	+	+	+
<i>Kuhlia mugil</i>	+	?	—	—
<i>Carangoides orthogrammus</i>	+	?	+	+
<i>Caranx lugubris</i>	—	+	+	+
<i>Caranx melampygus</i>	+	+	+	+
<i>Caranx sexfasciatus</i>	+	+	—	+
<i>Forcipiger flavissimus</i>	+	?	+	+
<i>Cirrhitichthys oxycephalus</i>	+	+	—	—
<i>Novaculichthys taeniourus</i>	+	+	+	+
<i>Stethojulis bandanensis</i>	—	+	—	—
<i>Thalassoma purpureum</i>	+	+	+	+
<i>Scarus rubroviolaceus</i>	+	?	+	+
<i>Zanclus cornutus</i>	+	+	+	+
<i>Acanthurus achilles</i>	+	+	+	+
<i>Acanthurus nigricans</i>	+	+	+	+
<i>Acanthurus triostegus triostegus</i> ²	—	+	—	—
<i>Acanthurus xanthopterus</i>	+	+	—	+
<i>Ctenochaetus marginatus</i>	+	+	+	—
<i>Naso annulatus</i>	+	?	—	+
<i>Naso hexacanthus</i>	+	?	+	+
<i>Naso lituratus</i>	+	?	+	+
<i>Bothus mancus</i>	+	?	+	+
<i>Melichthys niger</i>	+	+	+	+
<i>Xanthichthys mento</i>	—	?	—	+
<i>Aluterus scriptus</i>	+	?	+	+
<i>Cantherhines dumerilii</i>	+	?	+	+
<i>Ostracion meleagris</i> ³	+	?	—	—
<i>Arothron meleagris</i>	+	+	+	+
<i>Diodon holacanthus</i>	—	?	—	+
<i>Diodon hystrix</i>	+	?	+	+
Total ⁴ known at each site	38	22	32	40

1. Marquesian form probably is a separate subspecies

2. Three subspecies – Hawaiian;

Marquesian; Line Islands plus eastern Pacific

3. Different subspecies in the Hawaii region and the remainder Indo-Pacific

4. Includes only shared species and subspecies

Sources: Chave and Eckert 1974 (Fanning Island only), Randall 1981, Randall and Gueze 1981, Tinker 1982, Randall 1985a, b, Randall et al. 1985, Kosaki et al. 1991, Myers 1991, DR Robertson personal observations in the Marquesas in 1995

elsewhere in that island group (Randall, pers. comm., 1995). Even so, there is some evidence of a particular affinity of the Clipperton fish fauna to that of the Line Islands, as two of Clipperton's transpacific species or subspecies (*Stethojulis bandanensis* and *Acanthurus triostegus triostegus*) occur at the Line Islands but not at any of the other three Oceanian sites. In addition, 23 of the Clipperton transpacific shorefishes are lacking at one or two of the other three sites (Table 3). Glynn et al., (this

issue) note that among the same set of Oceania sites, the coral fauna of Clipperton is most closely allied to that of Johnston Island and has great affinities to the faunas of Hawaii and Polynesia. However, the Clipperton transpacific coral fauna is very small (six species) and, as with fishes, the coral fauna has been examined at only Fanning within the Line Islands. Thus, apparent dissimilarities between both the fish and coral faunas of Clipperton and the Line Islands could be a result of sampling artifacts.

The only surface current between the TEP and the Hawaiian region is the North Equatorial Current (NEC), which flows westward from the northern part of the TEP (see Fig. 2 in Glynn et al., this issue). In Oceania, the boundary of that current extends well below the latitude of Johnston Island. Thus both Hawaii and Johnston Island seem to be unlikely sources for recruitment to the TEP (Grigg and Hey 1992). Rosenblatt and Waples (1986) suggested that high levels of genetic similarity between Hawaiian and TEP populations of some of the 11 transpacific shorefishes they examined is due to ongoing gene flow, and proposed that those sites are connected by indirect west to east movements of recruits (from the Hawaiian region to the Line Islands and from there to the TEP?). However, the fish fauna of the Hawaiian region is sufficiently distinct from that of locations to the south (Randall et al. 1985) that southward recruitment from Hawaii or Johnston Island to the Line Islands does not seem likely. The repeated appearance of the TEP endemics, *Sectator ocyurus* and *Balistes polylepis*, as vagrants in Hawaii (Randall 1985a, JE Randall pers. comm. 1995), presumably results from recruitment in the NEC. Clipperton could very well provide recruits for this east- to west connection. Resident populations of *Priacanthus alalaua*, which appear to be restricted to the Revillagigedos and Hawaii (Starnes 1988, Fischer et al. 1995), might also be connected by way of the NEC. Such an east to west movement of recruits could also explain similarities in the transpacific fish and coral faunas of Clipperton and the Hawaiian region.

Under non-ENSO conditions, the currents that are most likely to carry recruits from Oceania across the EPB are the NECC, the flow of which spans $\sim 5^{\circ}$ – 10° N at the eastern edge of Oceania, and the subsurface Equatorial Undercurrent (EUC), which extends within a couple of degrees of both sides of the equator (Richmond 1990, Glynn et al., this issue). At such times the NECC could carry fish recruits from the northern Line Islands, while the EUC could capture recruits from the southern part of those islands (Clarke 1995). The chance of transpacific recruitment from the Line Islands seems likely to increase during ENSOs because then the flow of the NECC extends from 10° N to at least 5° S, completely spanning the latitudinal range of these islands. That the Line Islands are the most likely potential source of recruitment from Oceania across the EPB on the NECC is well recognized (Hubbs and Rosenblatt 1961, Richmond 1990, Grigg and Hey 1992, Clarke 1995).

Under non-ENSO conditions, the Marquesas (7° – 10° S) experience the South Equatorial Current (SEC), which flows from the eastern Pacific between 4° N– 20° S. The occurrence of the TEP species *Sectator ocyurus* as a vagrant on the SW side of the EPB (Randall 1961) is probably due to dispersal on the SEC. During non-ENSO periods there is no eastbound surface or subsurface water flow close to the latitude of the Marquesas, and eastward dispersal from those islands is very unlikely (Grigg and Hey 1992). However, the extension of the southern limit of the NECC to 5° S, and perhaps further south, during ENSOs, might allow fish recruits from the Marquesas to reach the TEP. Because Marquesian recruits would have

to travel 1,500 km (28%) less distance than those from the Line Islands to reach the TEP, the Marquesas could be important as a source of transpacific recruits during ENSOs.

Variability in the strength of ocean currents may have a major influence on long distance dispersal, with extreme conditions being particularly important (Richmond 1990, Leis 1991, Grigg and Hey 1992). Due to increased strength of the NECC during ENSOs, average and minimum passage times across the EPB appear to decline from ~ 150 d and ~ 100 d to ~ 80 d and ~ 45 d, respectively (Richmond 1990, Glynn et al., this issue). Such changes could mean that fish recruits with only moderate periods of competency could recruit to the TEP during ENSOs (Richmond 1990, Grigg and Hey 1992). Larval durations of a number of taxa of transpacific fishes are near the lower end of this range (45 d) (Leis 1984, Brothers and Thresher 1985). There is evidence that the 1982–1983 ENSO produced recruitment of transpacific organisms in the southern half of the TEP, where eastward flow was very strong. Five Indo-Pacific fishes previously unrecorded in the TEP were observed as vagrants at the Galapagos, and another three at Cocos Island (Grove 1989) immediately following that event. Examination of the otoliths of one individual of *Naso annulatus* that we collected at Clipperton indicate that it was ~ 5 – 11 y old and had a larval life of ~ 150 d (EB Brothers pers. comm.). Thus, this fish could have arrived at Clipperton during either the 1982–1983 ENSO or the 1987 ENSO. Transpacific species of other taxa also appear to have become established in the TEP during 1982–1983 ENSO (eg echinoids—Lessios et al., this issue). Thus, recruitment from Oceania clearly has the potential to regularly influence the biota of Clipperton and the remainder of the TEP.

In summary, what is known about surface current systems in the EPB points to the Line Islands as the most important source for fish recruits dispersing eastward across the EPB, although intermittent recruitment from the Marquesas remains a possibility. The limited information on affinities of the fish faunas of Clipperton and various other sites in eastern Oceania is consistent with such a Line Islands connection. Recruitment of shorefishes from the Hawaiian region to the TEP is unlikely under present conditions. Recruitment from Oceania to the TEP is an ongoing process associated, at least to some extent, with ENSO produced enhancement of eastward current flow. Recruitment of shorefishes from the TEP to Hawaii and to southern Oceania currently occurs, perhaps more frequently than is generally thought.

Much more work is needed to resolve the issues of the effectiveness of the EPB in isolating eastern and western populations of transpacific fishes, to determine source(s) of recruitment in Oceania to the TEP, and to define the impact of ENSOs on recruitment across the EPB. Accumulating evidence strongly indicates that the barrier is much more permeable, particularly to west- to east, than formerly believed (Ekman 1953, Mayr 1954). Unfortunately, because transpacific fishes are most common on remote offshore islands in the TEP (Rosenblatt et al. 1972), observations useful for establishing the spatial and temporal relationship of such recruitment to ENSOs will always be

difficult. At this stage two things would be particularly useful for the zoogeography of transpacific fishes: (1) a comprehensive assessment of the composition of the shorefish fauna of the Line Islands, and (2) a detailed comparison of the genetic similarities of populations of transpacific fishes in the TEP and in the Hawaiian province, the Line Islands and the Marquesas Islands.

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References

- Allen GR, Robertson DR (1994) Fishes of the tropical eastern Pacific. U Hawaii Press, Honolulu
- Allen GR, Smith-Vaniz WF (1994) Fishes of the Cocos (Keeling) Islands. Atoll Res Bull 412:1–21
- Briggs JC (1961) The Eastern Pacific Barrier and the distribution of marine shore fishes. *Evolution* 15:545–554
- Brogan MW (1994) Distribution and retention of larval fishes near reefs in the Gulf of California. *Mar Ecol Prog Ser* 115:1–13
- Brothers EB, Thresher RE (1985) Pelagic duration, dispersal, and the distribution of Indo-Pacific coral-reef fishes. In: Reaka ML (ed) *The Ecology of Coral Reefs*. NOAA Symp Ser Undersea Res 3:53–68. NOAA Undersea Research Program, Maryland
- Clark TA (1995) Larvae of nearshore fishes in oceanic waters of the central equatorial Pacific. *Pacif Sci* 49:134–142
- Chave EH, Eckert DB (1974) Ecological aspects of the distributions of fishes at Fanning Island. *Pacif Sci* 28:297–317
- Ekman S (1953) *Zoogeography of the Sea*. Sidgwick and Jackson, London
- Emerson WK (1994) A zoogeographic summary of the marine molluscs of Clipperton Island (tropical eastern Pacific). *Festiva* 26:62–71
- Fischer W, Krupp F, Schneider W, Sommer C, Carpenter KE, Niem VH (1995) *Guia FAO para la identificacion de especies para los fines de la pesca. Pacifico centro-oriental*. Vols II–III, FAO, Rome
- Galzin R, Planes S, Dufour V, Salvat B (1994) Variation in diversity of coral reef fish between French Polynesian atolls. *Coral Reefs* 13:175–180
- Glynn PWG, Veron JEN, Wellington GM (1996) Clipperton Atoll (Eastern Pacific): oceanographic setting, geomorphology, reef-building coral communities and zoogeographic relationships. *Coral Reefs* 15:71–99
- Grigg RW, Hey R (1992) Paleooceanography of the tropical eastern Pacific Ocean. *Science* 255:172–178
- Grove JS (1984) The influence of the 1982–1983 El Niño on the ichthyofauna on the Galapagos Archipelago. *Trop Ocean-Atmos Newsl* Nov 1984:18–19
- Grove JS (1989) El Niño 1982–1983 and new records of Indo-west Pacific fishes at the Galapagos. *Ann Rept West Malacol Soc* 21:5
- Guzman HM, Robertson DR (1989) Population and feeding responses of the corallivorous pufferfish *Arothron meleagris* to coral mortality in the eastern Pacific. *Mar Ecol Prog Ser* 55:121–131
- Herre AW (1940) Distribution of fish in the tropical Pacific. *Proc 6th Pacif Sci Congr Oceanogr Mar Biol*:587–592
- Hourigan TF, Reese ES (1987) Mid-ocean isolation and the evolution of Hawaiian reef fishes. *Trends Ecol Evol* 2:187–191
- Hubbs CL, Rosenblatt RH (1961) Effects of the equatorial currents of the Pacific on the distribution of fishes and other marine animals. *10th Pacif Sci Congr Abs*:340–341
- Jokiel PL (1990) Long-distance dispersal by rafting: re-emergence of an old hypothesis. *Endeavour* 14:66–73
- Koblentz-Mishke OJ, Volkovinsky VV, Kabanova JG (1970) Plankton primary production of the World Ocean. In: *Scientific Exploration of the South Pacific*. Wooster WS (ed), Nat Acad Sci, Washington DC
- Kosaki RK, Pyle RL, Randall JE, Irons DK (1991) New records of fishes from Johnston Atoll, with notes on biogeography. *Pacif Sci* 45:186–203
- Leis JM (1983) Coral reef fish larvae (Labridae) in the East Pacific Barrier. *Copeia* 1983:826–828
- Leis JM (1984) Larval fish dispersal and the East Pacific Barrier. *Oceanogr Trop* 19:181–192
- Leis JM (1986) Ecological requirements of Indo-Pacific larval fishes: a neglected zoogeographic factor. *Proc 2nd Int Conf Indo-Pacif Fish* 759–766
- Leis JM (1991) The pelagic stage of reef fishes: the larval biology of coral reef fishes. In: Sale PF (ed) *The Ecology of Coral Reef Fishes*. Academic Press, New York, pp 183–230
- Leis JM (1993) Larval fish assemblages near Indo-Pacific coral reefs. *Bull Mar Sci* 53:362–392
- Leis JM, Rennis DS (1983) The larvae of Indo-Pacific coral reef fishes. U Hawaii Press, Honolulu
- Leis JM, Trinski T (1989) The larvae of Indo-Pacific shorefishes. U Hawaii Press, Honolulu
- Lessios HAL, Kessing BD, Wellington GM, Graybeal A (1996) Indo-Pacific echinoids in the tropical eastern Pacific. *Coral Reefs* 15:133–142
- MacArthur RH (1972) *Geographical Ecology*. Harper and Row, New York
- MacArthur RH, Wilson EO (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton
- Mayr E (1954) Geographic speciation in tropical echinoids. *Evolution* 8:1–18
- Myers RF (1991) *Micronesian reef fishes*. Coral Graphics, Guam
- Randall JE (1956) A revision of the surgeonfish genus *Acanthurus*. *Pacif Sci* 10:159–235
- Randall JE (1961) A record of the kyphosid fish *Sectator ocyurus* (= *azureus*) from the Society Islands. *Copeia* 1961:357–358
- Randall JE (1985a) *Guide to Hawaiian Reef Fishes*. Treasures of Nature, Kaneohe
- Randall JE (1985b) Fishes. *Proc 5th Int Coral Reef Congr* 1:462–481
- Randall JE (1992) Endemism of fishes in Oceania. *UNEP Regional Seas Repts Studs* 147:55–67
- Randall JE, Earle JL, Pyle RL, Parrish JD, Hayes T (1993) Annotated checklist of the fishes of Midway atoll, northwestern Hawaiian islands. *Pacif Sci* 47:356–400
- Randall JE, Lobel PS, Chave EH (1985) Annotated checklist of fishes of Johnston Island. *Pacif Sci* 39:24–80
- Randall JE, Gueze P (1981) The holocentrid fishes of the genus *Myripristis* of the Red Sea, with clarification of the *murdjan* and *hexagonus* complexes. *Nat Hist Mus LA County Contrib Sci* 334:1–16
- Randall JE, Randall HA (1978) Annotated checklist of the fishes of Enewetak Atoll, and other Marshall Islands. In: Devany DM, Reese ES, Burch BL, Helfrich P (eds) *The Natural History of Enewetak Atoll*. Vol II Biogeography and Systematics, Dept Energy, Off Sci Tech Inf, Washington, pp 289–324
- Richmond RH (1990) The effects of the El Niño/Southern Oscillation on the dispersal of corals and other marine organisms. In: Glynn

- PW (ed) Global Ecological Consequences of the 1982–83 El Niño-Southern Oscillation. Elsevier, Amsterdam, pp 153–190
- Rosenblatt RH (1967) The zoogeographic relationships of the marine shore fishes of tropical America. *Stud trop Oceanogr* 5:579–592
- Rosenblatt RH, McCosker JE, Rubinoff I (1972) Indo-West Pacific fishes from the Gulf of Chiriqui, Panama. *Contrib Sci Nat Hist Mus LA County* 234:1–18
- Rosenblatt RH, Waples RS (1986) A genetic comparison of allopatric populations of shore fish species from the eastern and central Pacific Ocean: dispersal or vicariance? *Copeia* 1986:275–284
- Rubio EA, Suarez A, Estupian F, Henao W, Vargas B (1992) Los recursos ictiológicos de la Isla Malpelo (Colombia). I. Una revisión de su conocimiento y nuevos reportes para la ictiofauna de la Isla. VIII Seminario nacional de las ciencias y las tecnologías del mar y congreso Centroamericano y del Caribe en ciencias del Mar. Mem Tomo II:642–658
- Springer VG (1958) Systematics and zoogeography of the clinid fishes of the subtribe Labrisomini Hubbs. *Pub Inst Mar Sci U Texas* 5:417–492
- Starnes WC (1988) Revision, phylogeny and biogeographic comments on the circumtropical marine percoid fish family Priacanthidae. *Bull Mar Sci* 43:117–203
- Tinker SW (1982) Fishes of Hawaii. Hawaiian Service, Honolulu
- Victor BC (1987) Growth, dispersal, and identification of planktonic labrid and pomacentrid reef-fish larvae in the eastern Pacific Ocean. *Mar Biol* 95:145–152
- Wyrтки K (1965) Surface currents of the eastern tropical Pacific Ocean. *Bull IATTC* 9:271–304