Tropical Transpacific Shore Fishes[1]

D. Ross Robertson,[2] *Jack S. Grove,*[3] *and John E. McCosker*[4]

Abstract: Tropical transpacific fishes occur on both sides of the world's largest deep-water barrier to the migration of marine shore organisms, the 4,000- to 7,000-km-wide Eastern Pacific Barrier (EPB). They include 64 epipelagic oceanic species and 126 species of shore fishes known from both the tropical eastern Pacific (TEP) and the central and West Pacific. The broad distributions of 19 of 39 circumglobal transpacific species of shore fishes offer no clues to the origin of their TEP populations; TEP populations of another 19 with disjunct Pacific distributions may represent isthmian relicts that originated from New World populations separated by the closure of the Central American isthmus. Eighty species of transpacific shore fishes likely migrated eastward to the TEP, and 22 species of shore fishes (12 of them isthmian relicts) and one oceanic species likely migrated westward from the TEP. Transpacific species constitute ~12% of the TEP's tropical shore fishes and 15–20% of shore fishes at islands on the western edge of the EPB. Eastward migrants constitute ~7% of the TEP's shore-fish fauna, and a similar proportion of TEP endemics may be derived from recent eastward immigration. Representation of transpacific species in different elements of the TEP fauna relates strongly to adult pelagic dispersal ability—they constitute almost all the epipelagic oceanic species, ~25% of the inshore pelagic species, but only 10% of the demersal shore fishes. Taxa that have multiple pelagic life-history stages are best represented among the transpacific species. Among demersal teleosts that have pelagic larvae, pelagic spawners are better represented than demersal spawners among transpacific species, perhaps because offshore larval development and longer pelagic larval durations provide the former with greater dispersal capabilities. There are strong phylogenetic effects on representation in the transpacific fauna: (1) elasmobranchs are proportionally better represented than teleosts, even teleosts with more pelagic life-history stages; (2) a pelagic juvenile stage with great dispersal potential allows tetraodontiforms that produce demersal or pelagic eggs to be well represented; and (3) various speciose central Pacific families with "adequate" larval dispersal characteristics lack transpacific species. El Niños potentially enhance eastward migration by increasing eastward flow and halving transit times across the EPB. However, that effect may be offset by low productivity and high temperatures in those eastbound flows. There is little clear evidence of strongly increased migration across the EPB during El Niños, including recent extreme events (1982–1983 and 1997–1998). During such events shore fishes in the TEP experience range expansions and become locally abun-

---

[1] This research was supported by a National Geographic Society Grant (5831-96) to D.R.R. and general research funds from STRI. Manuscript accepted 20 October 2003.

Pacific Science (2004), vol. 58, no. 4:507–565

[2] Smithsonian Tropical Research Institute (Panama), Unit 0948, APO AA 34002-0948 (phone: (+507) 212 8704; fax: (+507) 212 8714; e-mail: drr@stri.org).

[3] Section of Ichthyology, Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, California 90007 (e-mail: jsgIMAGES@aol.com).

[4] California Academy of Sciences, San Francisco, California 94118 (e-mail: jmccosker@calacademy.org).

dant at marginal areas such as the Galápagos, changes that can be confused with increased migration across the EPB. Although there is a strong bias toward eastward migration among the transpacific shore fishes, there likely is much more westward migration than previously realized: 20–25% of transpacific species may have migrated in that direction. Stronger eastbound than westbound currents can account for this bias. Westward migrants have better developed pelagic dispersal characteristics than many eastward migrants, suggesting that westward migration is more difficult. Many westward migrants associate with flotsam and flotsam-mediated migration is more likely to be westward. All westward migrants occur at Hawai'i, but only about one-fifth of them at the Marquesas. This bias may be due to: Hawai'i being a larger target and in the path of most of the flotsam dispersal from the TEP; an eastward current that impinges on the Marquesas, reducing westward arrivals; and most propagules dispersing toward the tropical Marquesas originating in the temperate eastern Pacific. However, the Hawaiian Islands also are much better sampled than the Marquesas. Although the TEP reef-fish fauna may be depauperate relative to that of the Indo-Malayan "center of diversity," it is as rich as the faunas of islands on the western side of the EPB. Hence a preponderance of eastward migration does not represent a response to a richness gradient across that barrier. There is little evidence that a paucity of ecological groups in the native TEP fauna is primarily responsible for the structure of the eastward-migrant fauna. Rather, eastward migrants may simply represent a cross section of those in the donor fauna, tempered by phylogenetic variation in dispersal ability. Because few central Pacific fishes can live only on live corals and coral reefs, the rarity of such reefs in the TEP is unlikely to strongly limit eastward migration. Differences between oceanic and adjacent continental reef-fish faunas in the West Pacific indicate that each is strongly tied to its respective habitat. Hence, the rarity in the TEP of the (overwhelmingly) most abundant habitat present in the central Pacific—tropical oceanic reefs—may strongly limit migration in both directions across the EPB: there is little suitable habitat for eastward migrants in the TEP and few suitable species and tiny source populations for westward migrants. The global effects that oceanic/continental habitat differences have on reef-fish biogeography need further assessment. Genetic data on ~18% of the transpacific species indicate: that conspecific populations of oceanic species (especially) and shore fishes are genetically well connected across the EPB; that circumtropical taxa in the TEP include isolated isthmian relicts and recent eastward migrants; that all five TEP species of one circumtropical genus (*Thalassoma*) were derived by several eastward invasions after the closure of the Isthmus of Panama; that some isolated Hawaiian central Pacific populations were established by postisthmian invasion from the TEP; and that Indo-central Pacific species unsuspectedly can co-occur with their endemic sibling sisters in the TEP. Genetic data support distributional data that indicate a strong preponderance of eastward migration across the EPB but also more westward migration than previously thought. Future genetic studies should resolve a question that distributional data cannot: how many widespread presumed eastward-migrant transpacific species actually originated by westward migration from the TEP?

THE TROPICAL EASTERN PACIFIC (TEP) biogeographic region encompasses the tropical and subtropical Pacific coast and offshore islands of central and northern South Amer-

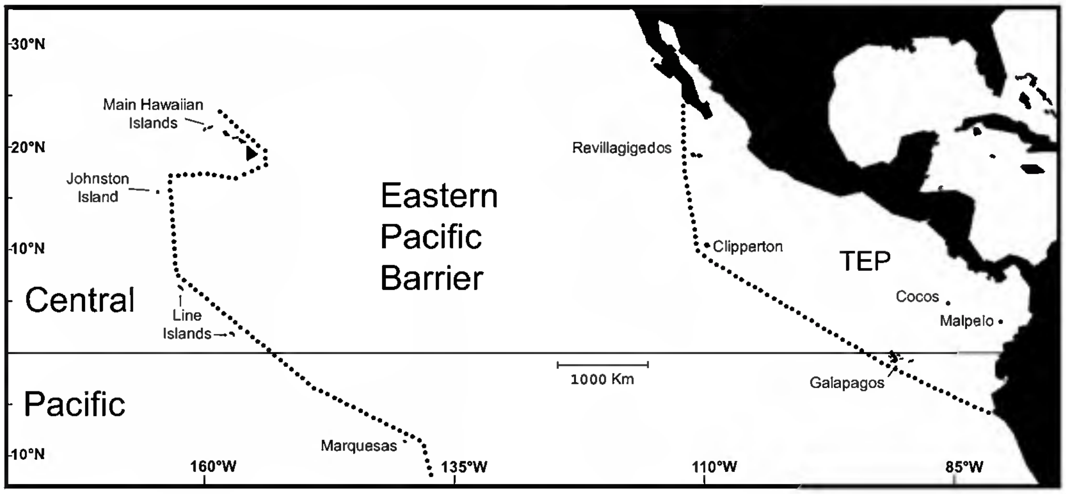

Figure 1. The tropical eastern Pacific (TEP) biogeographic region and its isolation from other regions by the Eastern Pacific Barrier and the Central American isthmus.

ica. The continental portion of this region extends from the tip of Baja California and the lower two-thirds of the Gulf of California (south of ~29° N) to the northern coast of Peru, at about 5° S (Briggs 1974, Hastings 2000, Robertson and Allen 2002). The latitudinal limits of the region are set by western extensions of the continental coastline, where cool currents that flow toward the equator turn offshore toward the central Pacific. In addition to the continental shore there are five oceanic islands and archipelagos scattered through most of the latitudinal range of this region (see Figure 1): the Revillagigedo Islands (at ~18° N, ~400 km S of Baja California), Clipperton Atoll (at 10° N, ~1,100 km SW of central Mexico), Cocos Island (at 5.5° N, 450 km W of Costa Rica), Malpelo Island (at 3.9° N, 350 km W of Colombia), and the Galápagos Archipelago (between 1.7° N and 1.5° S, ~1,000 km W of Ecuador).

The TEP is the most isolated tropical marine biogeographic region. It has been separate from the tropical Atlantic since the closure of the isthmus of Panama, about 3.1 million yr ago (Ma) (Coates and Obando 1996). It also is isolated from the central and western Pacific by the world's widest deep-water marine barrier to the dispersal of marine shore organisms, the 4,000- to 7,000-km Eastern Pacific Barrier (EPB) (Ekman 1953; see Figure 1), which may have existed for the past 65 myr (Grigg and Hey 1992). Although initially the EPB was thought to be completely impenetrable to dispersal by contemporary marine taxa (Darwin 1872, Mayr 1954), many members of various major taxa now are known to occur on both sides of this barrier. These include corals (Glynn and Ault 2000), sea urchins (Ekman 1953, Lessios et al. 1998, 1999, 2003), mollusks (Vermeij 1987, Emerson 1994), polychaetes (Fauchald 1977), and fishes (Briggs 1961, 1964, Rosenblatt et al. 1972, Leis 1984). There is direct evidence of the transport of invertebrate larvae across the EPB (Scheltema 1988), and accumulating genetic data demonstrate ongoing connections between conspecific populations separated by the EPB in some invertebrates and fishes (Rosenblatt and Waples 1986, Lessios et al. 1998). Briggs (1961) compiled the first list of transpacific fishes, species that occur on both sides of the EPB. That list has expanded considerably (Briggs 1964, Rosenblatt 1967, Rosenblatt et al. 1972, Springer 1982), and in the most recent review Leis (1984) listed 54 transpacific shore fishes (five of them erroneous). Most attention to movements across the EPB has been given to eastward migration, due largely to the assumption that species tend to migrate from areas of higher diversity (the Indo-Malayan area in the western Pacific) to areas of lower diversity in the central and eastern Pacific (e.g., Briggs 1995, 1999*a,b*, Mora et al. 2003).

This paper has several purposes: (1) to summarize current information on the occurrence, distributions, and population status of tropical transpacific shore fishes on each side of the EPB, and the contribution that they make to the faunas on each side of that barrier; (2) to review genetic studies dealing with patterns of connections of populations across the EPB and the role of transpacific migration in the origin of TEP populations; and (3) to examine factors potentially affecting the current level, direction, and routes of migration across the EPB and the establishment of resident populations of immigrants in the TEP.

MATERIALS AND METHODS

Tropical Transpacific Shore Fishes

Transpacific shore fishes occur in the central and/or West Pacific as well as the TEP. The great majority of the species discussed here have all or most of their ranges within the Tropics; however, a few mainly warm temperate species with ranges extending into at least one tropical area are included. Transpacific warm temperate species that apparently enter the Tropics only as vagrants (e.g., the sharks *Hexanchus griseus*, *Carcharodon carcharias*, and *Galeorhinus galeus* and the tuna *Thunnus orientalis*) are excluded. Here, shore fishes include demersal and coastal pelagic species living at <100 m depth. Oceanic epipelagic species also are included mainly to assess the effectiveness of the EPB as a barrier to shore fishes and how dispersal potential affects representation of different types of fishes in the transpacific fauna.

RESIDENTS AND VAGRANTS. A vagrant on one side of the EPB likely does not have a self-replenishing population there because only a few isolated individuals have been seen at scattered locations and times or a few same-sized individuals once at a single site. A regional resident likely has a self-sustaining population because it is relatively common at at least one location, has been recorded repeatedly at the same site(s) over intervals of decades, and at least one local population includes juveniles and adults of various sizes.

EASTWARD AND WESTWARD MIGRANTS, AND ISTHMIAN RELICTS. Eastward migrants to the TEP are widely distributed in the central Pacific, including the Line Islands at the upcurrent end of eastbound currents on the western edge of the EPB, and are either residents or vagrants in the TEP. Residents restricted to areas at the termini of the eastbound currents or to the offshore islands likely are such immigrants. Except for *Heteropriacanthus cruentatus* (see section on Genetic Studies in Discussion), eastward migrants are exclusively Indo-Pacific. Most also lack a "look-alike" likely sister species in the West Atlantic because such would indicate that the TEP populations might be isthmian relicts (cf. Vermeij and Rosenberg 1993). Westward migrants to the central Pacific are residents in the TEP, where they occur near the upcurrent ends of westbound currents and at the offshore islands. Elsewhere in the Pacific they are restricted to islands at or near the downcurrent ends of those currents (e.g., Hawai'i, Johnston Island, and the Marquesas). Isthmian relicts: Before the rise of the Isthmus of Panama (~3.1 Ma) (Coates and Obando 1996), the biotas of the TEP and the Greater Caribbean are presumed to have had extensive connections. This common history is reflected in the similarities of their fish faunas (Rosenblatt 1967, Thresher 1991, Robertson 1998). In many marine organisms, populations on the Atlantic and Pacific sides of the isthmus represent geminate species pairs (Jordan 1908) (i.e., sister species formed subsequent to the separation of TEP and Caribbean populations of a single species). Isthmian relicts in the TEP arose through the division of a neotropical population by the rise of the isthmus.

Sources of Data

As well as older material on transpacific fishes (Briggs 1960, 1961, 1964, Rosenblatt et al.

1972, Leis 1984), we draw on information summarized in Robertson and Allen (2002) from both primary sources and regional works on the shore-fish fauna of the TEP (Thompson et al. 1979, Rubio et al. 1992, Allen and Robertson 1994, Fischer et al. 1995, Bearez 1996, Grove and Lavenberg 1997, Garrison 2000); a checklist of fishes from the Hawaiian Islands (Mundy in press); unpublished data on Line Islands fishes (R. Pyle, pers. comm., 1996; B. C. Mundy, pers. comm., 2003); a checklist of Marquesan fishes (Randall and Earle 2000, and see Randall et al. 2003); and more general references for sharks (Compagno 1984*a,b*), clupeids (Whitehead 1985), lutjanids (Allen 1985), scombrids (Collette and Nauen 1983), and istiophorids (Nakamura 1985). In addition, D.R.R. has recorded shore fishes at the Hawaiian Islands (at various times between 1987 and 2003), Kiritimati (Christmas Island) in the Line Islands (1996), the Marquesas (1996, 1999, and 2003), and in the TEP: Clipperton (1994, 1998), Cocos (1992 and 1997), the Galápagos (1990, 1992), Malpelo (1992), the Revillagigedos (1991, 1994), Mexico (1990, 1998, 2002), most of the coast of Panama (many times between 1977 and 2003), and El Salvador (2000). J.S.G. has extensive diving experience in the Galápagos since 1975. J.E.M. has been involved in numerous ichthyological surveys (using scuba and submersibles to 1,000 m depth) since 1967 off Baja California, Costa Rica, Panama, Cocos Island, the Galápagos, and various island groups spread throughout Oceania and the West Pacific. A few records of transpacific fishes already known to occur in the TEP but not previously recorded in the Galápagos are included from work by J.E.M. (unpubl. data).

Sampling effort has been unevenly spread in areas of interest on both sides of the EPB. There now exists reasonably comprehensive information on the fishes of the continental shore of all countries and offshore islands in the TEP except for the Revillagigedos Islands and the continental shoreline between Colombia and northern Peru. In the central Pacific the fauna of the Hawaiian Islands is well characterized thanks to a long history of intensive research (Mundy in press). Less information is available on the fishes of the Line Islands, and what is known about the Marquesan fauna (Randall and Earle 2000) derives from a few short visits by ichthyologists to a few of those islands. Hence the lack of records at those two island groups of several widespread species of transpacific shore fishes found in adjacent parts of the central Pacific could well reflect inadequate sampling.

G tests of independence were used to compare the relative abundances of different types of species in the faunas of the TEP and the central Pacific.

RESULTS

Distributions of Transpacific Shore Fishes in the TEP and Elsewhere

Currently 126 species of transpacific shore fishes are known from the TEP, including 114 tropical species, 10 species with tropical to warm temperate distributions, and two species with largely warm temperate distributions. In addition there are 64 species of transpacific epipelagic oceanic fishes that enter nearshore waters. The distributions of transpacific species on both sides of the EPB and their general ecology are summarized in Table 1, with supplementary information on some species in Appendix 1.

The 126 shore-fish species include 22 elasmobranchs and 104 bony fishes. Three of the elasmobranchs and 28 of the bony fishes have resident populations on only one side of the EPB: three elasmobranchs and five bony fishes occur as vagrants on the western side of that barrier and 23 teleosts as vagrants on the eastern side (Table 1). Ten species of transpacific shore fishes are found in the West Pacific but not the central Pacific, and the remainder occur in both areas (Table 1). The 116 species found in both the central and eastern Pacific belong to 55.8% of 77 families of shore fishes present in both the TEP and central Pacific, 44.3% of 97 shore-fish families found in the central Pacific, and 38.7% of 111 families present in the TEP (Table 2).

TABLE 1

Tropical Transpacific Oceanic and Shore Fishes

			TEP Distribution[c]	TEP	
Family	Species[a]	Range outside TEP (H,L,M)[b]	Oceanic Islands/ Mainland	Residency[d]	Comments[e]
Hexanchidae	**Notorynchus cepedianus* (te)	Circumglobal, disjunct (–,–,–)	-/Calif—GofC, Col—Chile	Resident	DC
Rhincodontidae	*Rhincodon typus*	Circumtropical	All/all	Resident	Oceanic, PL
Carcharhinidae	**Carcharhinus albimarginatus*	Indo-C Pacific (?,–,+)	All/Baja—Ecuador	Resident	Semipelagic, MC/DC
	C. altimus (te/tr)	Circumtropical, disjunct (+,–,–)	Rev, Gal/Mex, CR—Peru	Resident	Isthmian relict, E to W migrant, DC, soft + hard
	**C. brachyurus* (te/tr)	Circumglobal, disjunct (–,–,–)	Rev/Calif—central Mex, Ecuador	Resident	Semipelagic, MC/DC
	C. falciformis	Circumtropical	All/GofC—Ecuador	Resident	Oceanic, MC
	**C. galapagensis*	Circumtropical, disjunct (+,–,–)	All/Baja—Peru	Resident	Semipelagic, DC/MC
	**C. leucas*	Circumtropical, disjunct (–,–,–)	Mal/Calif—Peru	Resident	Isthmian relict, soft + hard, DC
	**C. limbatus*	Circumtropical (+,–,+)	All/Calif—Peru	Resident	E to W migrant, semipelagic, MC/DC, soft + hard
	C. longimanus	Circumtropical	All/GofC—Ecuador	Resident	Oceanic, MC
	**C. obscurus* (tr/te)	Circumglobal, disjunct (?,–,–)	Rev/Calif—Mexico	Resident	Isthmian relict, semipelagic, DC/MC
	Galeocerdo cuvier	Circumtropical (R,+,+)	All?/Calif—Peru	Resident	Semipelagic, MC/DC
	Prionace glauca (tr/te)	Circumglobal	All?/Calif—Ecuador	Resident	Oceanic, MC
	**Triaenodon obesus*	Indo-C Pacific (R,R,R)	All but Clip/ Baja—Ecuador	Resident	DC, soft + hard
Sphyrnidae	**Sphyrna lewini* (tr/te)	Circumtropical (R,+,R)	All/Calif—Peru	Resident	Semioceanic, MC/DC
	**S. mokarran*	Circumtropical, disjunct (V,–,–)	Gal, Mal/Baja, GofC—Peru	Resident	Isthmian relict, E to W migrant, semioceanic, DC/MC
	**S. zygaena* (tr/te)	Circumsubtropical, disjunct (+,–,–)	Gal, Mal/Calif—Ecuador	Resident	Isthmian relict, E to W migrant, semioceanic, DC/MC
Odontaspidae	**Odontaspis ferox* (tr/te)	Circumglobal, disjunct (R?,–,–)	Mal/Calif—Baja	Resident	E to W migrant, soft + hard, DC
Alopiidae	*Alopias pelagicus*	Indo-C Pacific	Gal/CofC—Ecuador	Resident	Oceanic, MC
	A. superciliosus	Circumtropical	Gal/GofC—Ecuador	Resident	Oceanic, MC
	A. vulpinus (tr/te)	Circumglobal	-/Calif—GofC, Guatemala—Peru	Resident	Oceanic, MC

Lamnidae	*Isurus oxyrinchus*	Circumtropical	Gal/Calif—Peru	Resident	Oceanic, MC
Echinorhinidae	*Echinorhinus cookei* (te/tr)	W-C Pacific, disjunct (R,–,–)	Mal, Rev/All	Resident	E to W migrant, soft + hard, DC
Dasyatidae	**Dasyatis dipterura*	C Pacific (V,–,–)	Mal, Gal/All	Resident	E to W migrant, soft, DC
	Pteroplaytrygon violacea	Circumtropical	All?/All	Resident	Oceanic, MC
	**Taeniurua meyeni*	Indo-central Pacific (–,+,+)	Coc, Gal/-	Resident	Soft + hard, DC
Myliobatidae	*Aetobatus narinari*	Circumtropical (R,+,+)	All—Clip/Calif—Ecuador	Resident	Soft, benthopelagic, DC
	Manta birostris	Circumtropical (+,+,+)	All/Baja, GofC—Ecuador	Resident	Semipelagic, PL
	Mobula japanica	Circumtropical, disjunct (–,–,–)	-/Calif—Peru	Resident	Isthmian relict, semipelagic, PL
	M. tarapacana	Circumtropical	Coc/Baja—Peru	Resident	Oceanic, PL
	M. thurstoni	Circumtropical, disjunct (–,–,–)	-/GofC—Ecuador	Resident	Isthmian relict, semipelagic, PL
Anguillidae	*Anguilla marmorata*	Indo-C Pacific (–,+,+); effectively disjunct?	Galapagos/-	Vagrant	Adults freshwater/estuarine
Muraenidae	*Echidna nebulosa*	Indo-C Pacific (R,+,+)	Clip, Coc, Mal, Gal/Baja—Colombia	Resident	DC
	**Enchelychore lichenosa*	Japan/Taiwan, very disjunct (–,–,–)	Gal/-	Resident?	DC
	**Enchelynassa canina*	Indo-C Pacific (R,+,+)	Clip/Pan	Resident	DC
	Gymnomuraena zebra	Indo-C Pacific (R,+,+)	All/Baja—Ecuador	Resident	DC
	**Gymnothorax buroensis*	Indo-C Pacific (V,+,+)	Clip, Coc, Gal/CR—Pan	Resident	DC
	**G. flavimarginatus*	Indo-C Pacific (R,+,+)	All/Baja—Pan	Resident	DC
	**G. javanicus*	Indo-C Pacific (V?,+,R)	Coc, Gal/Pan	Vagrant	DC
	**G. meleagris*	Indo-C Pacific (R,+,+)	Coc, Gal/-	Vagrant	DC
	**G. pictus*	Indo-C Pacific (R,+,+)	All—Mal/CR—Pan	Resident	DC
	**G. undulatus*	Indo-C Pacific (R,+,–)	Rev/CR—Pan	Resident	DC
	Scuticaria tigrina	Indo-C Pacific (R,+,+)	All—Gal, Mal/Baja—Col	Resident	DC
	Uropterygius macrocephalus	Indo-C Pacific (+,+,+)	All—Mal/Baja—Peru	Resident	DC
	**U. supraforatus*	Indo-C Pacific (+,+,–)	Clip/-	Resident?	DC
Clupeidae	**Etrumeus teres* (tr/te)	Circumglobal, disjunct (R,–,–)	Gal/Calif—GofC, CR—Peru	Resident	Isthmian relict, E to W migrant, pelagic, PL
Chanidae	*Chanos chanos*	Indo-C Pacific, (R,R,+)	All—Rev/Calif—Ecuador	Resident	BH, semipelagic
Carapidae	**Encheliophis dubius*	C Pacific (V,–,–)	-/GofC—Ecuador	Resident	E to W migrant, Pa
	**Encheliophis vermicularis*	Indo-W Pacific, very disjunct (–,–,–)	Coc, Gal/GofC—Ecuador	Resident	Pa
Ophidiidae	**Brotula multibarbata*	Indo-C Pacific (R,+,+)	Clip/-	Vagrant?	DC
Antennariidae	**Antennarius coccineus*	Indo-C Pacific (–,+,+)	Clip, Coc/Mex—Pan	Resident	DC
	**A. commerson*	Indo-C Pacific (R,?,?)	Rev, Coc, Mal/Mex—Col	Resident?	DC

TABLE 1 (continued)

Family	Species[a]	Range outside TEP (H,L,M)[b]	TEP Distribution[c] Oceanic Islands/ Mainland	TEP Residency[d]	Comments[e]
Belonidae	_Ablennes hians_	Circumtropical (R,+,?)	Gal, Mal/Baja—Peru	Resident	Semioceanic, MC
	Tylosurus imperialis melanotus	Indo-C Pacific (+,+,+)	All—Coc/Pan—Col	Resident	Pelagic, MC
Exocoetidae	_Cheilopogon atrisignis_	Indo-C Pacific	Rev, Gal/-	Resident	Oceanic, PL
	C. dorsomacula	C Pacific	All?/-	Resident	Oceanic, PL
	C. furcatus	Indo-C Pacific	All except Mal/-	Resident	Oceanic, PL
	C. spilonotopterus	Circumtropical	All/-	Resident	Oceanic, PL
	Cypselurus angusticeps	W-C Pacific	Rev/-	Resident	Oceanic, PL
	Exocoetus monocirrhus	Indo-C Pacific	All/Baja—Peru	Resident	Oceanic, PL
	E. volitans	Circumtropical	All/-	Resident	Oceanic, PL
	Hirundichthys speculiger	Circumtropical	All/Baja—Ecuador	Resident	Oceanic, PL
	Oxyporhamphus m. micropterus	Indo-C Pacific	All/Baja—Peru	Resident	Oceanic, PL
	Parexocoetus b. brachypterus	Indo-C Pacific	-/Pan—Ecuador	Resident	Oceanic, PL
	Prognichthys seali	Indo-C Pacific	All/-	Resident	Oceanic, PL
	P. tringa	Pacific	Gal/GofC—Ecuador	Resident	Oceanic, PL
Hemirhamphidae	_Euleptorhamphus viridis_	Indo-C Pacific	All/Calif—Ecuador	Resident	Oceanic, PL
Holocentridae	*_Myripristis berndti_	Indo-C Pacific (R,R,R)	All/Baja, CR—Pan	Resident	PL
	*_Plectrypops lima_	Indo-C Pacific (R,?,+)	Rev, Clip, Coc/-	Vagrant?	DC
Syngnathidae	*_Doryrhamphus e. excisus_	Indo-C Pacific (R,R,R)	All—Rev/GofC—Ecuador	Resident	PL/DC
Aulostomidae	*_Aulostomus chinensis_	Indo-C Pacific (R,R,R)	All/Baja, Pan—Ecuador	Resident	DC
Fistulariidae	_Fistularia commersonii_	Indo-C Pacific (R,+,R)	All/GofC—Peru	Resident	DC
Scorpaenidae	*_Taenianotus triacanthus_	Indo-C Pacific (R,+,+)	Gala/-	Vagrant	DC
Priacanthidae	_Cookeolus japonicus_	Circumtropical (R,+,?)	Rev, Coc, Mal/Baja—Ecuador	Resident	PL/PC
	Heteropriacanthus cruentatus	Circumtropical (R,R,R)	All/Baja—Ecuador	Resident	MC/DC
	*_Priacanthus alalaua_	C Pacific (R,–,–)	Rev/Baja	Resident	E to W migrant, PL/MC

Malacanthidae	*Malacanthus brevirostris*	Indo-C Pacific (R,R,R)	Coc, Gal, Mal/CR—Ecuador	Resident	Soft, DC
Echeneididae	*Echeneis naucrates*	Circumtropical	All/Calif—Peru	Resident	Semioceanic, MC/PL
	Phtheirichthys lineatus	Circumtropical	All?/Calif—Peru	Resident	Oceanic, MC/PL
	Remora australis	Circumtropical	All/Calif—Peru	Resident	Oceanic, MC
	R. brachyptera	Circumtropical	All/Calif—Peru	Resident	Oceanic, MC
	R. osteochir	Circumtropical	All/Calif—Peru	Resident	Oceanic, MC
	R. remora	Circumtropical	All/Calif—Peru	Resident	Oceanic, MC
	Remorina albescens	Circumtropical	All/Calif—Peru	Resident	Oceanic, MC
Coryphaenidae	*Coryphaena equiselis*	Circumtropical	All/Baja—Peru	Resident	Oceanic, MC
	C. hippurus	Circumtropical	All/Calif—Peru	Resident	Oceanic, MC
Carangidae	*Alectis ciliaris*	Circumtropical (R,+,+)	Coc, Gal, Mal/GofC—Peru	Resident	Semipelagic, MC
	**Carangoides caballus*	C Pacific (+,−,−)	All/Calif—Ecuador	Resident	E to W migrant, semipelagic, MC/DC
	C. orthogrammus	Indo-C Pacific (R,+,R)	All/Mex	Resident	Semipelagic, MC
	**C. lugubris*	Circumtropical (R,R,R)	All/Baja—Pan	Resident	Semipelagic, MC
	**C. melampygus*	Indo-C Pacific (R,R,R)	All/Baja—Ecuador	Resident	Semipelagic, MC/DC
	**C. sexfasciatus*	Indo-C Pacific (R,R,R)	All/GofC—Ecuador	Resident	Semipelagic, MC
	Decapterus macarellus	Circumtropical (R,+,+)	All/Baja, CR	Resident	Pelagic, PL
	**D. macrosoma*	Indo-C Pacific (+,+,−)	-/GofC—Peru	Resident	Pelagic, PL
	**D. muroadsi* (tr/te)	Circumglobal, disjunct (+,−,−)	Rev, Gal/Calif—central Mex, Ecuador	Resident	Isthmian relict, E to W migrant, pelagic, PL
	**Elagatis bipinnulata*	Circumtropical (R,R,R)	All/Baja—Ecuador	Resident	Semioceanic, PL/MC
	Gnathanodon. speciosus	Indo-C Pacific (R,+,+)	Coc, Mal, Gal/GofC—Ecuador	Resident	Benthopelagic, adult—soft, DC
	Selar crumenophthalmus	Circumtropical (R,+,+)	All/GofC—Ecuador	Resident	Pelagic, PL
	**Seriola lalandi* (tr/te)	Circumglobal, disjunct (V,−,−)	Gal, Mal/Calif—GofC, CR—Peru	Resident	Isthmian relict, E to W migrant, antitropical, semipelagic, MC/DC
	**S. rivoliana*	Circumtropical (V,+,−)	All/Calif—Peru	Resident	Isthmian relict, E to W migrant, semipelagic, MC/DC
	**Trachurus murphyi* (te/tr)	SW-southCentral Pacific (−,−,−)	Mal, Gal/Ecuador—Peru	Resident	E to W migrant, pelagic, PL
	**Uraspis helvola*	Circumtropical, disjunct (+,−,+)	All—Clip/Pan	Resident	Isthmian relict, E to W migrant, pelagic, PL/PC
	Naucrates ductor	Circumtropical	All?/Calif—Peru	Resident	Oceanic, PC
Bramidae	*Brama dussumieri*	Circumtropical	Gal, Coc, Mal/Nicaragua—Peru	Resident	Oceanic, MC
	Taractes rubescens	W-C Pacific, Atlantic	Gal, Coc, Mal/Nicaragua—Peru	Resident	Oceanic, MC

TABLE 1 (continued)

			TEP Distribution[c]	TEP	
Family	Species[a]	Range outside TEP (H,L,M)[b]	Oceanic Islands/ Mainland	Residency[d]	Comments[e]
Lutjanidae	**Aphareus furca*	Indo-C Pacific (R,R,+)	Coc/-	Resident	MC
	Prisitpomoides zonatus	Indo-C Pacific (R,R,R)	Gal/-	Vagrant	DC/PL
Mullidae	**Mulloidichthys vanicolensis*	Indo-C Pacific (R,R,R)	Clip/Baja, Pan	Resident	Soft + hard, DC
Chaetodontidae	**Chaetodon auriga*	Indo-C Pacific (R,R,R)	Gal/-	Vagrant	BO
	**C. kleinii*	Indo-C Pacific (R,R,–)	Gal/-	Vagrant	BO
	**C. lunula*	Indo-C Pacific (R,R,R)	Coc, Gal/-	Vagrant	BO
	**C. meyeri*	Indo-C Pacific (–,R,–)	Rev, Gal/-	Vagrant	CO
	**C. unimaculatus*	Indo-C Pacific (R,R,R)	Gal/-	Vagrant	CO/BO
	**Forcipiger flavissimus*	Indo-C Pacific (R,R,R)	All—Coc/Baja—Ecuador	Resident	DC
Kyphosidae	**Sectator ocyurus*	W-C Pacific (V,–,R)	All/Baja, GofC—Peru	Resident	E to W migrant, semipelagic, PL
Kuhliidae	*Kuhlia mugil*	Indo-C Pacific (–,+,–)	All/Calif—Ecuador	Resident	Pelagic, PL
Cirrhitidae	**Cirrhitichthys oxycephalus*	Indo-C Pacific (–,R,R)	All/GofC—Ecuador	Resident	DC/PL
	**Oxycirrhites typus*	Indo-C Pacific (R,+,+)	Gal, Mal/Baja—Col	Resident	DC/PL
Mugilidae	**Mugil cephalus* (tr/te)	Circumglobal, disjunct (R,–,–)	Gal/All	Resident	Isthmian relict, E to W migrant, BD
Labridae	**Iniistius pavo*	Indo-C Pacific (R,?,+)	All—Clip/GofC – Col	Resident	Soft, PL/DC
	**Novaculichthys taeniourus*	Indo-C Pacific (R,R,R)	All/GoC—Col	Resident	Soft + hard, DC
	**Stethojulis bandanensis*	Pacific (–,R,–)	All/Baja, CR—Col	Resident	DC
	**Thalassoma purpureum*	Indo-C Pacific (R,R,R)	Clip, Coc, Gal/Pan	Resident	DC
Scaridae	**Calotomus carolinus*	Indo-C Pacific (R,R,R)	Rev, Gal/-	Resident	BH
	**Scarus ghobban*	Indo-C Pacific (–,R,–)	Coc, Gal, Mal/GofC—Ecuador	Resident	BH
	**S. rubroviolaceus*	Indo-C Pacific (R,R,R)	All/GofC—Ecuador	Resident	BH
Luvaridae	*Luvarus imperialis* (tr/te)	Circumglobal	All?/N & S fringes?	Resident	Oceanic, PL/MC
Zanclidae	*Zanclus cornutus*	Indo-C Pacific (R,R,R)	All/Baja—Peru	Resident	BO

Acanthuridae	**Acanthurus achilles*	W-C Pacific (R,R,R)	Clip/Baja	Vagrant	BH
	**A. nigricans*	Indo-C Pacific (R,R,R)	All/Baja, CR—Ecuador	Resident	BH
	**A. triostegus triostegus*	Indo-C Pacific (−,+,−)	All/Baja—Ecuador	Resident	BH
	**A. xanthopterus*	Indo-C Pacific (R,R,R)	All—Rev/Baja—Ecuador	Resident	Soft + hard, BH/BD
	**Ctenochaetus marginatus*	C Pacific (−,R,R)	All/CR—Col	Resident	BD
	**Naso annulatus*	Indo-C Pacific (R,+,+)	Clip, Coc/-	Vagrant	BH/PL
	**N. brevirostris*	Indo-C Pacific (R,R,+)	Gal/-	Vagrant	BH/PL
	**N. hexacanthus*	Indo-C Pacific (R,+,+)	Clip, Coc/-	Vagrant	BH/PL
	**N. lituratus*	Indo-C Pacific (R,R,R)	Clip/-	Vagrant	BH
	**N. vlamingii*	Indo-C Pacific (−,+,+)	Gal/-	Vagrant	BH/PL
Sphyraenidae	**Sphyraena barracuda*	Circumtropical (R,+,+)	Gal/Pan	Vagrant	Pelagic, MC
	**S. genie*	Indo-C Pacific (V,+,+)	Clip/central Mex, Pan—Col	Resident	Pelagic, MC
Gempylidae	*Gempylus serpens*	Circumtropical	All/Calif—Peru	Resident	Oceanic, MC
	Nealotus tripes	Circumtropical	All?/Baja—Peru	Resident	Oceanic, MC
	Ruvettus pretiosus	Circumtropical	Mal/Calif—Baja, Guat—Ecuador	Resident	Oceanic, MC
Trichiuridae	**Trichiurus lepturus*	Circumglobal, disjunct (−,−,−)	All—Clip, Coc/Calif—Peru	Resident	Semipelagic, isthmian relict, MC
Scombridae	*Acanthocybium solandri*	Circumtropical	All/Baja—Peru	Resident	Oceanic, CM
	Euthynnus affinis	Indo-C Pacific	Rev/-	Vagrant	Oceanic, MC
	Euthynnus lineatus	C Pacific (V,−,−)	All/Calif—Peru	Resident	Oceanic, E to W migrant, MC
	Katsuwonus pelamis	Circumtropical	All/Calif—Peru	Resident	Oceanic, MC
	Sarda orientalis	Indo-C Pacific	All—Clip/Baja—Peru	Resident	Oceanic, MC
	**Scomber australasicus* (te/tr)	Indo-C Pacific (+,−,−)	Rev/-	Resident	Pelagic, MC
	**S. japonicus* (te/tr)	Indo-W Pacific, very disjunct (?,−,−)	All—Clip, Coc/Cal—GofC, Pan—Peru	Resident	Pelagic, MC
	Thunnus alalunga (tr/te)	Circumglobal	-/Baja & Peru	Vagrant	Oceanic, MC
	T. albacares	Indo-C Pacific	All/Calif—Peru	Resident	Oceanic, MC
	T. obesus	Circumtropical	All/Calif—Peru	Resident	Oceanic, MC
Xiphiidae	*Istiophorus platypterus*	Indo-C Pacific	All?/Calif—Peru	Resident	Oceanic, MC
	Makaira indica	Indo-C Pacific	All?/Calif—Peru	Resident	Oceanic, MC
	M. mazara	Indo-C Pacific	All?/Calif—Peru	Resident	Oceanic, MC
	Tetrapterus angustirostris	Indo-C Pacific	All?/Calif—Peru	Resident	Oceanic, MC
	T. audax	Indo-C Pacific	All?/Calif—Peru	Resident	Oceanic, MC
	Xiphias gladius	Circumtropical	All?/Calif—Peru	Resident	Oceanic, MC

TABLE 1 (continued)

Family	Species[a]	Range outside TEP (H,L,M)[b]	TEP Distribution[c] Oceanic Islands/ Mainland	TEP Residency[d]	Comments[e]
Nomeidae	*Cubiceps pauciradiatus* (tr/te)	Circumglobal	All?/-	Resident	Oceanic, MC/PL
	Nomeus gronovii	Circumtropical	All?/Calif—Peru	Resident	Oceanic, MC/PL
	Psenes arafurensis	Circumtropical	All except Rev/CR—Peru	Resident	Oceanic, MC/PL
	P. cyanophrys (tr/te)	Circumglobal	Coc, Mal, Gal/CR—Ecuador	Resident	Oceanic, MC/PL
	P. pellucidus	Circumtropical	Gal, Mal/Ecuador—Peru	Resident	Oceanic, MC/PL
Bothidae	*Bothus mancus*	Indo-C Pacific (R,R,R)	All/Baja, western Pan	Resident	Soft + hard, DC
Balistidae	**Balistes polylepis*	C Pacific (+,–,V)	All/Calif—Peru	Resident	E to W migrant, DC
	**Canthidermis maculatus*	Circumtropical	All/central Mex—Peru	Resident	Semioceanic, PL
	**Melichthys niger*	Circumtropical (R,R,R)	All/Baja, GofC, CR—Col	Resident	PL/BO
	**M. vidua*	Indo-C Pacific (R,R,+)	All—Rev, Mal/western Pan	Resident?	PL/BO
	**Xanthichthys caeruleolineatus*	Indo-C Pacific (R,+,+)	Coc, Gal/-	Resident?	PL
	**X. mento* (antitropical)	W-C Pacific, disjunct (R,–,–)	All/Baja, central Mex, Col	Resident	E to W migrant, PL
Monacanthidae	**Aluterus monocerus*	Circumtropical (+,?,?)	All—Clip, Gal/Baja—Peru	Resident	BO
	A. scriptus	Circumtropical (R,R,+)	All/GofC—Ecuador	Resident	BO
	**Cantherhines dumerilii*	Indo-C Pacific (R,R,R)	All/CR—Col	Resident	CO/BO
Ostraciidae	**Ostracion meleagris meleagris*	Indo-C Pacific (–,R,R)	All/Baja – Col	Resident	BO
	**Lactoria diaphana*	Indo-C Pacific	All?/Baja—Peru?	Resident?	PL?
Tetraodontidae	*Arothron hispidus*	Indo-C Pacific (R,R,R)	All—Clip/Calif—Ecuador	Resident	Soft + hard, BO
	A. meleagris	Indo-C Pacific (R,R,R)	All/GofC—Ecuador	Resident	BO/CO
	**Canthigaster amboinensis*	Indo-C Pacific (R,+,R)	Gal/western Pan	Vagrant	BO
	**C. janthinoptera*	Indo-C Pacific (–,+,+)	Gal/-	Vagrant	BO
	**C. valentini*	Indo-C Pacific, disjunct (–,–,–)	Gal/-	Vagrant	BO

	Lagocephalus lagocephalus	Circumtropical	All?/Calif—Col	Resident	Semioceanic, PL
Diodontidae	**Chilomycterus reticulatus*	Circumtropical (R,V,V)	All—Clip/Calif—Peru	Resident	Isthmian relict, E to W migrant, DC
	**Cyclichthys spilostylus*	Indo-W Pacific, very disjunct (−,−,−)	Gal/-	Vagrant	DC
	**Diodon holocanthus*	Circumtropical (R,+,−)	All/Califa—Ecuador	Resident	DC
	D. hystrix	Circumtropical (R,+,R)	All/Calif—Peru	Resident	DC, soft + hard
	D. eydouxi	Circumtropical	All?/GofC—Col	Resident	DC, oceanic, MC
Molidae	*Mola mola* (tr/te)	Circumglobal	All?/Calif—Peru?	Resident	Oceanic, PL
	Ranzania laevis (tr/te)	Circumglobal	All?/Calif—Peru	Resident	Oceanic, PL

---

* See Appendix 1 for additional information on distribution.

[a] tr/te, tropical and temperate range; te, primarily temperate range; all others are tropical; Underlined species are oceanic epipelagics, remainder are shore fishes.

[b] (Nonoceanic species only) (H,L,M), (Hawaiian Islands, Line Islands, Marquesas Islands); −, apparently absent; ?, occurrence or limits thereof uncertain; V, vagrant; +, present, insufficient data on residency; R, apparent resident.

[c] (Shore fishes only) Oceanic islands: Rev, Revillagigedos; Clip, Clipperton; Coc, Cocos Island; Gal, Galápagos Archipelago; Mal, Malpelo; "All—a," species at all except specified island(s). Mainland: Calif, California; GofC, Gulf of California; Baj, west coast of Baja California peninsula, Mexico; Me, central to southern Mexico; CR, Costa Rica; Pan, Panama; Col, Colombia; "a—b" indicates limits of range.

[d] Resident and vagrant, see Materials and Methods.

[e] East to West migrant, occurrence on west side of EPB likely due to migration from TEP, remaining species likely migrated from central Pacific to TEP; isthmian relict, TEP population likely derived from Neotropical population divided by closure of Central American isthmus; demersal habitat usage: soft, lives primarily on soft bottoms; soft + hard, lives on soft and hard (reef) bottoms; all others restricted to hard bottom; semioceanic, offshore and inshore; diet: MC, midwater-feeding carnivore; DC, demersal-feeding carnivore; PL, planktivore; BH, benthic-feeding herbivore; BO, benthic-feeding omnivore; BD, benthic-feeding detritivore; Pa, parasitic; CO, corallivore.

TABLE 2

Numbers of Indigenous, Circumtropical and Transpacific Shallow-Water Shore Fishes per Family in the TEP, the Greater Caribbean*, and the Central Pacific

Family	TEP: Indigenous (Indo-Pacific/ circumtropical)	Caribbean Native (circumtropical)	Central Pacific: Total (Hawaiian, Line, Marquesas)	Characteristics Affecting Tropical Dispersal Potential[a]
Hexanchidae	- (-/1)	—	1 (H1)	Live birth, no pelagic phase, antitropical
Heterodontidae	3	—	—	Demersal egg, no pelagic phase
Ginglymostomidae	1	1	1	Live birth, no pelagic phase
Odontaspidae	- (-/1)	1	1 (H1)	Live birth, no pelagic phase, warm-temperate
Scyliorhinidae	1	—	—	Live birth, no pelagic phase
Triakidae	10	—	—	Live birth, semipelagic, mainly antitropical
Carcharhinidae	4 (2/7)	7 (8)	12 (H8, L5, M6)	Live birth, demersal to semipelagic
Sphyrnidae	3 (-/3)	3 (3)	3 (H3, L1, M1)	Live birth, semipelagic to pelagic
Echinorhinidae	- (1/-)	—	1 (H1)	Live birth, no pelagic phase, antitropical
Pristidae	1–2	2	—	Live birth, no pelagic phase, estuarine
Rhinobatidae	7	2	—	Live birth, no pelagic phase
Torpedinidae	1	1	—	Live birth, some semipelagic
Narcinidae	5	1	—	Live birth, no pelagic phase
Rajidae	5	8	—	Live birth, no pelagic phase
Urolophidae	10	2	—	Live birth, no pelagic phase
Dasyatidae	3 (1/-)	7	5 (H2, L1, M2)	Live birth, no pelagic phase, soft bottom; most demersal
Gymnuridae	2	2	—	Live birth, no pelagic phase, soft bottom
Myliobatidae	2 (-/4)	4 (2)	4 (H3, L2, M2)	Live birth, benthopelagic or pelagic
Elopidae	1	2	3 (H2, L1)	Benthopelagic
Megalopidae	—	1	1 (M1)	Benthopelagic
Albulidae	3	3	2 (H2, L1, M2)	Soft bottom
Anguillidae	- (1)	1	2 (L1, M1)	Estuarine, freshwater, marine larvae
Heterenchelyidae	1	1	—	Soft bottom
Moringuidae	1	2	3 (H1, L1, M2)	Soft bottom
Chlopsidae	3	5	5 (H3, L1, M2)	
Myrocongridae	1	—	—	
Muraenidae	15 (10/-)	28	>50 (H49, L26, M34)	Most reef, some soft bottom
Ophichthidae	37	52	40 (H21, L7, M14)	Most soft bottom
Congridae	12	18	8 (H6, L2, M2)	Soft bottom
Muraenesocidae	1	1	—	Soft bottom
Engraulidae	20	21	4 (H2)	Pelagic
Clupeidae	18 (-/1)	18 (1)	4 (H2, L1, M1)	Pelagic; TEP: demersal eggs; CP: pelagic eggs
Chanidae	- (1/-)	—	1 (H1, L1, M1)	Semipelagic
Ariidae	20	15	—	Brooded egg, no pelagic phase, soft bottom, many estuarine
Argentinidae	2	3	—	Benthopelagic
Synodontidae	5	8 (1)	17** (H15, L2, M4)	Soft bottom

TABLE 2 (continued)

Family	TEP: Indigenous (Indo-Pacific/ circumtropical)	Caribbean Native (circumtropical)	Central Pacific: Total (Hawaiian, Line, Marquesas)	Characteristics Affecting Tropical Dispersal Potential[a]
Carapidae	3 (2/-)	2	8** (H8, L4, M1)	Transpacifics demersal
Ophidiidae	18 (1/-)	27	2 (H2, L1, M1)	
Bythitidae	14	28	10 (H2, L1)	Live birth, pelagic larvae
Moridae	2	1	3 (H3)	Soft bottom
Batrachoididae	14	12	—	Demersal egg, no pelagic phase, soft bottom
Lophiidae	2	7	—	Soft bottom
Antennariidae	3 (2/-)	7	10 (H10, L1, M1)	
Ogcocephalidae	2	9	2 (H1, L2)	Reef and soft bottom
Gobiesocidae	31	20	1 (L1)	Demersal egg
Atherinidae	13	23	6 (H1)	Pelagic, demersal egg
Belonidae	6 (1/1)	5 (1)	5 (H4, L3, M3)	Pelagic, demersal egg
Hemirhamphidae	5	5	9 (H2, L4, M2)	Pelagic
Anomalopidae	1	1	2	
Holocentridae	4 (2/-)	11	29 (H19, L20, M15)	
Pegasidae	—	—	2** (H1, M1)	Soft bottom
Syngnathidae	5 (1/-)	24	25 (H10, L4, M4)	Live birth, some with pelagic young
Aulostomidae	- (1/-)	1	1 (H1, L1, M1)	
Fistulariidae	1 (1/-)	2	2 (H2, L2, M1)	Reef and soft bottom
Dactylopteridae	—	1	1 (H1, M1)	Soft bottom
Scorpaenidae	11 (1/-)	20	35 (H22, L12, M9)	Reef and soft bottom
Triglidae	10	18	1 (L1)	Soft bottom
Platycephalidae	—	—	5 (L2, M2)	Soft bottom
Centropomidae	6	5	—	Soft bottom, many estuarine
Serranidae	51	84+	83** (H17, L40, M16)	Some genera soft bottom
Pseudochromidae	—	—	5 (L1)	Demersal egg
Opistognathidae	12	17	—	Demersal egg, soft bottom
Priacanthidae	2 (1/1)	3 (1)	5 (H4, L2, M2)	
Apogonidae	6	21 (1)	52** (H10, L18, M14)	Brooded egg
Epigonidae	1	—	2 (H2)	Brooded egg?
Malacanthidae	3 (1/-)	10	5 (H1, L2, M1)	Soft bottom
Nematistiidae	1	—	—	Semipelagic
Carangidae	19 (5/9)	25 (6)	29 (H24, L12, M14)	Semipelagic to pelagic
Lutjanidae	10 (2/-)	14	15 (H11, L7, M9)	Transpacifics benthopelagic
Caesionidae	—	—	10 (L4, M2)	Benthopelagic
Lethrinidae	—	—	7 (H1, L7, M5)	Soft bottom
Lobotidae	1	- (1)	1 (H1)	Semipelagic
Gerreidae	11	12	3	Soft bottom, many estuarine
Haemulidae	35	23	5	Many soft bottom
Sparidae	3	19	—	Soft bottom
Polynemidae	2	3	3 (H1, M2)	Soft bottom
Sciaenidae	76	58	—	Many soft bottom, many estuarine
Mullidae	2 (1/-)	4	20 (H10, L10, M11)	Soft bottom but reef associated
Pempheridae	—	2	3 (L1, M1)	Benthopelagic
Chaetodontidae	3 (6/-)	7	41** (H22, L23, M14)	
Pomacanthidae	4	7	25 (H9, L9, M3)	
Kyphosidae	7 (1/-)	2	4 (H4, L2, M4)	Benthopelagic to pelagic
Scorpididae	—	—	1 (H1)	Antiequatorial
Kuhliidae	- (1/-)	—	5 (H2, L1, M1)	Pelagic
Cirrhitidae	1 (2/-)	1	17 (H6, L8, M6)	
Pomacentridae	19	17	72 (H17, L29, M22)	Demersal egg

TABLE 2 (continued)

Family	TEP: Indigenous (Indo-Pacific/ circumtropical)	Caribbean Native (circumtropical)	Central Pacific: Total (Hawaiian, Line, Marquesas)	Characteristics Affecting Tropical Dispersal Potential[a]
Mugilidae	5 (-/1)	7 (1)	10 (H2, L5, M5)	Benthopelagic
Labridae	26 (4/-)	31	103** (H44, L50, M30)	Reef and soft bottom
Scaridae	3 (3/-)	14	31 (H7, L19, M6)	
Pinguipedidae	—	—	7 (H1, L4, M1)	Soft bottom
Creediidae	—	—	4 (H2)	Soft bottom
Ammodytidae	1	—	3** (H1)	Soft bottom
Uranoscopidae	2	1	—	Soft bottom
Trypterygiidae	15	9	10 (H1, L3, M2)	Demersal egg
Dactyloscopidae	24	15	—	Soft bottom
Labrisomidae	36	45	—	Demersal egg or live birth + pelagic young
Chaenopsidae	34	52	—	Demersal egg
Blenniidae	12	15	62 (H13, L21, M16)	Demersal egg
Callionymidae	1	4	13** (H8, M3)	Soft bottom
Gobiidae	89	108	156** (H26, L27, M23)	Demersal egg, many soft bottom
Microdesmidae	14	8	5** (H3, L4, M5)	Demersal egg
Schindleridae	—	—	2 (H2)	Spawning mode unknown
Ephippididae	2	1	2	Reef and soft bottom
Siganidae	—	—	5 (L1, M1)	Demersal egg
Zanclidae	- (1/-)	—	1 (H1, L1, M1)	
Acanthuridae	2 (10/-)	3	41** (H25, L30, M21)	Mainly reef, some soft bottom
Sphyraenidae	4 (1/1)	3 (1)	5 (H3, L3, M4)	Pelagic
Trichuridae	- (-/1)	- (1)	—	Benthopelagic
Scombridae	4 (2/-)	6	1 (H1)	Pelagic
Stromateidae	3	3	—	Pelagic
Bothidae	4 (1/-)	14	8** (H8, L4, M3)	Soft bottom
Sammaridae	—	—	3 (H1, M1)	Soft bottom
Paralichthyidae	22	31	—	Soft bottom
Pleuronectidae	—	—	2 (H1, L2, M1)	Soft bottom
Achiridae	7	9	—	Soft bottom
Soleidae	1	—	7** (H3, L1, M1)	Soft bottom
Cynoglossidae	15	12	—	Soft bottom, deep-living in central Pacific
Balistidae	2 (4/2)	4 (2)	19 (H11, L13, M11)	Demersal egg
Monacanthidae	- (3/-)	8 (2)	17 (H8, L6, M4)	Demersal egg
Ostraciidae	- (1/-)	5	6 (H4, L2, M4)	
Tetraodontidae	9 (5/-)	10	21** (H13, L8, M6)	Demersal egg, reef and soft bottom
Diodontidae	- (1/3)	4 (2)	5 (H3, L1, M1)	

* Caribbean plus Gulf of Mexico, Bahamas, Florida, and Bermuda. Data on numbers of central Pacific species are from Springer (1982), except for families indicated by **.

** Numbers are increased due to new information from the Hawaiian, Line, or Marquesas Islands.

[a] Unless otherwise indicated members of the family are tropical, demersal, shallow-water reef fishes that produce pelagic eggs and pelagic larvae. Exceptions to this pattern: (1) no pelagic phase: live-bearing demersal fishes; (2) adults nondemersal (benthopelagic to pelagic); (3) adults use habitats other than shallow reefs: deep-living, demersal on soft bottoms, in estuaries and freshwater; (4) demersal/brooded eggs: species with benthic or parentally brooded eggs and pelagic larvae; (5) families predominantly contain non-tropical species: temperate, antitropical.

Transpacific Species with Endemic Subspecies in the TEP

Sardinops sagax: Genetic analyses (Grant and Bowen 1998) indicate that two antitropical populations in the eastern Pacific represent a single endemic subspecies (*S. sagax sagax*) of a single widespread Indo-Pacific species. *Platybelone argalus* and *Tylosurus crocodilus: P. argalus pterura* and *T. crocodilus fodiator* are TEP endemic subspecies of circumtropical inshore-pelagic species (Collette 1995). *Auxis rochei* and *A. thazard: A. rochei eudorax* and *A. thazard brachydorax* are TEP endemic subspecies of two circumtropical oceanic species (Collette and Aadland 1996). *Doryrhamphus excisus: D. e. paulus* is an endemic subspecies of an Indo-Pacific species that is restricted to the Revillagigedo Islands. The widespread Indo-Pacific subspecies, *D. e. excisus*, occurs throughout the remainder of the TEP (Dawson 1985).

Recent Erroneous and Questionable Records of Transpacific Species in the TEP

Carcharhinus amblyrhynchos: Photographs of sharks in the Galápagos that were thought to be this species are of melanistic individuals of *C. galapagensis* (see Grove and Lavenberg 1997; J. E. Randall, pers. comm., 1999). No specimens have been collected anywhere in the region. *Carcharhinus plumbeus:* Records of the possible occurrence of this species in the TEP, at the Revillagigedos and the Galápagos (Compagno 1984*b*), are not based on collected specimens. *Pristis* spp.: The systematics of *Pristis* are confused. Compagno and Cook (1995) briefly discussed the status of the TEP population of large-tooth sawfish, *P. zephyreus*, and suggested that it is synonymous with either the Atlantic species *P. perotetti* or *P. microdon* from the Indo-West Pacific. Because *Pristis* spp. are continental fishes found in estuaries and freshwater, and do not occur between the western and eastern continental margins of the Pacific, the TEP population most likely is an isthmian relict. Compagno and Cook (1995) also listed the circumtropical species *P. pectinata* from the TEP. However, records of that seem to be based entirely on saws of *P. pectinata* purchased at sites in the TEP (e.g., Acapulco), to which they may have been imported for the tourist trade. *Albula "vulpes":* From genetic evidence, Colborn et al. (2001) concluded that the TEP contains two endemic members of the *A. vulpes* species complex, whereas *A. neoguinaica*, the name previously used for the TEP population, refers to a West and central Pacific species, and *A. vulpes* is restricted to the Caribbean. *Gymnothorax eurostus*: J. E. Randall (pers. comm., 1998) identified as *G. buroensis* the specimen from Cocos Island on which the report of *G. eurostus* in the TEP by Randall and McCosker (1975) is based. *Gymnothorax panamensis*: Lavenberg (1992) described specimens from Easter Island identified by Randall and McCosker (1975) as *G. panamensis* as a new species, *G. australicola*, which does not occur in the TEP. *Gymnothorax rueppellii*: Grove and Lavenberg's (1997) report of this species from the Galápagos is an error that was resolved by McCosker and Rosenblatt (1975*b*). *Myrichthys maculosus*: The report of this Indo-West Pacific species in the TEP by Allen and Robertson (1994) refers to *M. tigrinus*, a TEP endemic (McCosker and Rosenblatt 1993, Fischer et al. 1995). *Scorpaenopsis diabolus*: Grove and Lavenberg's (1997) report of this Indo-central Pacific species from the Galápagos is based on the misidentification of a juvenile of the TEP endemic *Scorpaenodes xyris* (McCosker 1998). *Priacanthus meeki*: The record of this Hawaiian species from the Galápagos (Grove and Lavenberg 1997) is based on a single juvenile specimen of uncertain identity that Starnes (1988) said resembles *P. meeki*. *Lobotes surinamensis:* Allen and Robertson (1994) used this name for the TEP population, which also has been described as an endemic, *L. pacificus*. According to Springer (1982), *L. surinamensis* is an Indo-West Pacific and Atlantic species that has populations as far east as Fiji and is thought to occur as vagrants at Hawai'i and Tahiti. Because the taxonomy of this genus is uncertain (P. Heemstra, pers. comm., 1997), the identity of not only the TEP population but also the vagrants at Hawai'i and Tahiti needs clarification. We follow Heemstra (1995) and treat the TEP population as

TABLE 3

Amounts of Shallow Habitat[a] at the Oceanic Islands and the Continental Shore of the Tropical Eastern Pacific[b]

	Substrate <100 m deep			Substrate <200 m deep		
Location	km²	% of Island Total	% of TEP Total	km²	% of Island Total	% of TEP Total
Revillagigedos	158	3.0	0.08	222	2.1	0.08
Clipperton	7	0.1	<0.01	18	0.2	<0.01
Cocos	111	2.1	0.05	235	2.2	0.08
Malpelo	6	0.1	<0.01	12	0.1	<0.01
Galápagos	4,900	94.7	2.3	10,150	95.4	3.6
Continental shore	205,300	NA	97.5	270,700	NA	96.2
Total	~210,500			~281,500		

[a] Calculated from nine digitized medium-scale (1:~600,000) nautical charts spanning the continental portion of the region and the Galápagos, plus a smaller-scale chart (1:50,000) covering each of the remaining oceanic islands.

[b] Lower Baja California and the lower two-thirds of the Gulf of California to Cabo Blanco, northern Peru.

L. pacificus. *Cirrhitichthys serratus*: Specimens from the TEP reported as this species by Randall (1963) are *C. oxycephalus*, and *C. serratus* is a synonym of *C. falco* from the West Pacific (Randall 1997). *Pseudojuloides cerasinus*: Allen and Robertson's (1994) report of this species from Cocos Island in the TEP was based on the incorrect identification of an unidentified labrid that is not in that genus (Allen and Robertson 2002). *Pseudojuloides cerasinus* is not known from Cocos (W. Bussing, pers. comm., 1999) or elsewhere in the TEP.

DISCUSSION

Transpacific Fishes in the Faunas of Each Side of the EPB

Currently known transpacific species constitute ~12.5% of the 1,088 tropical shore fishes known from the TEP (Robertson and Allen 2002) and higher percentages of the shore-fish faunas of islands on the western side of the EPB: 19.7% of the Hawaiian fauna, 14.7% of that of the Line Islands, and 20% of that of the Marquesas Islands (Table 2). According to Leis (1984), ~7% of the TEP shore-fish fauna consists of endemics that are derived from Indo-central Pacific species that migrated eastward after the rise of the isthmus of Panama; if correct, that figure indicates that ~20% of the TEP shore fishes have recent Indo-central Pacific origins.

All shore-fish habitat in the central Pacific consists of oceanic islands, which are spread over an enormous area. In contrast there are few such islands in the TEP. The overwhelming majority of shore-fish habitat in the TEP consists of continental shoreline and a few clusters of continental islands, mainly at Panama and the Gulf of California (Table 3). It was first thought that eastward-migrant transpacific fishes are largely restricted to the oceanic islands in the TEP (Briggs 1961, 1964). However, Rosenblatt et al. (1972) showed that the inshore islands of western Panama support many such species and that nearly half of them are widely distributed in the TEP. The distributions of the 80 eastward migrants discussed here follow the pattern described by Rosenblatt et al. (1972): 30% are widely distributed on the mainland and the oceanic islands. However, almost half the species are limited exclusively (32.5%) or largely (16.3%) to those islands and small parts of the mainland (Table 4). Further, only a fifth of those species are primarily continental, and only one (*Decapterus macrosoma*) is known solely from the continental shore. Because oceanic islands provide such a tiny proportion (~2.5%, Table 3) of the shore-fish habitat in the TEP, they are disproportionately much more important, in terms of the abundance of transpacific species per unit area, as habitat for transpacific immigrants than is the mainland. All five oceanic islands

TABLE 4

Occurrence of Putative Eastward-Migrant Tropical Transpacific Shore Fishes[a] at the Offshore Oceanic Islands[b] and Mainland of the TEP

	% of Species Found at				
Transpacifics	Islands Only	Mainly at Islands[c]	Islands + Mainland[d]	Mostly Mainland[e]	Mainland Only
Residents in TEP (57)	10.5	22.8	36.0	28.1	1.8
Vagrants in TEP (23)	87.0	0	13.0	0	0
Total (80)	32.5	16.3	30.0	20.0	1.3

[a] Tropical species listed in Table 1.

[b] The Revillagigedos, Clipperton, Cocos, Malpelo, and the Galápagos.

[c] Present at most of the islands and only a limited part of the mainland; with notably dense populations at one or more islands.

[d] Present at most of the islands and much of the mainland or a few islands and a limited part of the mainland; not notably more abundant at islands.

[e] Present at most of the mainland and few islands.

in the TEP host many eastward-migrant transpacific shore fishes: 60 (including 12 vagrants) at the Galápagos, 51 (5 vagrants) at Cocos, 46 (5 vagrants) at Clipperton, 39 (1 vagrant) at the Revillagigedos, and 35 at Malpelo. Those transpacific species are much more important components of the oceanic-island fauna than they are in the continental fauna (Table 5). Although the Galápagos contain 95% of the oceanic-island habitat for shore fishes in the TEP (Table 3) and may be in the best position to receive migrants on the main eastbound currents, they support fewer eastward migrants than the other islands together (60 versus 78). Further, the Galápagos host a resident population of only one transpacific species (*Enchelychore lichenosa*) found nowhere else in the TEP, but then so do Clipperton (*Uropterygius supraforatus*), Cocos (*Aphareus furca*), and the Revillagigedos (*Scomber australasicus*). Thus tiny oceanic islands that provide <0.1% of the shore-fish habitat in the TEP (Table 3) are of major regional importance for eastward-migrant shore fishes.

TABLE 5

Relative Importance of Transpacific Species in the Shore-Fish Faunas of Oceanic Islands and the Continental Shore in the TEP

Island	No. species	% Transpacifics	% Eastward Migrants[a]
Revillagigedos	176	38.6	22.7
Clipperton	102	60.8	45.1
Cocos	235	32.3	21.7
Malpelo	213	29.1	16.4
Galápagos	349	26.6	16.9
Combined islands	510	23.9	14.9
Mainland	971	10.3	5.4

[a] From Table 6.

Transpacifics in the TEP Shore Biota: Fishes versus Other Groups

For shore fishes, eastward migrants constitute ~7% of the TEP fauna. Similarly low levels occur in most groups of invertebrates: the TEP molluscan and crustacean faunas each contain <5% transpacific species (Garth 1974, Shasky 1985, Paulay 1997). Ekman (1953) noted the paucity of transpacific echinoderms (~2% of 240 Indo-central Pacific species [see also Lessios et al. 1996]). In strong contrast, 95% of the TEP coral fauna is the result of recent eastward migration: ~75% of 41 zooxanthellate corals in the TEP likely are such transpacific species (Glynn and Ault 2000) and <5% of the TEP coral fauna appears to be derived from isthmian relicts. The rarity of coral reefs in the TEP (only ~25 km^2), the small regional coral fauna, and the importance of transpacific species in that fauna reflect postisthmian extinction of the native coral fauna and destruction of reefs by a variety of environmental stresses (Glynn and Ault 2000). Such stresses, to which reef fishes may be relatively resistant (see Mora and Ospina 2001, Nilsson and Ostlund-Nilsson 2004), evidently had much less effect on the TEP's reef fishes: the latter include over 300 regional endemics, and eastward migrants represent only ~15% of the region's resident reef fishes. If Leis' (1984) estimate that ~7% of the endemic TEP shore fishes are derived from past eastward transpacific migration is correct, then ~85% of the shore-fish fauna of the region (tropical and temperate species combined) is derived from taxa present before the rise of the isthmus.

Among the 31 transpacific corals, 38.7% are known only or mainly from the mainland, 38.7% are well represented on both the oceanic islands and the mainland, and 22.6% are entirely or largely restricted to the oceanic islands, which provide ~4% of the region's habitat suitable for coral reef development (Glynn and Ault 2000). Most of the transpacific mollusks also are most common at the oceanic islands of the TEP (Paulay 1997). Thus, the few small oceanic islands in the TEP are disproportionately important as supporters of transpacific species of a range of major taxa.

Eastward versus Westward Migration by Shore Fishes across the EPB

Early studies of transpacific shore fishes emphasized eastward migration (Briggs 1961, Hubbs and Rosenblatt 1961, Rosenblatt and Walker 1963, Rosenblatt et al. 1972), and Briggs (1961, 1974, 2003) asserted that there was no evidence of any westward dispersal. Rosenblatt et al. (1972) concurred in general with this conclusion, but they noted one probable westward migration, by *Sectator ocyurus* to the Hawaiian and Society Islands. Later, Jokiel (1984) found evidence of westward dispersal of TEP corals by rafting. Rosenblatt and Waples (1986) maintained that connections between the TEP and the Hawaiian populations of 10 transpacific fish species indicated by their genetic data are eastward and indirect, with another central Pacific site acting as a stepping-stone. Briggs (1961, 1999*a,b*, and see Mora et al. 2003) proposed that eastward dispersal is more likely because it reflects dispersal from the Indo-Malayan center of diversity and speciation to more depauperate areas such as the TEP. Rosenblatt et al. (1972) thought that dispersal across the EPB predominantly should be eastward because of adverse effects of low temperatures in the higher-latitude westbound currents on tropical organisms. However, Scheltema (1988) found larvae of tropical shore invertebrates in westbound currents, which he noted have surface temperatures experienced by organisms in the TEP. Vermeij (1991) stated that all trans-EPB invasions are eastward, even though westward currents can support immigration. Here we address the issue of directions of migration across the EPB by shore fishes.

EASTWARD MIGRANTS. There are 80 shore-fish species whose current distributions and, in several cases, genetic evidence (see section on Genetic Studies later in Discussion) indicate that they likely migrated to the TEP from the central or western Pacific (Table 6). Those include 73 widespread Indo-Pacific species and one widespread circumtropical species (*Heteropriacanthus cruentatus*) found at the western edge of the EPB. Three of the remainder also occur at the western edge of the EPB: two from the central and western Pacific (*Stethojulis bandanensis* and *Acanthurus achilles*) and one (*Ctenochaetus marginatus*) from the central Pacific. Three other eastward migrants (*Encheliophis vermicularis*, *Cyclichthys spilostylus*, and *Scomber japonicus*) are entirely absent from the central Pacific, and another (*Canthigaster valentini*) occurs in the central Pacific but ~2,000 km west of the western edge of the EPB.

Among the 57 eastward migrants that have resident populations in the TEP, 54 are present at one or more of the Hawaiian, Line, and Marquesas Islands, 42 of them at all three sites (Table 6). Ten are absent from the Hawaiian fauna (three others occur there only as vagrants), 10 are absent from the Marquesas, and only one (*Carcharhinus albimarginatus*, a large, readily recognizable shallow-water reef shark) almost certainly does not occur at the Line Islands. The apparent absences of four others from the Line Islands may reflect inadequate sampling. Twenty-three species of

TABLE 6

Occurrence of Supposed Eastward-Migrant[a] Tropical Transpacific Shore Fishes at Hawai'i, Johnston Island, the Line Islands, and the Marquesas Islands

Family	Transpacific Species	Hawaiian Is.	Johnston I.	Line Is.	Marquesas Is.
Carcharhinidae	*Carcharhinus albimarginatus*	Vagrant?	No	No	+
	Triaenodon obesus	+	+	+	+
Dasyatidae	*Taeniura meyeni*	No	No	+	+
Anguillidae	*Anguilla marmorata*	No	No	+	+
Muraenidae	*Echidna nebulosa*	+	+	+	+
	Enchelynassa canina	+	No	+	+
	Gymnomuraena zebra	+	+	+	+
	Gymnothorax buroensis	Vagrant	+	+	+
	G. flavimarginatus	+	+	+	+
	G. javanicus	+	+	+	+
	G. meleagris	+	+	+	+
	G. pictus	+	+	+	+
	G. undulatus	+	+	+	No
	Scuticaria tigrina	+	+	+	+
	Uropterygius macrocephalus	+	+	+	+
	U. supraforatus	+	+	+	No
Chanidae	*Chanos chanos*	+	No	+	+
Carapidae	*Encheliophis vermicularis*	No	No	No	No
Ophidiidae	*Brotula multibarbata*	+	+	+	+
Antennariidae	*Antennarius coccineus*	No	No	+	+
	A. commerson	+	No	?	No
Belonidae	*Tylosurus imperialis melanotus*	+	No	+	+
Holocentridae	*Myripristis berndti*	+	+	+	+
	Plectrypops lima	+	+	?	+
Syngnathidae	*Doryrhamphus excisus excisus*	+	+	+	+
Fistulariidae	*Fistularia commersonii*	+	+	+	+
Aulostomidae	*Aulostomus chinensis*	+	+	+	+
Scorpaenidae	*Taenianotus triacanthus*	+	No	+	+
Priacanthidae	*Heteropriacanthus cruentatus*[b]	+	+	+	+
Malacanthidae	*Malacanthus brevirostris*	+	+	+	+
Carangidae	*C. orthogrammus*	+	+	+	+
	Caranx melampygus	+	+	+	+
	C. sexfasciatus	+	+	+	+
	Decapterus macrosoma	+	No	+	No
	Gnathanodon speciosus	+	No	+	+
Lutjanidae	*Aphareus furca*	+	+	+	+
	Pristipomoides zonatus	+	+	?	+
Mullidae	*Mulloidichthys vanicolensis*	+	+	+	+
Chaetodontidae	*Chaetodon auriga*	+	+	+	+
	C. kleinii	+	No	+	No
	C. lunula	+	+	+	+
	C. meyeri	No	No	+	No
	C. unimaculatus	+	+	+	+
	Forcipiger flavissimus	+	+	+	+
Kuhliidae	*Kuhlia mugil*	No	No	+	No
Cirrhitidae	*Cirrhitichthys oxycephalus*	No	No	+	+
	Oxycirrhites typus	+	No	+	+
Labridae	*Iniistius pavo*	+	+	?	+
	Novaculichthys taeniourus	+	+	+	+
	Stethojulis bandanensis	No	No	+	No
	Thalassoma purpureum	+	+	+	+
Scaridae	*Calotomus carolinus*	+	+	+	+
	Scarus ghobban	No	No	+	No
	S. rubroviolaceus	+	+	+	+
Zanclidae	*Zanclus cornutus*	+	+	+	+

TABLE 6 (continued)

Family	Transpacific Species	Hawaiian Is.	Johnston I.	Line Is.	Marquesas Is.
Acanthuridae	*Acanthurus achilles*	+	+	+	+
	A. nigricans	+	+	+	+
	A. triostegus triostegus	No (different subspecies)	No (different subspecies)	+	No (different subspecies)
	A. xanthopterus	+	No	+	+
	Ctenochaetus marginatus	No	+	+	+
	Naso annulatus	+	+	+	+
	N. brevirostris	+	+	+	+
	N. hexacanthus	+	+	+	+
	N. lituratus	+	+	+	+
	N. vlamingii	No	No	+	No
Sphyraenidae	*Sphyraena barracuda*	+	+	+	+
	S. qenie	Vagrant	No	+	+
Scombridae	*Scomber australasicus*	+	No	No	No
	Scomber japonicus	No	No	No	No
Bothidae	*Bothus mancus*	+	+	+	+
Balistidae	*M. vidua*	+	+	+	+
	Xanthichthys caeruleolineatus	+	No	+	+
Monacanthidae	*Cantherhines dumerilii*	+	+	+	+
Ostraciidae	*Ostracion meleagris meleagris*	No (different subspecies)	No (different subspecies)	+	+
Tetraodontidae	*Arothron hispidus*	+	+	+	+
	A. meleagris	+	+	+	+
	Canthigaster amboinensis	+	No	+	+
	C. janthinoptera	No	No	+	+
	C. valentini	No	No	No	No
Diodontidae	*C. spilostylus*	No	No	No	No
Total	80	59 (+3 vagrants)	49	70 (+4?)	64

[a] Species other than those labeled as circumtropical or westward migrants in Table 1.

[b] Circumtropical, but see text on this species.

transpacific species (Table 6) that are vagrants in the TEP must be very recent eastward migrants. Twelve of them occur at the Hawaiian, Line, and Marquesan Islands and two at none of those islands. One (*Chaetodon meyeri*) occurs only at the Line Islands, and the apparent absence of one of those species from the Lines may be a sampling artifact. Four do not occur in the Hawaiian Islands and three are absent from the Marquesas. Thus there are more occurrences at the Line Islands than at either the Hawaiian or Marquesas Islands, and there is only one major absence from the Lines (*C. albimarginatus*, which is also absent from Hawai'i). This pattern is generally consistent with eastward migrants being transported from the Line Islands on the only major eastbound warm surface current that flows across the EPB, the North Equatorial Counter Current (NECC). The few eastward migrants not found at any of the islands at the western edge of the EPB occur farther west in the path of the NECC. The only notable inconsistency with this pattern that is not readily attributable to a sampling artifact is the distribution of *C. albimarginatus*. The two *Scomber* species are basically temperate species, only one of which (*S. australasicus*) occurs at Hawai'i. Both could have taken the same route eastward from Japan, on extensions of the cool Kuroshio Current that reach to Baja California.

Four of the 80 species (*Heteropriacanthus cruentatus*, *Fistularia commersonii*, *Plectrypops lima*, and *Bothus mancus*) that we include as eastward immigrants are widely distributed in the Indo-central Pacific and have Atlantic sister species with similar morphology and ecology. Thus their TEP populations could represent either isthmian relicts that have remained connected to Indo-central Pacific populations or recent (postisthmus) eastward immigrants. *Heteropriacanthus cruentatus* currently is recognized as a circumtropical species in a monotypic genus. The genus *Plectrypops* includes only *P. lima* and *P. retrospinnis* (tropical Northwest Atlantic). The fact that *P. lima* has only been recorded three times in the TEP suggests that it is a vagrant there and hence an eastward migrant. *Fistularia commersonii* has an Atlantic sister, *F. tabacaria*. If Fritsche's (1976) scenario is correct, the TEP population of *F. commersonii* is an isthmian relict. *Bothus mancus* has a West Atlantic look-alike congener, *B. lunulatus*, that, like *B. mancus*, lives in reef environments. There is no information bearing on the origin of the TEP population of *B. mancus*. Vermeij and Rosenberg (1993) noted that tropical marine invaders often have limited distributions in areas they invade and occur at offshore islands or small sections of the available mainland. The distribution of *B. mancus* in the TEP fits this scenario. Although gene flow evidently occurs between TEP and central Pacific populations of *H. cruentatus* (see section on Genetic Studies later in Discussion), the origin of its TEP population remains unclear. No genetic studies have been done on the other three genera that would clarify the origins of their TEP populations.

WESTWARD MIGRANTS. The distributions of 22 shore-fish species and one oceanic species, supplemented in one case by genetic data, indicate that they are or may well be westward migrants (Table 1). The only central Pacific area at which 16 of them are known are the Hawaiian Islands: 10 shore-fish species as likely Hawaiian residents (*Carcharhinus altimus*, *Sphyrna zygaena*, *Echinorhinus cookei*, *Odontaspis ferox*, *Etrumeus teres*, *Mugil cephalus*, *Priacanthus alalaua*, *Carangoides caballus*, *Decapterus muroadsi*, *Uraspis helvola*) and five shore-fish species (*Sphyrna mokarran*, *Dasyatis dipterura*, *Encheliophis dubius*, *Seriola lalandi*, and *Seriola rivoliana*) and one oceanic species (*Euthynnus lineatus*) as vagrants. Six species are present at Hawai'i and the Marquesas (or nearby islands) but not in the remainder of the central Pacific: *Carcharhinus limbatus* and *Sphyrna lewini* (residents at both sites), *Sectator ocyurus* (resident at the Marquesas and a vagrant on the equator west of the Line Islands), *Balistes polylepis* (vagrant at both sites), *Xanthichthys mento* as a resident of Hawai'i and islands south of the Marquesas, and *Chilomycterus reticulatus* as a resident in Hawai'i and a vagrant at the Marquesas, Line, and other islands. The case for westward migration from the TEP is strongest for 11 species that are residents of the TEP and occur only at central Pacific sites at the western side of the EPB, particularly as vagrants. However, the other 12 species have populations in the West Pacific that may have provided central Pacific migrants or those central Pacific populations may be remnants of a once more-continuous population. Hawai'i, for example, has connections with the Japanese fauna, mediated by dispersal on the eastward-flowing Kuroshio Current to the NW Hawaiian Islands (e.g., Fritsche 1976, Mundy in press). If the TEP form of *Ostracion meleagris* is shown to be the subspecies currently thought to be endemic to Hawai'i (see Appendix 1), the number of westward-migrant shore fishes would increase to 23 and decrease the number of eastward migrants to 79. If vagrants of *Lobotes* from Hawai'i and French Polynesia prove to be *L. pacificus* (see section on Recent Erroneous and Questionable Records in Results), the number of westward migrants would increase to 24.

Transpacific Species with Highly Disjunct Pacific Distributions

Twelve species of transpacific shore fishes occur in the TEP and the West Pacific but nowhere in between (Table 1). TEP populations of seven of those, all circumtropical species, likely represent isthmian relicts (see next section) that lack ongoing contact across the Pacific. The remaining five most probably are not isthmian relicts and we attribute their occurrence in the TEP to ongoing or recent eastward migration: Two of those five (*Cyclichthys spilostylus* and *Canthigaster valentini*) occur in the TEP as vagrants and two others that either have (*Encheliophis vermicularis*) or may have (*Enchelychore lichenosa*) resident populations in the TEP lack Atlantic look-alike sister species. Genetic data on the fifth, *S. japonicus* (see under Shore Fishes in Genetic Studies later in Discussion), indicate that it arrived in the eastern Pacific well after the rise of the isthmus. *Canthigaster valentini* and *C. spilostylus* evidently have long-lived pelagic larvae or juveniles able to migrate 9,000–11,000 km to the TEP. The range of *S. japonicus* is primarily temperate (Grant and Bowen 1998), and its pelagic adults likely made the migration between Japan and the eastern Pacific on extensions of the Kuroshio Current that span the northern Pacific and extend to off Baja California. There is no information on the pelagic larval durations of carapids, although they do have large larvae and a pelagic juvenile stage that has been collected far beyond adult ranges (Markle and Olney 1990). Hence, whether ongoing connections occur between western and eastern populations of *E. vermicularis* is an open question; they may represent currently disjunct populations of a previously more widespread species. The situation is unclear for *E. lichenosa*. It is a resident in the NW Pacific, around Taiwan and Japan, but has an uncertain population status in the Galápagos, where specimens have been collected over 28 yr (see Appendix 1). If it is resident in both areas those populations could represent disjunct survivors of a previously more widespread species. However, moray eels are thought to generally have pelagic larval durations on the order of many months (see later in Discussion under What Types of Fishes Are Transpacifics?), and it is conceivable that ongoing pelagic dispersal across the entire Pacific could lead to the repeated arrival of vagrants of *E. lichenosa* in the Galápagos. This could be accomplished by two main surface routes: first, extensions of the cool Kuroshio Current could carry larvae eastward to Baja California (cf. the situation with *Scomber*), which then make their way south to the Galápagos. Alternatively, propagules could make their way south from Taiwan to the eastern Philippines, the origin of the main eastward equatorial currents flowing to the TEP, the Equatorial Undercurrent (EUC) and the North Equatorial Counter Current (NECC) (cf. *Anguilla*, see later in this section). There are difficulties with both those routes, which are roughly similar in distance (~16,000 km). The Kuroshio Current is a cool one, and larvae carried by it to Baja would have to move south 30° of latitude through a region dominated by westward-flowing currents and lacking major southerly currents. On the second route the main surface oceanic flow across the 12° of latitude separating the Philippines and Taiwan is counter to the direction larvae would need to move to get to the eastbound equatorial flow. Another substantial problem for the ongoing-dispersal scenario is why such activity has not resulted in records of this species at any of the many sites scattered along either route between the NW Pacific and the Galápagos. Hence, currently it seems more likely that the Galápagos harbor a relict population of *E. lichenosa*. Although *Anguilla marmoratus* occurs in the central Pacific, including islands on the western edge of the EPB, it probably effectively has a disjunct distribution, because its only known Pacific spawning grounds lie immediately east of the Philippines and of Papua (Arai et al. 2002). The NECC and EUC both originate near the northern spawning ground and to reach the TEP from there larvae of this species, which have very long pelagic larval durations (Table 9), would have to travel ~15,000 km. The eastbound current originating around the southern spawning area (the South Equatorial Counter Current [SECC]) likely only delivers larvae to the central Pacific (see section on Transport Potential later in Discussion).

Transpacific Fishes as Isthmian Relicts in the TEP

The best candidates for transpacific species whose TEP populations represent isthmian relicts are circumtropical species that have disjunct Pacific distributions, Atlantic geminates, and are likely westward migrants. Twenty of the 39 circumglobal shore fishes have disjunct Pacific distributions and either are absent from the central Pacific (*Carcharhi-*

nus brachyurus, *C. leucas*, *C. obscurus*, *Sphryna mokkaran*, *Notorynchus cepedianus*, *Mobula japanica*, *Mobula thurstoni*, and *Trichiurus lepturus*) or may be westward migrants to there (*Carcharinus altimus*, *C. limbatus*, *Sphyrna zygaena*, *Odontaspis ferox*, *Echinorhinus cookei*, *Etrumeus teres*, *Mugil cephalus*, *Decapterus muroadsi*, *Seriola lalandi*, *S. rivoliana*, and *Uraspis helvola*) (Table 1). *Chilomycterus reticulatus* also falls into the latter group as a resident of Hawai'i and a vagrant in the rest of the central Pacific. However, its large pelagic juvenile may also have allowed long-distance eastward migration from the West Pacific similar to that by its confamilial *Cyclichthys spilostylus*. One "circumtropical" species (*Sphyraena barracuda*) is a vagrant in the TEP and hence not an isthmian relict. The broad Pacific distributions of another 18 circumglobal species provide no clues to the status of their TEP populations, which may be clarified by genetic data (e.g., *Heteropriacanthus cruentatus*, see under Genetic Studies later in Discussion).

Ocean Current Systems and Migration across the EPB

TRANSPORT POTENTIAL OF EASTWARD AND WESTWARD CURRENTS. Because tropical shore-fish larvae seem to be restricted to the upper 100 m, and probably much shallower levels (Leis and McCormick 2002), surface and shallow subsurface currents are those most relevant to trans-EPB migration. Information on such currents in the EPB is derived from published analyses plus post-1993 satellite data (see http://www.oscar.noaa.gov). There are two eastbound currents in the central part of the EPB: the NECC, a warm, surface current that flows between ~5° and 10° N and carries about 30% of the eastward flow, and the EUC, a narrow (~2° of latitude wide), cool, subsurface current flowing along the equator that gradually shoals as it progresses eastward. The EUC carries 70% of the eastward flow (Wyrtki 1967) and is about twice as fast as the NECC (Wyrtki 1965, 1967, Firing and Lukas 1983, Chavez et al. 1999). Surface eastward flow through the central Pacific also occurs on the SECC. In the central Pacific this current is narrow (~1° wide) and slow, with flows wandering between ~8 and 17° S to the Marquesas (7–10° S). The SECC seems to have little influence in the EPB, although it may extend east to the longitude of the Galápagos but well south of those islands (Eldin 1983, and see http://www.oscar.noaa.gov). Westbound currents include the North Equatorial Current (NEC) and South Equatorial Current (SEC). Divergence associated with a thin band of upwelling from the EUC along the equator cuts the flow of the SEC into two sections, to the north and south of that band, with stronger flow on the northern arm. Although the SEC extends down to at least 17° S, its strongest flow is above 8° S. The NEC is notably slower than the SEC, and the speed of the northern arm of the SEC is similar to that of the NECC. Flows of the NEC and SEC are weaker at higher latitudes and stronger on the western side of the EPB than on the eastern side.

These trans-EPB current systems are dynamic, changing seasonally and in relation to the El Niño/Southern Oscillation (ENSO) cycle, as well as over periods of decades (Chavez et al. 2003). Seasonal changes include more vigorous surface flow in both directions in the second half of the year, when the NECC extends eastward into the TEP (early in the year it terminates well to the west). Current flows during the two extremes of the ENSO cycle (El Niño and La Niña) differ as follows: During El Niños eastward flow is greatly enhanced and westward flow reduced, particularly during the latter three-fourths of the year. The speed of the NECC can double, and during a strong El Niño, the transit time for a water mass across the EPB can be cut from a normal ~100–155 days to ~50–80 days (Wyrtki et al. 1981, Firing et al. 1983, Wyrtki 1985, Richmond 1990). During a strong El Niño the latitudinal spread of the NECC also increases southward, to ~5° S, and eastward flow replaces the usual westward flow by the northern arm of the SEC. In addition, during a strong El Niño the EUC (and its associated upwelling) can disappear (Firing et al. 1983, Chavez et al. 1999). During a La Niña, westward flow of the SEC strengthens, as does flow of the EUC and the upwelling above it (Chavez et al. 1999). The increase in eastward flow was greater during the intense 1997–1998 El Niño than during the weaker 2002–2003 event, the increase in flow of the SEC during the 1999 La Niña was less than that of the NECC during the 1997–1998 El Niño, and there was little change in the NEC during either type of event (http://www.oscar.noaa.gov). The 1999 La Niña was much weaker than six other La Niñas that occurred between 1950 and 1990 (http://www.cdc.noaa.gov/ENSO/enso.mei_index.html). Satellite data on currents are available only since 1993 (http://www.oscar.noaa.gov), so it is unclear what effect strong La Niñas have on westward flow.

Oceanographic and biologic conditions vary greatly in different parts of the EPB that contain the major currents and the islands on each side of that barrier, to the extent that Longhurst (1998) included different latitudinal zones of the barrier in four separate pelagic biogeographic provinces. A thin band (<5° of latitude wide) of cool upwelling from the EUC that extends west from the Galápagos along the equator across most of the EPB produces an overlying strip of increased productivity (http://seawifs.gsfc.nasa.gov/SEAWIFS/IMAGES/SEAWIFS_GALLERY.html, Chavez and Smith 1995, Chavez et al. 1999). The level of productivity in that upwelling band, although higher than in areas to the north and south, is much lower than that of productivity resulting from coastal upwelling, due to iron limitation (Chavez and Smith 1995, Longhurst 1998). Productivity in the EPB declines with increasing latitude away from the equatorial upwelling band. In addition there are two zones of notably low productivity in the northern part of the EPB, one along the center of the NECC and the other, which is very low, spanning half or more (depending on the season) of the area between the Hawaiian Islands and the TEP. Thus productivity is higher in the SEC than in most of the NEC and very low in the entire zone occupied by the greatly expanded NECC during an intense El Niño. The NECC is a warm, surface current, but the EUC is cool for tropical organisms (15–20°C at its center, at ~100 m depth), although warmer near the surface. Temperatures are cooler in both the NEC and the SEC than in the NECC, although (see Scheltema 1988) they are suitable for tropical organisms. However, because the northern arm of the SEC is fed partly by warm water from the equatorial TEP and the southern arm by flow from the cold Peru current, the southern arm is distinctly cooler (at ~22°C near the southern Galápagos) than the northern arm when it leaves the TEP during the season of peak flow.

Whether currents carry pelagic propagules of shore organisms across the EPB depends not only on transit times and the duration of the larval life (and the ability of larvae to extend their pelagic lives) but also on conditions within the currents for larval sustainment. How might variation in conditions in east- and westbound currents affect all these aspects of transit potential for fish propagules? In most accounts eastward migration is assumed to occur on the NECC (e.g., Rosenblatt et al. 1972, Briggs 1974, Scheltema 1988, Vermeij 1991), although the EUC route has also been considered (e.g., Grigg and Hey 1992, Clarke 1995). Under non–El Niño conditions the EUC could deliver a propagule to the TEP in about half the time it would take via the NECC. The limited information available on depth distributions of tropical shore-fish larvae (Leis and McCormick 2002) suggests that they remain above 100 m depth and often much shallower. Although shallow larvae could take advantage of warmer, higher productivity conditions above the core of the EUC, they would do so away from the high speed of the cold core in a zone where they could be advected into the westbound SEC, to the north and south of the upwelling strip. Thus eastward transport on the EUC seems problematic. More information on the depth distributions of shore-fish propagules should indicate whether it is a realistic possibility. The SECC likely is irrelevant for eastward migration to the TEP; it is very slow and whatever propagules of tropical species it picked up from the Marquesas would be carried to an unsuitable, temperate area of the eastern Pacific. Rather, it may act more as a hindrance to the Marquesas receiving propagules from the TEP on the SEC. For westbound transits the combination of higher speeds and productivity in the SEC than in the NEC suggests that potential for transits should be higher in the SEC. During a La Niña, a transit from the Galápagos to the southern Line Islands on the faster northern arm of the SEC likely would be shorter than one to the Marquesas on the slower southern arm of that current, despite the substantially greater distance of the former route (see Figure 1). Westward migration from the equatorial section of the TEP to the Line Islands, which has not been considered previously, is a realistic possibility given that westward migration does occur to both Hawai'i and the Marquesas in current systems that seem less conducive to such events.

POTENTIAL EFFECTS OF EL NIÑOS ON TRANS-EPB MIGRATION. El Niños are thought to enhance migration of tropical shore fishes and other organisms across the EPB to the TEP, largely due to the doubling in the velocity of the NECC during such events (e.g., Richmond 1990, Leis 1991, Grigg and Hey 1992). This increased flow rate should increase the number of potential migrants to include species with moderate pelagic larval durations, and the tripling of the latitudinal spread of that current should mean that more propagules can be drawn from a larger area of reefs. However, conditions in the center of the EPB change during strong El Niños in ways that may limit eastward dispersal. First, during an El Niño the equatorial productivity produced at other times by upwelling from the EUC (Chavez et al. 1999) is nearly eliminated. Second, during El Niños the surge of water moving eastward across the EPB has temperatures 2–3°C above normal. The development and growth of pelagic larvae of tropical reef fishes is strongly temperature dependent (McCormick and Molony 1995, Leis and McCormick 2002), with faster-growing individuals having shorter pelagic larval durations (Wellington and Victor 1992). The age at metamorphosis of fishes decreases with increasing temperature (Benoit et al. 2000) and tropical reef-fish larvae have increased growth rates and decreased pelagic larval durations at higher temperatures (McCormick and Molony 1995, Wilson and Meekan 2002, Meekan et al. 2003). Further, marine fishes tend to produce smaller eggs at higher temperatures (e.g., Chambers 1997, Kokita 2003). It is unclear how long the larvae of tropical fishes can delay settlement after achieving competency. Although some widely distributed taxa (including acanthurids, labrids, and flatfishes) can do so, extensive delays may not be the rule (McCormick 1994, Leis and McCormick 2002). Further, <1% of individuals surviving to settlement may have extended larval durations (Leis and McCormick 2002), and such extension may reduce subsequent survival (McCormick 1999). Thus, although eastward transit times may be halved during strong El Niños, that enhanced transit potential may be offset by reduced larval provisioning in the egg, low food availability in the eastbound flow, and "premature" achievement of settlement potential. A direct test of this scenario may not be feasible, but comparison of variation in egg content and pelagic larval durations of reef fishes under normal and El Niño conditions at the likely origin of eastbound propagules (the Line Islands) could act as a partial proxy; partial because conditions for larval development around an island differ from those in the middle of the EPB.

Based on observations of vagrant transpacific fishes in the TEP around the time of an El Niño event, it has been proposed that transpacific recruitment to the TEP is enhanced by such events (Grove 1984, 1986, Robertson and Allen 1996, Glynn and Ault 2000). What evidence is there of El Niño-enhanced migration across the EPB? Widespread observations on reef fishes in the TEP only began ~25 yr ago. Since then there have been two intense El Niños (1982–1983 and 1997–1998), plus several weaker events (1987, 1991–1995, 2003). There are few records of the precise timing of appearances of transpacific shore fishes on either side of the EPB relative to those events.

Arrivals of transpacific species in the TEP: El Niño related? The dates of the first record of each of 10 species in the TEP are relevant to this question. Two arrivals are associated with El Niño events: *Anguilla marmorata*: McCosker et al. (2003) estimated that the individual of this vagrant freshwater eel they examined arrived in the Galápagos in 1993 (i.e., in the center of a 5-yr period of sustained El Niño conditions [see http://www.cdc.noaa.gov/ENSO/enso.mei_index.html]). *Brotula multibarbata*: The first record for this species in the TEP consists of two small juveniles collected by D.R.R. at Clipperton in March 1998, at the end of the 1997–1998 El Niño. This is the best record of an El Niño–associated arrival in the TEP. However, other records do not clearly demonstrate such associations: *Uropterygius supraforatus*: The first specimens of this species were taken at Clipperton by D.R.R. in March 1998; however, because they included both adults and juveniles it is unlikely that this species first arrived during the 1997–1998 El Niño. *Chaetodon auriga* and *C. lunula*: Individuals of these species were first observed in the TEP in the northern Galápagos in mid-1987 (Merlen 1988); however lack of size data makes it unclear whether they arrived during the 1987 El Niño. *Chaetodon kleinii:* The first record of this species in the TEP was by J.S.G. in the Galápagos in mid-1984 (Grove 1986) (i.e., more than a year after the 1982–1983 El Niño had finished). Three other individuals were observed at other sites in the Galápagos in 1988. *Canthigaster amboinensis*: A single medium-sized adult was collected in the northern Galápagos in February 1967, a year after the 1965–1966 El Niño. *Canthigaster janthinoptera*: A single individual of this species was found in the Galápagos in mid-1984, over a year after the 1982–1983 El Niño. *Canthigaster valentini*: Two individuals of this species were found in different parts of the Galápagos, in late 1983 and late 1984. The earlier record could represent an El Niño–mediated arrival. *Naso vlamingii*: A small adult of this species was photographed in the Galápagos in 1990 (Robertson and Allen 2002), several years after an El Niño.

Arrivals at Hawai'i: El Niño related? Mundy (in press) suggested that changes in the abundance of two carangids in Hawai'i have resulted from El Niño–enhanced westward migration. First, *Carangoides caballus*, which was first collected in Hawai'i early in the twentieth century (Fowler 1928), became very abundant there at the end of the 1997–1998 ENSO (Randall and Carlson 1999), but within several years was no longer being caught by fishers (B. C. Mundy, pers. comm., 2003). Second, records of vagrant adult *Seriola lalandi* at the southern Hawaiian islands are during El Niño years (Mundy in press).

Effects of El Niños on intraregional distributions. Rather than being due to El Niño–enhanced migration across the EPB, local increases in abundances of transpacific species on either side of the EPB could arise through other mechanisms. El Niño–related environmental changes strongly affect the fish faunas of peripheral parts of the TEP, with the Galápagos providing the best documented example. These islands are at the junction of the temperate Peruvian province and the TEP, and have both a strong north/south gradient and strong seasonal variation in environmental conditions and local faunal composition (Rosenblatt and Walker 1963, McCosker et al. 1978). In the Galápagos during El Niños there are both declines of local endemics and increases in the abundance of species widely distributed in the TEP, including both regional endemics and transpacific species (Grove 1984, 1986, Ruttenberg 2000, Victor et al. 2001). Similar changes in resident transpacific populations have occurred at the northern edge of the TEP (Victor et al. 2001). Dramatic environmental changes that occur in the TEP during El Niños evidently affect both larval and adult survivorship and produce local changes in abundances and shifts in distributions by established residents within a region. Thus, rather than being due to enhanced trans-EPB migration, local increases in transpacific species during El Niños could be due to either (a) environmental changes that favor short-term population increases of usually uncommon resident transpacific species, or (b) species whose propagules transit across the EPB at other stages of the ENSO cycle as well as El Niños experiencing conditions favorable for their development to adulthood at the arrival point only during an El Niño.

Interpretation of new records of vagrant transpacific species in a region immediately after El Niños as evidence of enhanced trans-EPB migration needs to be treated with caution for another reason. The intense 1982–1983 El Niño produced large changes in many TEP reef environments, particularly at the Galápagos, which have large areas of temperate habitat (Glynn and Ault 2000). That was the first El Niño during which large-scale changes in oceanographic conditions and current flows in the central and eastern Pacific were revealed by satellite data. This event stimulated a heightened awareness of the impact of El Niños that has undoubtedly affected the effort expended in looking for changes in fish populations (e.g., Victor et al. 2001) and for "new" arrivals. The intensity of scuba diving in the Galápagos and elsewhere in the TEP also greatly increased beginning shortly before the 1982–1983 El Niño and continues to do so. As a result divers are more likely to expect immigrants during El Niños and interpret increases in the abundance of transpacific species during them to enhanced trans-EPB migration.

In conclusion, contrary to previous impressions (e.g., Grigg and Hey 1992, Glynn and Ault 2000) equivocal evidence suggests at most a limited enhancement of migration by shore fishes in both directions across the EPB during seven El Niños since 1982–1983, a period when the frequency and intensity of those events has been increasing. Given that El Niños typically recur at 2- to 7-yr intervals and last for 1–5 yr, some sightings of vagrant immigrants are bound to be associated with such events by chance alone. Even though some vagrants may well have arrived during El Niños, there is no evidence of a large influx of immigrants of any species leading to the establishment of a "new" transpacific population in the TEP during a period that included the two most intense El Niños (1982–1983 and 1997–1998) of the past century. The 1997–1998 event is particularly informative because ample prior warning of its occurrence undoubtedly led to increased surveillance of its effects in the TEP. Thus the long-term impact of such events on the composition of the TEP shore-fish fauna remains unclear. Until more is known about the "background" level of immigration it will be hard to determine the effect El Niños may have on trans-EPB immigration of new faunal elements and thus on long-term changes in regional faunas. If only about 50–60 eastward migrants have established themselves in the TEP so recently that they retain specific continuity with central Pacific populations, then influxes of central Pacific species in sufficient numbers to establish a new resident population in the TEP must occur very infrequently.

What Types of Fishes Are Transpacifics?

TAXONOMIC BIASES. Previous authors noted strong taxonomic biases in the representation of different families of Indo-central Pacific fishes among transpacifics (e.g., Rosenblatt et al. 1972, Leis 1984). However, when those papers were written comprehensive lists of the shore fishes of the central Pacific and the three island groups at the western edge of the EPB were not available. New information makes such a compilation possible (see Table 2). Three families (Carcharhinidae, Muraenidae, and Carangidae) that are well represented in the TEP and central Pacific faunas, including the faunas of the Hawaiian, Line, and Marquesas Islands, contribute many transpacific species, and transpacifics represent major proportions of the members of those families in the faunas on both sides of the EPB. In contrast, other families that have many species in the central Pacific and Hawaiian, Line, and Marquesan faunas lack transpacific representatives, most notably Ophichthidae, Scorpaenidae, Serranidae, Apogonidae, Pomacanthidae, Pomacentridae, Blenniidae, and Gobiidae. Most of those families also have substantial numbers of species in the TEP (Table 2). In further contrast, all five families in one order (Tetraodontiformes: Balistidae, Monacanthidae, Ostraciidae, Tetraodontidae, and Diodontidae) that have relatively few species on each side of the EPB also are well represented among the transpacifics. Thus these additional data strengthen previous conclusions of strong taxonomic biases in the representation of different potential "donor" families in the

TABLE 7

Representation of Different Fishes in the Transpacific and Indigenous Faunas of the TEP Fauna and of Transpacifics in Each Part of the TEP Fauna

Fish Type	% of Transpacifics Represented by	% of Indigenous Fauna Represented by	Transpacifics as % of Each Group in Total TEP Fauna
Oceanic epipelagic	33.7	0.1	98.4
Inshore pelagic	19.5	9.5	26.1
Inshore demersal	47.9	90.4	9.7
n	190	949	1,139

transpacific fauna: the occurrence of transpacific species in different families is largely unrelated to family richness on either side of the EPB.

Although much of this pattern of biases is real, some part may represent sampling artifacts. Members of two genera (*Chaetodon* and *Naso*) include a substantial number of the transpacifics recorded as vagrants in the TEP. These fishes are large, diurnally active, conspicuous, and readily recognizable as different from indigenous TEP species. Vagrant individuals of those and various other taxa are likely to be readily noticed on eastern Pacific reefs and offshore islands frequented by scuba divers. In contrast, other families for which no transpacifics are known have characteristics that greatly reduce the likelihood that any vagrants present in the TEP or the central Pacific would be recorded. For example synodontids are cryptic soft-bottom fishes that look very similar to one another. Ophichthids and scorpaenids are cryptic, sedentary fishes and most of the former burrow within soft bottoms. In other cases different species on each side of the EPB resemble one another closely enough that migrants from one side of the EPB might well pass unrecognized on the other side (e.g., species of *Kyphosus*, which often associate with flotsam [e.g., Hunter and Mitchell 1966] and are good candidates to be such migrants, look much the same worldwide). *Mulloidichthys vanicolensis* and *M. dentatus* are so similar, morphologically, that the unsuspected penetration of the former into the TEP has only been revealed by genetic analyses (see section on Genetic Studies later in the Discussion).

PELAGIC DISPERSAL POTENTIAL: TRANSPACIFIC SPECIES VERSUS NONTRANSPACIFICS. Distances across the EPB are vast (4,500–7,000 km) and minimal transit times under the best of conditions are on the order of a couple of months. Rosenblatt et al. (1972) pointed out that transpacific fishes generally belong to taxa that have either pelagic adults or pelagic larvae that likely are relatively long-lived. Leis (1984) extended this analysis and found that, although transpacific species do generally have long-lived larvae many families that have similar larvae lack transpacifics. To assess how variation in dispersal characteristics may have shaped the structure of the transpacific fauna we compared such characteristics of the transpacific fauna and the nontranspacific faunas on both sides of the EPB.

Effects of different pelagic life-history stages. The representation of different fishes in the transpacific fauna and different segments of the TEP fauna relates strongly to the degree to which their adults are pelagic (Table 7). At one extreme, oceanic epipelagic species represent <1% of the indigenous TEP fauna but almost one-third of the transpacific fauna and almost all the oceanic species in the TEP fauna. In contrast, demersal shore fishes represent 90% of the indigenous TEP fauna and about half the transpacific fauna, but only ~10% of demersal species in the TEP are transpacifics. Inshore pelagic species are intermediate between these two extremes. Hence, the pelagic habits of adults enhance

TABLE 8

Occurrence of Different Pelagic Life-History Phases among Transpacific and Nontranspacific Shore Fishes

	% of Fauna[a] Represented by Each Group			
Dispersal Characteristics	Transpacifics[b]	Indigenous TEP	Indigenous Central Pacific	TEP + Central Pacific
No pelagic phase	3.3	8.4	1.3	4.5
Demersal adult and egg[c], pelagic larva	11.6	33.9	37.1	35.7
Demersal adult, pelagic egg and larva	52.1	44.9	58.7	52.6
Pelagic adult, no pelagic larva	10.7	2.4	0.5	1.4
Pelagic adult, demersal egg, pelagic larva	1.7	4.0	0.9	2.2
Pelagic adult, egg, and larva	20.7	6.4	2.0	3.6
n	121	949	1,194	2,143

[a] Faunal data from Table 2.

[b] Excludes transisthmian relicts not occurring in the central Pacific.

[c] Includes species with brooded eggs and live bearers.

their long-distance dispersal capabilities and increase their representation in the transpacific fauna and their section of the TEP fauna.

The vast majority of tropical reef teleosts have pelagic larvae, which are released from either pelagic eggs (most species) or demersal (including brooded) eggs (Leis and Carson-Ewart 2000). In the TEP, ~94% of the shore fishes have pelagic larvae and 61% of such species produce them from pelagic eggs (Robertson and Allen 2002). Indo-Pacific reef fishes that produce pelagic larvae from demersal eggs tend to have smaller geographic ranges than do pelagic spawners (Thresher and Brothers 1985, Thresher 1991, Pyle 1999, Hughes et al. 2002, Jones et al. 2002). Demersal spawners may have a reduced dispersal ability due to their larvae (1) tending to remain inshore (while those of pelagic spawners often develop offshore) (Leis 1986, Brogan 1994), and (2) having short pelagic larval durations (Thresher and Brothers 1985, 1989, Thresher 1991). Although most analyses of zoogeographic patterns of tropical fishes in relation to dispersal modes have focused on contrasts between demersal- and pelagic-spawning teleosts that produce pelagic larvae, Pyle (1999) included species that lack any pelagic life-history phase in his analysis of the distributions of shore fishes in Oceania. He found the largest ranges to be among pelagic-spawning teleosts but no difference between the range sizes of demersal spawners and species that lack a pelagic phase. Because all of the latter are elasmobranchs he suggested that the more ancient origins of elasmobranchs had effectively "compensated" for the lack of a pelagic dispersal phase by giving them more time to enlarge their ranges. Regardless of the causes of this pattern, his study demonstrates the need to include entire faunas in such analyses. We made an entire-fauna comparison of the reproductive and dispersal modes of the transpacific fauna and nontranspacific fauna of the fringes of the EPB (i.e., the three central Pacific island groups plus the TEP). There are strong differences between the structure of those two faunas (Table 8: G test, $G = 14.3$, $P < 0.001$): relative to their abundance in the nontranspacific fauna (1) demersal species with demersal eggs and pelagic larvae are strongly underrepresented; (2) demersal species with pelagic eggs and larvae are neutrally weighted (in terms of their proportional abundance); (3) species with pelagic adults (including types with and without pelagic eggs and larvae) are strongly overrepresented; (4) species that lack a pelagic stage and pelagic species that have demersal eggs and pelagic larvae are about neutrally weighted (sample sizes for these two groups are very small). As with Pyle's (1999) comparison, there is a strong phylogenetic component to these patterns—all demersal transpacific species that lack a pelagic stage or that have pelagic adults but not pelagic larvae are elasmobranchs, and all species that have pelagic larvae are teleosts. Among teleosts, having pelagic adults has a strong additive effect over having only pelagic eggs and larvae: the ratio of the abundances of the former in the transpacific versus the nontranspacific fauna is much higher than the ratio for demersal species with pelagic eggs and larvae (Table 8: 5.8:1 versus <1:1). The ratio of the relative abundance of transpacifics to nontranspacifics among species in which all three stages are pelagic (Table 8: teleosts, 5.8:1) is less than the ratio among species with pelagic adults but not larvae (elasmobranchs, 7.8:1). Thus having a pelagic adult provides a dispersal advantage for both teleosts and elasmobranches, but teleosts that have pelagic larvae and adults do not have a greater achieved dispersal than elasmobranchs with pelagic adults. These patterns extend Pyle's (1999) finding by indicating that elasmobranchs have achieved greater dispersal than teleosts despite the latter having additional dispersive life-history stages. That difference could be due to the time available for dispersal (as mediated by the age of a species), as Pyle suggested, and/or to biological attributes of elasmobranchs (e.g., large size and mobility of adults and greater ability for adults to survive in offshore waters).

Differences in reproductive mode generally are family specific, and families of teleosts vary greatly in their contribution to the faunas on both sides of the EPB and the transpacific fauna. Thus assessment of the effect of egg type on dispersal using total numbers of species with each spawning mode is confounded by a phylogenetic effect. To control for that effect on dispersal potential among demersal shore fishes that produce pelagic larvae from the two types of eggs, we compared the proportions of demersal-spawning and pelagic-spawning families found on both sides of the EPB that have transpacific representatives (see Table 2). The difference, 0.21 of 17 versus 0.34 of 62, is in the same direction as that involving total numbers of species in Table 8 but is not significant (G test of independence: $G = 1.8$, ns). Tetraodontiform fishes, which produce demersal eggs (balistids, monacanthids, and tetraodontids) or pelagic eggs (ostraciids and diodontids), have a pelagic juvenile stage capable of an extended pelagic existence and long-distance dispersal. All five tetraodontiform families are well represented among the transpacifics (Table 1). Among nontetraodontiform teleosts there is a clear difference between pelagic- and demersal-spawning families in terms of representation in the transpacific fauna: 0.0 of 14 demersal-spawning families versus 0.32 of 60 pelagic-spawning families, $G = 4.72$, $P < 0.01$). Thus dispersal-related larval attributes associated with egg type do affect which families are represented in the transpacific fauna.

Larval dispersal characteristics of transpacific species versus other teleosts. Leis (1984) pointed out that certain speciose families of pelagic-spawning Indo-central Pacific fishes (chaetodontids, pomacanthids, mullids, synodontids, and scorpaenids) that were not then known to have transpacific representatives probably have pelagic larval durations and larval dispersal capabilities broadly similar to those of families that do. Newer analyses are consistent with that finding: Hughes et al.'s (2002) analysis of distribution patterns of Indo-Pacific reef fishes showed that five families of pelagic spawners (acanthurids, chaetodontids, holocentrids, lutjanids, and serranids) have proportionately more widespread species than expected, and that two others (pomacanthids and lethrinids) are neutrally weighted in this characteristic. Such patterns indicate that members of those 10 families have good powers of larval dispersal relative to other reef-fish families. However, although all 10 families have many species in the Line Island fauna (Table 2), only five of them have eastward-migrant transpacifics, and those mostly occur in the TEP as vagrants.

Leis (1984) was obliged to rely on informed guesstimates of the pelagic larval durations of transpacific fishes; figures he gave ranged from <1 to >6 months (for moray eels), with most ~2 months. The greatly increased availability of otolith-based data on pelagic larval durations (Table 9) allows us to

TABLE 9

Pelagic Larval Durations of Transpacific Fishes, Members of Genera of Nontranspacifics Present at the Line Islands, and Species of Shore Fishes Endemic to the TEP

Group	Family	Species	Range in Pelagic Larval Duration (days)	
Transpacifics at Line Islands	Anguillidae	*Anguilla marmorata*	145–160	
	Chanidae	*Chanos chanos*	14–29	
	Mugilidae	*Mugil cephalus*	29–67	
	Aulostomidae	*Aulostomus chinensis*	71–106	
	Chaetodontidae	*Chaetodon auriga*	40–53	
		Chaetodon kleinii	56	
		Forcipiger flavissimus	41–57	
	Cirrhitidae	*Cirrhitichthys oxycephalus*	36–45 (mean 39)	
	Labridae	*Novaculichthys taeniourus*	44–74	
		Iniistius pavo	42–77	
		Stethojulis bandanensis	22–44 (mean 29)	
		Thalassoma purpureum	50–62	
	Scombridae	*Scomber australasicus* and *S. japonicus*	21–28	
	Acanthuridae	*Acanthurus triostegus triostegus*	44–60	
		Naso brevirostris	80–120	
		Naso hexacanthus	82–111	
	Tetraodontidae	*Canthigaster valentini*	64–113 [found west of the Line Is.]	
			Range in maximum PLD	
Nontranspacifics (Indo-central Pacific)		Genus	Any species [*n*]	Species at Line Islands [with data/total present]
	Serranidae	*Epinephelus*	39–50 [4]	39–41 [2/15]
	Apogonidae	*Apogon*	<30 [11]	- [-/13]
	Lutjanidae	*Lutjanus*	25–62 [5]	62 [1/7]
	Caesionidae	*Caesio*	41 [1]	- [-/2]
		Pterocaesio	32–47 [2]	- [-/2]
	Lethrinidae	*Lethrinus*	30–37 [6]	30 [1/4]
	Mullidae	*Eupeneus*	37 [1]	- [-/1]
		Mulloidichthys	65 [1]	65 [1/3]
		Parupeneus	44–50 [3]	44–50 [3/5]
	Chaetodontidae	*Chaetodon*	20–90 [17]	30–54 [5/22]
		Heniochus	44 [1]	44 [1/1]
	Pomacanthidae	*Centropyge*	27–39 [11]	28–34 [3/5]
		Pomacanthus	<30 [6]	<30 [1/1]
	Pomacentridae	*Abudefduf, Chrysiptera, Dascyllus, Lepidozygous, Pomacentrus*	<30 [4,7,4,1,17]	<30 [1/4,2/2,1/3,1/1,2/3]
		Chromis	24–46 [17]	24–46 [5/9]
		Plectroglyphidodon	28–33 [4]	28–33 [2/5]
		Stegastes	23–35 [4]	24–32 [3/5]
	Labridae	*Anampses*	28–52 [2]	38 [1/4]
		Bodianus	23–78 [4]	<30 [1/5]
		Cheilinus	26–60 [8]	26–42 [3/4]
		Cirrhilabrus	<30 [1]	- [-/1]
		Coris	25–54 [5]	52–53 [2/3]
		Cymolutes	91 [1]	91 [1/1]
		Epibulus	38 [1]	38 [1/1]
		Gomphosus	72 [1]	72 [1/1]
		Halichoeres	22–56 [14]	22–56 [3/8]
		Hemigymnus	29–34 [2]	34 [1/1]
		Labroides	24–38 [4]	24–26 [2/3]
		Macropharyngodon	30–43 [3]	36 [1/1]

TABLE 9 (continued)

Group	Family	Genus	Range in Maximum PLD	
			Any species [*n*]	Species at Line Islands [with data/total present]
		Pseudocheilinus	46–72 [4]	46–55 [2/2]
		Pseudojuloides	52 [1]	52 [1/1]
		Thalassoma	55–121 [8]	55–99 [5/7]
	Scaridae	*Chlorurus*	40 [1]	40 [1/3]
		Scarus	45 [1]	- [-/12]
	Blenniidae	*Petroscirtes*	<30 [1]	- [-/1]
	Gobiidae	*Amblygobius*	41 [1]	- [-/3]
		Gobiodon	22–40 [3]	- [-/1]
		Paragobiodon	36–47 [3]	- [-/2]
	Acanthuridae	*Acanthurus*	34–64 [4]	34–64 [2/17]
		Ctenochaetus	60 [2]	60 [2/5]
		Naso	94 [1]	94 [1/4]
		Zebrasoma	62 [1]	62 [1/3]
TEP endemics	Mugilidae	*Mugil*	31 [data for 1 of/5 species present in TEP]	
	Serranidae	*Paralabrax*	<30 [1/8]	
	Apogonidae	*Apogon*	21–49 [2/6]	
	Lutjanidae	*Hoplopagrus*	<30 [1/1]	
		Lutjanus	24–44 [4/9]	
	Gerreidae	*Eucinostomus*	33 [1/4]	
	Haemulidae	*Haemulon*	<30 [1/5]	
	Pomacentridae	*Abudefduf*	<30 [3/3]	
		Chromis	20–43 [3/3]	
		Nexilosus	33 [1/1]	
		Microspathodon	30–34 [2/2]	
		Stegastes	25–48 [8/8]	
	Labridae	*Bodianus*	32–48 [2/2]	
		Halichoeres	29–80 [9/11]	
		Thalassoma	59–104 [4/4]	
		Xyrichtys	59–131 [5/6]	
	Tripterygiidae	*Axoclinus*	<30 [1/6]	
	Labrisomidae	*Malacoctenus*	<30 [2/9]	
	Blenniidae	*Ophioblennius*	58 [1/1]	
	Gobiidae	*Coryphopterus*	51 [1/1]	
		Bathygobius	39 [1/3]	

Sources: Arai et al. (2002); Bagarinao (1994); Bowen et al. (2001); Chang et al. (2000); Chen (1999); Doherty et al. (1995); Fowler (1989); Graves (1998); Leis (1989); McCormick (1994, 1999; unpubl. data on *Mulloidichthys flavolineatus*); C. Mora, F. Zapata, and A. Ospina. (unpubl. data on *Cirrhitichthys oxycephalus* and eastern Pacific species of *Apogon*, *Malacoctenus*, *Haemulon*, *Eucinostomus*, *Mugil*, *Chromis*, *Coryphopterus*, and *Bathygobius*); Planes (1993, 1998 [sources of pelagic larval duration values given in these papers are not indicated in many cases], 2002); Planes et al. (1998, 2002); Riginos and Victor (2001); Robinet et al. (2003); Stroud et al. (1989); S. Swearer and D.R.R. (unpubl. data on *Ophioblennius steindachner*); Thresher and Brothers (1985); Thresher et al. (1989; Victor 1986, 1987); Victor and Wellington (2000); Victor et al. (2001); Wellington and Robertson (2001); Wellington and Victor (1989, 1992); G. Wilson (2001); Wilson and McCormick (1999); Zapata and Herron (2002).

examine the relationship between pelagic larval duration variation and representation in the transpacific fauna. In 13 of 18 transpacific representatives of 10 families maximum pelagic larval durations exceed 50 days, and, in all but five cases, minima vary upward from 40 days. The exceptions are the milkfish *Chanos chanos*, the hawkfish *Cirrhitichthys oxycephalus*, the mackerels *Scomber australasicus* and *S. japonicus*, and the labrid *Stethojulis bandanensis*. The milkfish (pelagic larval duration 2–4 weeks) is widely distributed throughout the TEP and the rest of the tropical and subtropical Indo-Pacific. Although juvenile settlers develop in estuarine and other sheltered inshore habitats (Bagarinao 1994), adults occur in extremely isolated situations where conditions likely are lacking for settlers (e.g., oceanic islands such as Easter and Clipperton). Adult milkfish are large (to 1.8 m), fast swimming, pelagic fish, and adult dispersal could compensate for limited larval dispersal capabilities. However, larger juveniles of this species also associate with flotsam (J.E.M., pers. obs.), which could also facilitate long-distance dispersal. Adults of the two *Scomber* species (pelagic larval durations of 3–4 weeks) are nearshore pelagics that could well have accomplished the transpacific migration. *Cirrhitichthys oxycephalus* and *S. bandanensis*, in contrast, are small (to 10 cm and 15 cm, respectively), demersal reef fishes. Although *C. oxycephalus*, and other members of its genus, occasionally associate with flotsam (Randall 1997; C. Mora, pers. comm., 2003), such behavior is not known for *S. bandanensis.* Both species are resident in and widely distributed in the TEP. Data on *S. bandanensis* from three studies (Victor 1986, Victor and Wellington 2000, Victor et al. 2001) that included individuals from both the western Pacific and TEP showed a maximum pelagic larval duration of 44 days and an average of 29 days; the equivalent figures for *C. oxycephalus* are 45 and 39 days, respectively (C. Mora, pers. comm., 2003). The maximum pelagic larval duration of these two species is a little less than the minimum estimated time to transit the EPB on the NECC during an El Niño (~50 days). If we use the pelagic larval duration of *S. bandanensis* as the benchmark for the minimum pelagic larval duration needed for larvae of a demersal species to transit the EPB and establish a population in the TEP, then data in Table 9 indicate that many species and genera present in the Line Islands have not realized a pelagic larval duration capacity to migrate to and establish populations in the TEP. These include lutjanids, caesionids, mullids, chaetodontids, various genera of labrids, as well as acanthurids. On the other hand, some pelagic spawners (e.g., lethrinids, pomacanthids) as well as demersal spawners (e.g., apogonids and most pomacentrids) lack pelagic larval durations as long as that benchmark. The exception among the pomacentrids may be *Chromis*, which can have relatively long pelagic larval durations and which Clarke (1995) collected ~1,000 km east of the western side of the EPB. There are insufficient data on the pelagic larval durations of other speciose families in the Line Islands and central Pacific (serranids, scarids [with two species of transpacifics], blenniids, and gobiids) although some are close to the benchmark. The large goby fauna of the western side of the EPB includes one genus (*Gnatholepis*) whose Caribbean member has a maximum pelagic larval duration of at least 120 days (Sponaugle and Cowen 1994), so some likely have pelagic larval durations exceeding the benchmark.

Thus while short pelagic larval durations can account for the lack of transpacific species in some taxa, particularly among the demersal spawners, many other taxa lacking transpacifics have or likely have pelagic larval durations that greatly exceed the benchmark minimum. Variation in the representation in the transpacific fauna of five families that have a leptocephalus larva, which typically has a very long pelagic duration (elopids, albulids, muraenids, congrids, and ophichthids), provides the strongest case in point: moray eels have more transpacific species than any other family of demersal fishes (Table 1), but there are no transpacifics in any of the other four families. This is particularly notable for ophichthids, which have substantial numbers of species and genera on both sides of the EPB (Table 2). Large differences in rates of endemism among Hawaiian ophichthids and muraenids (22.7 versus 8.9% [Bohlke and McCosker 2001, McCosker 2002]) suggest that ophichthids in general have more limited dispersal potential than muraenids. Indirect estimates of the larval durations of muraenids (based on seasonal change in abundance of larvae at different stages of development) range from 3 to 10 months (Leis 1984, Bohlke 1989, Bohlke and McCosker 2001). Unfortunately there are no comparable estimates for ophichthids. Estimates of pelagic larval durations (using the same methodology) of West Atlantic congrids and moringuids from genera that occur in the TEP range from 3 to 12 months (Bohlke 1989), which are congruent with otolith-based determinations of a European *Conger* species (Correial et al. 2003). Estimates of the pelagic larval duration of western Atlantic *Elops* are 2–3 months, and those for members of the *Albula "vulpes"* circumtropical species complex range from 2 to 24 months (Bohlke 1989, Colborn et al. 2001), including 6–7 months for one TEP species (Pfeiler et al. 1988). Yet genetic data indicate that there have been no connections between TEP and central Pacific members of the *A.* "*vulpes*" complex for about 10 myr (Colborn et al. 2001). D. G. Smith (pers. comm., 2003) noted that although adult populations of many marine eels have precise distributional boundaries, their larvae range well beyond those boundaries. For example, Clarke (1995) collected muraenid and congrid larvae ~800 km east of the Line Islands on the western side of the EPB. Thus factors other than pelagic larval duration limitation clearly are involved in producing these differences in abundances of transpacific species among groups that share a pelagic larval form that characteristically has a very long pelagic duration.

Among the group of 22 likely westward migrants, 17 are elasmobranchs and/or have pelagic adults. The demersal remainder are members of families (Carapidae, Priacanthidae, Balistidae, and Diodontidae) known to have large, specialized pelagic larval stages and, in most cases, pelagic juvenile stages (Markle and Olney 1990, Leis and Carson-Ewart 2000). There are pelagic larval duration data for a limited range of nontranspacific TEP shore fishes (Table 9). Pelagic larval durations of TEP species are not shorter than those of congeners from the central Pacific in the two families (Labridae and Pomacentridae) where that has been examined (Mora et al. 2003). In a few cases such pelagic larval durations reach >100 days. However, because westward transits of the EPB may take twice as long as eastward transits, pelagic larval duration limitations probably have much stronger effects on westward migration. There is evidence (see section on Genetic Studies later in Discussion) that the Hawaiian population of *Mugil cephalus* could have been derived by westward migration from the TEP. Although this species has a pelagic larval duration of 29–67 days (Table 9), its adults reach 1 m in length, are fast swimming and semipelagic, and may have accomplished a transit to Hawai'i.

Since Leis' (1984) report there have been only two studies involving sampling for shore-fish larvae within the EPB but near its edges rather than in its center. Victor (1987) collected larvae of three genera of labrids that were >80 days old between the Galápagos and mainland Ecuador. Clarke (1995) sampled shore-fish larvae on the western side of the EPB and collected larvae of 14 families 750–1,100 km from the nearest shore-fish habitat: muraenids, congrids, holocentrids, scorpaenids, acropomatids, carangids, lethrinids, mullids, serranids, labrids, pomacentrids (*Chromis*), acanthurids, callionymids, and ostraciids. These two studies support the idea that a range of reef fish taxa that lack transpacific representatives have long-distance dispersal capabilities. As Clarke (1995) noted, net avoidance is likely to result in underestimates of the diversity and abundance of large fish larvae and pelagic juveniles far from their adult habitat.

Flotsam-mediated dispersal of shore fishes. Dispersal of large juveniles and adults of shore fishes across the EPB in association with flotsam likely is involved in some cases. Various known or potential westward migrants have been found with flotsam in the TEP: *Lobotes pacificus*, *Carangoides caballus*, *Seriola rivoliana*, *Uraspis helvola*, *Sectator ocyurus*, *Euthynnus lineatus*, and *Balistes polylepis* (see Hunter and Mitchell 1966). Other probable eastward migrants have also been found with durable flotsam, including *Chanos chanos* (J.E.M., pers. obs), *Fistularia commersonii* and *Cirrhitichthys oxycephalus* (C. Mora, pers. comm., 2003), *Sphyraena barracuda* (Gooding and Magnuson 1967), and *Caranx sexfasciatus* (Hunter and Mitchell 1967). Other transpacific species with unclear direction(s) of migration that associate with durable flotsam include *Elagatis bipinnulata* (Gooding and Magnuson 1967) and *Aluterus monocerus* and *A. scriptus* (Hunter and Mitchell 1966). Ages of demersal stages of TEP species associated with flotsam can reach over a year (*Hypsoblennius* [Mora et al. 2001]), which should make them capable of a westward transit of the EPB. Because long transit times would strongly limit westward larval dispersal, flotsam dispersal may be proportionately much more important for westward migration than for eastward migration.

POTENTIAL ECOLOGICAL LIMITATIONS ON IMMIGRANTS. *Availability of equivalent habitats on both sides of the EPB.* Access to equivalent habitats affects the colonization ability of organisms moving in either direction across the EPB (Rosenblatt et al. 1972, Scheltema 1988). This includes conditions for larvae as well as adults. Leis (1986) noted that taxa whose larvae typically occur in continental habitats on the Australian Great Barrier Reef are less well represented on the (central) Pacific Plate than those whose larvae occur in oceanic habitats on the Great Barrier Reef. There are strong differences between the fish faunas of continental and outer barrier (oceanic) reefs of the Great Barrier Reef in terms of both species composition and the abundances of fishes in different feeding groups (Williams 1991). Because those differences occur across tens of kilometers, they are much more likely to be related to interspecific differences in adult and/or larval requirements than to variation in pelagic larval durations and larval dispersal capabilities.

Leis (1986) recognized the difficulty of distinguishing between effects of adult versus larval habitat requirements in limiting faunal exchange between continental and oceanic reefs. Adult-habitat limitations relating to the paucity of coral reefs in the TEP (cf. Rosenblatt et al. 1972) can reasonably be invoked to explain lack of establishment of a few eastward migrants that reach the TEP as vagrants. First, central-Pacific *Chaetodon* species that feed on live corals regularly disperse to the TEP but lack established populations. Second, if scarids are strongly tied to a food base provided by carbonate substrata on coral reefs (cf. Streelman et al. 2002), this could explain why the TEP and the other tropical Pacific region that has few coral reefs (the Marquesas) have small parrotfish faunas (see Robertson 1998). However, there are many noncorallivorous *Chaetodon* species in the Line Islands (Table 2), and there is no evidence that the vast majority of "coral-reef" fish species are directly dependent on live corals or coral reefs. Overall similarities in taxonomic structure of the reef-fish faunas of the TEP and the Caribbean (which has twice as many coral species and a ~1,000 times greater area of coral reefs as the TEP) indicate that a lack of coral reefs in the TEP is not likely to be a major limiting factor on successful eastward migration for most taxa. The occurrence of vagrants of various species of *Naso* and various noncorallivorous species of *Chaetodon* at different locations in the TEP does suggest that their ability to establish is limited more by suitability of conditions for self-sustaining populations in the TEP than by their ability to disperse across the EPB. What those conditions might be is far from obvious. Large fluctuations in the abundance of the westward-migrant carangid *Carangoides caballus* in Hawai'i, where it increased greatly following the 1997–1998 El Niño, then declined sharply, clearly demonstrate environmental limitations on successful invasion of Hawai'i in addition to any effects El Niños might have on its rate of immigration. If this species experiences a similar increase at Hawai'i during a future El Niño, then assessing the reproductive state of adults there and comparing their growth rates (using otolith analyses) with those occurring in the TEP could help clarify why it fails to establish in Hawai'i. Another Hawaiian example of possible island-environment limitations on establishment of a continental TEP species derives from the fate of three species of nonnative lutjanids introduced in large numbers in the 1950s. Two Indo-central Pacific reef-dwelling species successfully established substantial resident populations, but a continental TEP species that lives mainly on soft bottoms did not (Oda and Parrish 1981).

The biggest difference between the central Pacific and the TEP in terms of habitat availability is in the abundance of equivalent offshore habitats. The pelagic and benthic environments of the Line Islands and the oceanic islands of the TEP share physical and biological characteristics that are very different from those along the mainland of the TEP (Longhurst 1998). Oceanic reefs provide 100% of habitats for shore fishes in the equatorial part of the central Pacific, and all potential immigrants from there to the TEP are adapted to life in that type of environment. In contrast, in the TEP the amount of oceanic-island habitat is very small in both absolute and relative terms, where such islands provide only ~2.5% of shallow, inshore habitat (Table 5). Further, ~97.5% of the oceanic-island habitat in the TEP is situated at the cooler latitudinal limits of the region: the Revillagigedos in the north and the Galápagos in the south (Table 5). The largest (southern and western) islands in the Galápagos have a marine environment that is warm temperate rather than equatorial (Glynn and Wellington 1983, Grove and Lavenberg 1997). Further, the second-largest area of oceanic-reef habitat (the subtropical Revillagigedos) have a reduced ability to receive eastward migrants because they lie well to the north of the flow path of the NECC, in an area where westbound currents predominate. Consequently the amount of tropical oceanic-reef habitat likely not only to receive immigrants on the NECC but also to support continuing populations of those immigrants is miniscule: it consists of the northern Galápagos, Cocos, Clipperton, and Malpelo, which together provide ~0.5% of the shallow inshore habitat in the TEP. Some suitable habitat for oceanic-island species occurs at a moderate-sized cluster of coastal islands in western Panama (see Glynn et al. 1972, Rosenblatt et al. 1972) and at few small similar islands on the coast of Costa Rica. However, inclusion of those islands only marginally increases the total amount of reef habitat suitable for resident populations of central Pacific immigrants. That the TEP's oceanic islands are disproportionately important (relative to their number and size) as supporters of transpacific shore fishes is consistent with their requiring equivalent habitat to that on the western side of the EPB. However, the offshore islands of the TEP also are substantially closer to the western edge of the EPB (by ~1,000 km in the cases of the Galápagos and Clipperton) and more directly influenced by eastbound currents than is the continental coast of that region and particularly the continental islands at Panama and Costa Rica. Hence greater accessibility of the offshore islands may also affect the extent to which they support transpacific fishes.

The paucity of tropical oceanic-reef habitat in the TEP can also be expected to limit westward emigration in two ways. First, it reduces the pool of TEP species adapted to ocean-island life and thus capable of establishing populations in the central Pacific: only 99 TEP species of shore fishes (11.4% of the regional fauna) are ocean-island endemics and <30% of the remainder of the region's endemic shore fishes probably have self-sustaining insular populations (Robertson and Allen 1996, 2002). Second, the small size of the TEP's tropical oceanic islands must be reflected in small adult populations of fishes and relatively small numbers of emigrant propagules being released.

How differences in oceanic-reef and continental-reef environments affect the faunal composition of reef-fish assemblages throughout the Indo-Pacific and what different adaptations are required of members of the fish fauna of each environment are questions of major biogeographic significance that need to be addressed. Explanations of latitudinal gradients in diversity across the Indo-Pacific have emphasized the importance of dispersal ability and the geologic history of the Indo-Philippine center of diversity (e.g., Hughes et al. 2002, Mora et al. 2003). Yet although the West Pacific contains an abundance of both continental and oceanic reefs, the vast majority of the reef habitat in the central Pacific and central Indian Oceans, and particularly the habitat that can act as stepping-stones for dispersal, consists of oceanic reefs.

Interactions between the indigenous fauna and potential immigrants? Eco-evolutionary factors that are thought to affect the level and pattern of invasion of a fauna by immigrants include (1) the relative size of the recipient fauna, (2) the extent to which it has become depauperated by mass-extinction events, and (3) whether invaders have biological characteristics that provide them with an advantage over members of the native fauna. Vermeij (1978, 1987, 1991) and Vermeij and Rosenberg (1993) examined the pattern of transpacific invasion of the TEP molluscan fauna from this perspective. They attributed a preponderance of eastward migration of mollusks across the EPB to higher levels of prior extinction in the TEP and the possession by the western invaders of ecological characteristics possessed by extinct members of the TEP but lacking in the contemporary native fauna. Lacking a recent fossil record for tropical fishes in the TEP, West Atlantic, and central Pacific, we cannot assess the relative level of any extinction in the TEP versus those other regions or whether the TEP fish fauna has become depauperate. Although the reef-fish fauna of the TEP is much smaller than that of the area used as the global standard (the Indo-Malayan center of diversity [e.g., see Hughes et al. 2002, Mora et al. 2003]), it is similar in size to the fauna of its sister region, the tropical Northwest Atlantic (e.g., Robertson 1998, Robertson and Allen 2002, Smith 1997). Those two regions shared a common history and marine biota until the closure of the isthmus of Panama, and their shore-fish faunas share a substantial number of Neotropical endemic genera and families (Rosenblatt 1967, McCosker and Robertson 2001).

To provide an indication of which families in the indigenous TEP shore-fish fauna might be functionally depauperate we compared the relative abundance of each in the faunas of the TEP and the greater Caribbean, and assumed that families with proportionately fewer (or no) species in the TEP are depauperate. To assess whether eastward migration is more common in those depauperate families we examined the occurrence of successful (i.e., resident) eastward-migrant transpacific species in each family present in the TEP, the Caribbean, and the Line Islands (the most likely source of such migrants). These data (Table 2) show that the proportion of "depauperate" TEP families that have resident transpacific species does not differ from the proportion of nondepauperate families that do: 0.54 of 50 versus 0.47 of 15, respectively (*G* test: $G = 0.33$, $P > 0.05$). It is also possible that immigration occurs more often in families that have relatively fewer species in the TEP than in the central Pacific. In that comparison eastward-immigrant transpacific species are present in 0.55 of 49 depauperate families and 0.31 of 16 nondepauperate families, a nonsignificant difference (*G* test: $G = 2.71$, $P > 0.05$).

Vermeij and Rosenberg (1993) found that in the Caribbean, where the mollusk fauna was subject to a mass extinction 2–5 Ma, recent immigrants are more common and widespread than in other nearby regions (including the TEP) that experienced fewer extinctions. There are 37 species of eastward-migrant shore fishes that are widely distributed residents in the TEP and 20 species of vagrants (Table 1). If interactions with indigenous species determine whether a transpacific species establishes a population in the TEP and how widespread it becomes, then the proportion of widely distributed resident transpacific species that are members of depauperate families should be greater than the proportion of vagrants that are members of such families. Because there is virtually no difference in those proportions (0.76 and 0.75, respectively), this is not the case.

To assess whether interactions with the indigenous TEP shore-fish fauna may have affected the success of eastward invasions we also compared the ecological composition (habitat usage and feeding groups) of the eastward-migrant transpacific fauna with the composition of the donor (Line Islands) and recipient (native TEP) faunas. As previously noted, oceanic and inshore pelagics are both overrepresented in the transpacific fauna relative to their abundances in the donor and recipient faunas. Among the demersal species, the relative abundances of reef fishes and soft-bottom fishes are almost identical in the transpacific and Line Island faunas. In contrast, soft-bottom species are much less abundant in the transpacific fauna than in the TEP fauna (Table 10: *G* test: $G = 25.5$, $P < 0.01$), in which they predominate over reef species. The relative abundances of species in eight feeding groups (Table 11) differs in the transpacific fauna from that in both the TEP and Line Islands faunas (*G* tests: $G = 39.1$, $P < 0.01$, and $G = 16.8$, $P < 0.05$, respectively). However, the overall structure of the transpacific fauna is more similar to that of the Line Islands fauna than the TEP fauna; Czekanowski similarity indices (Bloom 1981) are 0.78 and 0.66, respectively. These pat-

TABLE 10

Percentage of Different Groups of Demersal Shore Fishes among Eastward-Migrant Transpacific Species and in the Faunas on Both Sides of the EPB

Habitat Type	Transpacifics	TEP Indigenous Fauna	Line Islands Fauna
Demersal: soft bottom[a]	10.4	56.7	13.0
Demersal: reef[b]	89.6	43.3	87.0
No. of species	67	858	487

[a] Mud, sand, and gravel.
[b] Rock, rubble, and coral.

terns of dissimilarity between the structures of the transpacific and TEP faunas are what would be expected if transpacific species were being excluded from groups with many native species. However, the similarity of the transpacific and Line Islands faunas suggests a simpler explanation: that transpacific species are drawn largely at random, at least in terms of ecological groupings, from the Line Islands fauna, with differences between the transpacific fauna and the faunas of both the TEP and the Line Islands arising from phylogenetic differences in dispersal potential. Greater dispersal potential leads to overweighting of the following groups in the transpacific fauna: pelagic species among the inshore fishes, and among the trophic groups: midwater carnivores (all but one are pelagic or semipelagic species) and most of the benthic herbivores and omnivores (which are members of taxa with high dispersal capabilities: acanthurids, chaetodontids, and tetraodontiforms).

TABLE 11

Representation of Different Feeding Groups among Eastward-Migrant Transpacific Shore Fishes and the Shore-Fish Faunas on Each Side of the EPB

Feeding Group[a]	Transpacifics	TEP Indigenous	Line Islands
Midwater carnivores	12.5	3.3	2.1
Demersal carnivores	44.5	66.8	60.9
Planktivores	9.4	22.5	13.8
Benthic herbivores	11.9	2.7	7.4
Benthic omnivores	15.0	4.1	9.3
Benthic detritivores	2.5	0.8	3.9
Parasitic	1.3	0.2	1.2
Corallivores	1.9	0	1.4
No. of species	80	949	515

[a] Species in two feeding groups (see Table 1) were assigned half value for each.

We conclude that there are no clear indications that interactions with the native fauna have played a role in determining what taxa or ecological groups of eastward-immigrant fishes have established resident populations in the TEP. In only a few cases do eastward-migrant shore fishes have notable ecological characteristics lacking in the native TEP fauna: the TEP includes no indigenous members of the herbivorous surgeonfish genera *Acanthurus* or *Ctenochaetus* (both are abundant in the Indo-central Pacific and there are three species of *Acanthurus* in the Caribbean) and only one native member of the scraping/excavating herbivore/detritivore genus *Scarus*, which is abundant in both the Indo-central Pacific and Northwest Atlantic. In addition there are no native corallivores in the TEP, but two among the transpacific species. However, together those species that have characteristics lacking in the native TEP fauna represent only 15.5% of the resident eastward-migrant transpacific species in the TEP.

Genetic Studies and the Status of TEP Populations of Transpacific Taxa

The overall similarities of the shore-fish faunas of the Caribbean and the TEP and the occurrence of numerous transisthmian geminate species pairs suggest that TEP populations of many circumtropical species may be isthmian relicts. The alternative to that scenario is an eastward range expansion and immigration to the TEP, perhaps during periods with different climate conditions (cf. Bowen and Grant 1997). Because fossils of reef fishes are rare and not known from the Caribbean and eastern Pacific, a major source of historical information bearing on relationships within the coral and molluscan faunas of the New World is lacking for shore fishes. Hence data on genetic relationships of Neotropical and central Pacific fish taxa are vital for establishing how the TEP shorefish fauna was formed. Such data should help answer questions about the origin of TEP populations of transpacific fishes: Were TEP populations separated from those of putative West Atlantic sister taxa before or during the rise of the Isthmus of Panama? Are TEP and central Pacific populations of transpacific species currently in genetic contact? What is the relative importance of eastward versus westward migration across the EPB? To what extent have widely distributed Indo-Pacific species originated in the TEP and spread westward? Are the Line Islands both receiving westward migrants from and providing eastward migrants to the TEP (see discussion in the conclusions on directions of migration across the EPB)? There are data available relevant to these questions for a range of transpacific oceanic and shore fishes.

OCEANIC FISHES. *Isurus oxyrinchus:* Heist et al. (1996) examined relations between Pacific and Atlantic populations (including those in the Northeast Pacific) using mtDNA. They found "no evidence of multiple subspecies ... nor of past genetic isolation between ... populations." *Coryphaena hippurus:* Rosenblatt and Waples (1986) found virtually no difference (in allozymes) between populations in the TEP, Hawai'i, and the Atlantic, indicating gene flow across the EPB, as well as between the Pacific and the Atlantic. *Thunnus alalunga:* Graves and Dizon (1989: mtDNA) found no differences that could distinguish populations at South Africa and the Northeast Pacific and concluded that they are either connected or only recently isolated. *Thunnus albacares:* Ward et al. (1997: allozymes and mtDNA) examined global population structure of this species. They found three subdivisions (Atlantic, Indian Ocean, and Pacific) with no evidence of separation between East and West Pacific populations. *Xiphias gladius:* Chow and Takeyama (2000: mtDNA and nDNA) compared populations from locations scattered around the world. They identified four groupings (Mediterranean, Northwest Atlantic, South Atlantic, and Indo-Pacific) but no subdivisions within the Indo-Pacific. Istiophorid billfishes: Graves and McDowell (1995: mtDNA) examined relationships between Atlantic and Pacific sister species of three istiophorids: blue marlin (*Makaira nigricans* and *M. mazara*), sailfish (*Istiophorus albicans* and *I. platypterus*), and white and striped marlin (*Tetrapterus albidus* and *T. audax*). The TEP population was included among samples of sailfish and striped marlin. They concluded that all three Atlantic and Indo-Pacific pairs probably do not warrant the status of separate species and that populations in the two oceans are connected by recent gene flow. Although sampling was insufficient to assess the status of the TEP population versus that of the rest of the Pacific, connections between the Indo-Pacific and Atlantic indicate that isolation of the TEP population is unlikely.

SHORE FISHES. *Manta birostris:* Limited sampling of central Pacific, TEP, and Caribbean populations of *M. birostris* by T. Clark (pers. comm., 2003: mtDNA) indicated that the TEP population is an isthmian relict that has not had contact with central Pacific populations since before the rise of the Isthmus of Panama. *Sphyrna lewini:* Analysis of populations in the West Atlantic and the eastern, central, and West Pacific (K. Duncan, pers. comm., 2003: mtDNA) indicated that the TEP population is not an isolated isthmian relict and is genetically connected to central and western Pacific populations. *Albula "vulpes":* Colborn et al. (2001: mtDNA) assessed relationships among Indo-Pacific and Atlantic populations in the pantropical "*vulpes*" species complex. The TEP previously was thought to have one representative of this group, referred to as either *A. vulpes* (Eschmeyer et al. 1983, Whitehead and Rodriguez-Sanchez 1995, Grove and Lavenberg 1997) or *A. neoguinaica* (Allen and Robertson 1994). Colborn et al. (2001) concluded that (1) there might be up to eight species in this complex; (2) *A. forsteri* (a senior synonym of *A. neoguinaica* according to Randall and Bauchot [1999]) is restricted to the West and central Pacific and *A. vulpes* to the Caribbean; and (3) the TEP lineage contains a pair of sister species. They also noted (4) that the

TEP lineage separated from a lineage that contains two Atlantic and one Indo-central Pacific species ~10 Ma. This complexity means that it is not possible to determine whether the TEP lineage originated by an invasion from the central Pacific or from an Atlanto–East Pacific stock. The TEP lineage was formed well before the Isthmus of Panama closed, and the two TEP species separated ~4 Ma (about when that closure occurred) and represent isthmian relicts. *Gymnomuraena zebra:* Rosenblatt and Waples (1986: allozymes) found virtually no difference between populations of this species in the TEP and Hawai'i, indicating recent gene flow. *Sardinops sagax:* Bowen and Grant's (1997) and Grant and Bowen's (1998: mtDNA) analysis led them to propose that this genus contains a single widespread Indo-Pacific species that spread throughout its current range only within the last few hundred thousand years. They cited paleontological evidence indicating that the eastern Pacific endemic subspecies (*S. s. sagax*), which has an antitropical distribution that largely excludes the TEP, may have arrived in the northern part of its range less than 100,000 yr ago. Where the eastern Pacific population came from is unclear. *Fistularia commersonii:* Rosenblatt and Waples (1986:279: allozymes) found evidence of "relatively recent interruption of previously significant levels of geneflow" between Hawai'i and the TEP. *Tylosurus imperialis:* Collette and Banford (2001: mtDNA) found little differentiation between western and eastern Pacific populations of the Indo-Pacific subspecies (*T. i. melanotus*) of this circumtropical, inshore pelagic species. The deepest split in the *T. imperialis* lineage is between the Indo-Pacific and Atlantic, which was followed by separation of *T. pacificus* (a TEP endemic) and *T i. melanotus*. The simplest explanation for this pattern is that the Indo-Pacific lineage invaded the TEP twice after the Atlantic lineage became isolated, and neither TEP population is an isthmian relict. *Tylosurus crocodilus:* Currently two subspecies of this circumtropical species are recognized: *T. c. fodiator* from the TEP and *T. c. crocodilus* from the Atlantic and Indo-central Pacific (to the Hawaiian, Line, and Marquesas Islands). Collette and Banford (2001: mtDNA) concluded that there are three allopatric lineages (Atlantic, TEP, and Indo-central Pacific) of *T. crocodilus* with an initial separation of lineages between the New World and the Indo-central Pacific, followed by separation of the TEP and West Atlantic lineages. This sequence of events indicates that the TEP subspecies likely is an isthmian relict. *Aulostomus chinensis:* Bowen et al. (2001: mtDNA) found weak genetic structuring across the Indo-Pacific (East Africa to the TEP) and no substantial separation across the EPB. These data (and see also Rosenblatt and Waples [1986]) indicate ongoing to recent gene flow across the EPB. Levels of genetic difference between *A. chinensis* and the Caribbean species (*A. maculatus*) suggest that they were separated by the closure of the Isthmus of Panama. The fact that genetic diversity in *A. chinensis* is low in the TEP and that TEP haplotypes are a subset of those found elsewhere in the Indo-Pacific indicate that the TEP population originated by recent eastward migration and remains in genetic contact with central Pacific populations. *Hippocampus ingens:* Teske et al.'s (2003: nuclear and mtDNA) global phylogeny of the genus indicates that *H. ingens*, a TEP endemic (and the only member of its genus in that region), is a member of an Indo-Pacific lineage that invaded the Atlantic/eastern Pacific before the closure of the Central American isthmus and that *H. ingens* is an isthmian relict with a Caribbean geminate. Their data do not show how that lineage invaded the New World: from the central Pacific or from the western Indian Ocean around southern Africa. *Heteropriacanthus cruentatus:* Rosenblatt and Waples (1986: allozymes) found virtually no difference between populations of this species in the TEP and Hawai'i (indicating ongoing gene flow) but a large difference between Pacific and Atlantic populations of what is currently regarded as a circumtropical species. Bermingham et al. (1997: mtDNA) reported a large divergence between TEP and Atlantic populations of this species. These two data sets indicate that the TEP population is not an isolated isthmian relict and either was derived from an eastward migration after the rise of the Isthmus of Panama or was in the TEP before that event and has remained in genetic contact with the central Pacific population. *Gnathanodon speciosus:* Rosenblatt and Waples (1986:279: allozymes) found evidence of "relatively recent interruption of previously significant levels of geneflow" between Hawai'i and the TEP. *Trachurus murphyi:* The eastern Pacific populations of this primarily warm-temperate fish have a disjunct, antitropical distribution and sometimes are referred to as separate species. The southern form is a transpacific that extends westward to New Zealand. Stepien and Rosenblatt (1996: mtDNA) found indications of ongoing gene flow across the TEP and suggested that the two forms are conspecific. *Mulloidichthys vanicolensis:* The widespread Indo-central Pacific species *M. vanicolensis* is extremely similar in morphology to its TEP congener, *M. dentatus*. Stepien et al. (1994: allozymes) examined relationships between populations of *M. vanicolensis* from five Indo-central Pacific sites (including Hawai'i) and a population of *M. dentatus* from the Gulf of California. They found *M. dentatus* to be genetically distinguishable from *M. vanicolensis*. Bermingham et al. (1997) found very low mtDNA sequence divergence between *M. dentatus* and *M. martinicus* from the Caribbean, indicating that they separated very recently. Relationships between the three species and the timing of their separations (before or after the rise of the Isthmus of Panama) remain unclear. Lessios, D.R.R., and Kessing (unpubl. mtDNA sequence data) compared presumed *M. dentatus* at Baja California, Clipperton, and Panama in the TEP with *M. vanicolensis* at sites throughout the Indo-central Pacific, including Hawai'i, the Line Islands, and the Marquesas. They found that all three TEP populations contained sequences found only in that region but also sequences commonly found in Indo-central Pacific populations of *M. vanicolensis*. These results indicate that although the TEP population was previously isolated, *M. vanicolensis* recently invaded from the central Pacific. Given that it was found in all three populations sampled by those workers it likely is widespread in the TEP. *Mugil cephalus:* This circumtropical species has a disjunct distribution in the Pacific; the only central Pacific population is at Hawai'i. Crosetti et al. (1994: mtDNA) examined populations covering much of its range. Their data indicate that the TEP population is most closely related to the Hawaiian population and that the sister population of those two is in the Atlantic and Mediterranean. This pattern is consistent with westward migration to Hawai'i by an isthmian-relict TEP population, although further data are needed to determine whether the ancestral population was in the TEP. *Thalassoma* spp.: Bernardi et al. (2003: mtDNA and nDNA) constructed a phylogeny of this pantropical genus, which includes four endemics and one resident transpacific species, *T. purpureum*, in the TEP. The most ancient split occurred between the Atlantic and Indo-Pacific lineages, and the TEP endemics are much more recently derived from Indo-Pacific lineages. There are three lineages in the TEP: one containing the TEP sister endemics *T. lucasanum* and *T. robertsoni* plus the Indo-central Pacific *T. amblycephalum*, one consisting of *T. virens* (a TEP endemic) and *T. purpureum* (perhaps the most widespread Indo-Pacific wrasse), and one that includes the TEP endemic *T. grammaticum* and the Indo-central Pacific *T. lutescens*. The entire TEP fauna evidently is derived from four separate invasions from the Indo-central Pacific (the *T. purpureum* lineage having invaded twice) and lacks any isthmian relicts. *Acanthurus triostegus:* Planes and Fauvelot (2002: allozymes) examined relationships between Pacific populations of this species. Planes (2002) proposed that the species originated in French Polynesia and then spread east and west. The Clipperton population was most closely allied to (although distinct from) that of the Tuamotus among those they sampled, and the Marquesas and Hawaiian populations each were very distinct from all others. This pattern of genetic relationships parallels that of the three recognized subspecies of *A. triostegus*, which occur in Hawai'i, the Marquesas, and the remainder of the Indo-Pacific (Randall 1956). It also is consistent with the TEP being populated by migrants from the Line Islands. However, sampling of the continental TEP, the Line Islands, and islands to the west of the Line Islands is needed to clarify this situation and determine the extent of gene flow across the EPB. *Zanclus cornutus:* Rosenblatt and Waples (1986: allozymes) found low levels of differentiation between Hawaiian and TEP populations of this species, indicating ongoing or very recent gene flow. *Scomber australasicus:* This Indo-Pacific species occurs in the West Pacific, Hawai'i, and the Revillagigedo Islands in the TEP. Distributions of mtDNA haplotypes (Scoles et al. 1998) show that the Revillagigedos population has low genetic diversity and evidently was established by eastward immigration some time ago (it has unique haplotypes), but has experienced recent/ongoing eastward gene flow. *Scomber japonicus:* What was once regarded as a circumglobal species is now restricted to the Indo-Pacific with an Atlantic sister species (Collette et al. 2001). Geographically inadequate sampling precludes a clear assessment of the relationship of the eastern Pacific populations to those elsewhere in its range, although disjunct northern and southern populations in the eastern Pacific have been isolated from each other for several hundred thousand years (Stepien and Rosenblatt 1996: mtDNA). *Aluterus scriptus:* Rosenblatt and Waples' (1986:279: allozymes) data indicated "relatively recent interruption of previously significant levels of geneflow" between Hawai'i and the TEP. Bermingham et al. (1997: mtDNA) found very low divergence between populations in the TEP and the Caribbean. Together these data suggest that this is a circumtropical species with gene flow throughout its range. *Melichthys niger:* Bermingham et al. (1997: mtDNA) found a very low level of divergence between TEP and Caribbean populations, indicating a circumtropical species with gene flow throughout its range. *Arothron hispidus* and *Arothron meleagris:* Rosenblatt and Waples (1986:279: allozymes) found virtually no differences between the TEP and Hawai'i populations of the former species, indicating ongoing gene flow, and indications of "relatively recent interruption of previously significant levels of geneflow" between such populations in the latter. *Diodon holacanthus:* Rosenblatt and Waples (1986:279: allozymes) found evidence of "relatively recent interruption of previously significant levels of geneflow" between populations in Hawai'i and the TEP. *Diodon hystrix:* Using mtDNA sequences Bermingham et al. (1997) found extremely low divergence between TEP and Atlantic members of this species; this circumtropical species exhibits pantropical gene flow.

PATTERNS OF HISTORICAL RELATIONSHIPS. In summary these genetic data have shown the following: (1) TEP populations of eight large, highly mobile oceanic species (in four different families) with circumglobal distributions are connected to those elsewhere in the Pacific, and often the Atlantic, and do not represent isolated isthmian relicts. (2) Among the shore fishes there is good evidence of ongoing to recent genetic connections between the TEP and the central Pacific in 10 Indo-Pacific species from nine families, between the TEP and the western Pacific in three Indo-Pacific species, and between the TEP and the rest of the Indo-Pacific and the Atlantic in two circumtropical species. (3) Six TEP representatives of five circumtropical genera (*Manta*, *Albula*, *Tylosurus*, *Mugil*, *Hippocampus*) include isthmian relicts, and TEP populations in 10 species in five other such genera (*Sardinops*, *Tylosurus*, *Aulostomus*, *Mulloidichthys*, *Thalassoma*, *Scomber*) apparently are the result of eastward migration since the closure of the isthmus. The latter include species whose TEP populations range from having been isolated for a substantial amount of time, to having intermittent or ongoing contact with populations on the western side of the EPB. (4) In one genus (*Thalassoma*), multiple eastward invasions after the rise of the isthmus by several different Indo-Pacific lineages established the entire TEP fauna of four endemic and one transpacific species. (5) An isolated central Pacific population of a circumglobal species (*Mugil cephalus*) likely was established by westward migration from an isthmian-relict population in the TEP. (6) Indo-central Pacific species can co-occur with endemic siblings in the TEP (e.g., *Mullodichthys*). (7) Species with disjunct, antitropical distributions may have less gene flow between TEP populations and those elsewhere than do species with continuous tropical distributions (cf. Graves 1998). Northern and southern populations of antitropical species in the eastern Pacific range from being well connected to well isolated. (8) Genetic data are consistent with distributional data indicating a strong preponderance of eastward migration across the EPB but more westward migration than previously thought. However, existing genetic data in many cases are very sketchy, with few samples per site and a lack of samples from substantial parts of the geographic range. Hence there is a largely unrealized potential for such data to resolve many questions about the extent, timing, and routes of migration in both directions across that barrier and to assess historical patterns indicated by current geographic distributions. In particular, such data could determine the extent to which transpacific fishes that are widespread in the Indo-Pacific, including circumtropical species and many of those treated here as eastward migrants, originated by westward migration from the TEP.

OTHER TAXA. Besides shore fishes, there are genetic data on the status of TEP representatives of circumtropical taxa in only one other group of marine shore organisms: the echinoids. Data on five pantropical genera of sea urchins, which, geographically, are much more comprehensive than those for most of the fishes, show ongoing large-scale connections across the EPB in two genera represented in the TEP only by transpacifics (Lessios et al. 1998, 2003). In two genera, isthmian-relict species co-occur with resident eastward-migrant transpacific species in the TEP (Lessios et al. 1996, 2001). In one other genus the TEP fauna consists of a pair of endemics derived from an isthmian relict (Lessios et al. 1999). Thus the range of relationships in this small set of taxa parallels that among the shore fishes.

Conclusions: The Level and Pattern of Migration across the EPB

The extreme width of the EPB and the slowness of currents that traverse it have led to the conclusion that migration is limited to the few species with the longest larval durations (Scheltema 1988). However, additional information reinforces previous conclusions that many central Pacific shore-fish taxa that have pelagic larval durations that are adequate for an EPB transit and larval characteristics likely to facilitate long-distance dispersal are not represented among successful eastward migrants. Although data on pelagic larval durations are still lacking for many central Pacific taxa, there is enough to indicate that variation in that measure of dispersal capability does not explain some conspicuous absences of speciose taxa in the transpacific fauna. Absences of certain higher taxa whose members likely have adequate pelagic larval durations probably are due to phylogenetic variation in some other aspects of larval life histories, but chance may well affect which species in a particular taxon make their way across the EPB in sufficient numbers to establish successful immigrant populations. Transit times for westward migration are likely to be on the order of twice as long as for eastward migration; hence the pool of capable species must be much smaller for westward than for eastward migration. Flotsam migration across the EPB, which has been recognized for corals (Jokiel 1984, Grigg and Hey 1992), seems more likely to occur in a westward direction because the eastern source of flotsam (a continental shore spanning ~20° of latitude) is huge in comparison with the western source (small islands scattered over a vast area of ocean). Modeling of flotsam movements in the TEP indicate that most westward flotsam dispersal would occur on the NEC (Garcia et al. 1999), hence to the Hawaiian Islands (including Johnston Island). However, few species whose adults are demersal are known to associate with flotsam, which severely limits the potential importance of such dispersal. Flotsam dispersal may be important for pelagic shore fishes because many westward migrants have pelagic adults that are known to associate with flotsam.

Large differences in the availability of comparable habitat on the two sides of the EPB may be a major factor limiting overall levels of migration—the only shore-fish habitat present at the head of the eastbound currents on the western side of the barrier (tropical oceanic reefs) is rare in the TEP. The scarcity of that habitat in the TEP and the small fauna (number of species and individuals) it supports there also reduces the potential for westward migration. Conditions on each side of the EPB evidently limit the establishment of some immigrant shore fishes, which have appeared repeatedly as vagrants in a region or undergo large fluctuations in abundance there. However, other than effects of the scarcity of corals in the TEP on a few reef fishes it is unclear how such limitations might operate.

Distributional and existing genetic data support the prevailing view that eastward migration across the EPB is the predominant mode but indicate that westward migration has been substantially underestimated, with the ratio of eastward to westward movements probably being on the order of 3 : 1. A bias toward eastward migration previously has been attributed to: (1) eastward currents being stronger than westward flows; (2) the TEP having a depauperate fauna with few species capable of long-distance dispersal (the reverse of the situation in the Indo-central Pacific); and (3) adults of Indo-central Pacific species having broader ecological capabilities than adults of TEP endemics (summarized in Grigg and Hey [1992]). Although eastward migrants exhibit a range of dispersal characteristics, westward migrants comprise elasmobranchs, species with pelagic adults, and species with specialized larvae capable of extended dispersal. Such a difference in the composition of the eastward and westward migrant faunas is consistent with the idea that westward migration is more difficult than eastward migration. However, our analyses indicate that effective differences between eastbound and westbound currents may not be as great as previously thought. The TEP shore-fish fauna is only about one-third the size of that in the Indo-Malayan center of Indo-Pacific diversity and is substantially smaller than the shore-fish fauna of the entire central Pacific. However, because the reef-associated fauna of the TEP (~550 species [Robertson and Allen 2002]) is about the same size as that of any of the three main groups of islands on the western side of the EPB, there is no real support for the notion that a bias toward eastward migration reflects emigration from a richer to a poorer fauna. There are no indications that interactions with the indigenous TEP fauna have shaped taxonomic or ecologic biases in the structure of the eastward-immigrant fauna. Rather the ecologic structure of that fauna simply reflects the structure of the donor fauna, tempered by effects of taxonomic variation in dispersal ability. Although long-distance dispersal capabilities may be important to determining the taxonomic structure of the central Pacific fauna (e.g., Mora et al. 2003), currently there are no indications that TEP fishes have lower dispersal capabilities than central Pacific members of the same family. The TEP has one of the most dynamic environments of any tropical region in the world, a much more dynamic environment than that of its sister region, the tropical Northwest Atlantic. The native TEP coral fauna was largely wiped out by environmental stresses of various types, especially those associated with El Niños, leading to large differences between the coral faunas and abundance of coral reefs in those two regions. However, differences between the shore-fish faunas of those two regions are much smaller, and there is no evidence of a strong, widespread impact of those stresses on the TEP's shore-fish fauna. Hence, there is no reason to assume that limited ecological capabilities of TEP species might limit westward migration of fishes even if it does so for invertebrates.

Many more westward migrants are known from the Hawaiian Islands than from the Marquesas; in fact all 23 supposed westward migrants are found at Hawai'i and only five at the Marquesas. Several factors likely contribute to this bias. First, the Marquesas represent a much smaller target than the Hawaiian Islands. Second, even though westward flow toward the Marquesas is faster than that toward Hawai'i, the Marquesas may effectively be more isolated than Hawai'i by an eastward current that intermittently impinges on them. Third, although the westward current flowing toward Hawai'i has a tropical origin, the current carrying any propagules to the Marquesas originates in a cool part of the eastern Pacific with a largely temperate fauna. Fourth, flotsam migration seems more likely to occur toward Hawai'i (and Johnston Island) than to the Marquesas. However, a sampling bias may also contribute to this difference: with a long history of ichthyological studies and the large population of fishers and scuba divers likely to notice unusual fishes, the Hawaiian fauna is very well known. In contrast the Marquesas are isolated, with a small human population including very few people equipped to identify transpacific species, little recreational scuba activity, and a very short history of research on its fish fauna with substantial parts of the archipelago yet to be visited by professional ichthyologists.

Previous analyses relied on distributional data to indicate the likely direction of migration across the EPB by transpacific fishes. Recent genetic studies have revealed part of the history of range expansion among widespread transpacific taxa and indicate substantial variation in how the EPB has affected the composition of the TEP shore-fish fauna. However, most such studies lack sufficient geographic scope and analytical sensitivity to provide a general picture of the level of bias in the direction of historical and current migration across the EPB.

ACKNOWLEDGMENTS

We are indebted to Gerald R. Allen, Richard L. Pyle, John E. Randall, John L. Earle, Bruce C. Mundy, and Bruce B. Collette for sharing their information on the fish fauna of various parts of Oceania, including the Hawaiian, Line, and Marquesas Islands. Robert J. Lavenberg contributed to an early draft of this paper. Thanks to Giacomo Bernardi, Brian W. Bowen, John L. Earle, Haris A. Lessios, Bruce C. Mundy, and John E. Randall for reviewing the manuscript; to Bruce B. Collette, John E. Olney, and William F. Smith-Vaniz for comments on the status of several transpacific taxa; and to J. Howard Choat for information on pelagic larval durations. Ernesto Peña prepared the data for Table 5.

Literature Cited

Allen, G. R. 1985. An annotated and illustrated catalogue of the lutjanid species known to date. FAO Fish. Synop. No. 125, Vol. 6.

Allen, G. R., and J. E. Randall. 1977. Review of the sharpnose puffers (subfamily Canthigasterinae) in the Indo-Pacific. Rec. Aust. Mus. 30:475–517.

Allen, G. R., and D. R. Robertson. 1994. Fishes of the tropical eastern Pacific. University of Hawai'i Press, Honolulu.

———. 1996. An annotated checklist of the fishes of Clipperton Atoll, tropical eastern Pacific. Rev. Biol. Trop. 45:813–843.

———. 2002. *Halichoeres salmofasciatus*, a new species of wrasse (Labridae) from Isla del Coco, tropical eastern Pacific. Aqua 5:65–72.

Arai, T., M. Marui, M. J. Miller, and K. Tsukamoto. 2002. Growth history and inshore migration of the tropical eel *Anguilla marmorata* in the western Pacific. Mar. Biol. (Berl.) 140:309–316.

Bagarinao, T. 1994. Systematics, distribution, genetics and life history of milkfish, *Chanos chanos*. Environ. Biol. Fishes 39:23–41.

Bearez, P. 1996. Lista de los peces marinos del Ecuador continental. Rev. Biol. Trop. 44:731–741.

Benoit, H. P., P. Pepin, and J. A. Brown. 2000. Patterns of metamorphic age and length in marine fishes, from individuals to taxa. Can. J. Fish. Aquat. Sci. 57:856–869.

Bermingham, E., S. McCafferty, and A. P. Martin. 1997. Fish biogeography and molecular clocks: Perspectives from the Panamanian isthmus. Pages 113–128 *in* T. D. Kocher and C. A. Stepien, eds. Molecular systematics of fishes. Academic Press, New York.

Bernardi, G., G. Bucciarelli, D. Costagliola, D. R. Robertson, and J. B. Heiser. 2003. Ecology and evolution of the coral reef fish genus *Thalassoma* (Labridae): 1. Molecular phylogeography and biogeography. Mar. Biol. (Berl.) 144:369–375.

Bloom, S. A. 1981. Similarity indices in community studies: Potential pitfalls. Mar. Ecol. Prog. Ser. 5:125–128.

Bohlke, E. B., ed. 1989. Fishes of the western North Atlantic: Leptocephali. Mem. Sears Found. Mar. Res. No. 1, Pt. 9, Vol. 2. Yale University Press, New Haven, Connecticut.

Bohlke, E. B., and J. E. McCosker. 2001. The moray eels of Australia and New Zealand, with the description of two new species (Anguilliformes: Muraenidae). Rec. Aust. Mus. 53:71–102.

Bohlke, E. B., and J. E. Randall. 2000. A review of the moray eels (Anguilliformes: Muraenidae) of the Hawaiian Islands, with descriptions of two new species. Proc. Acad. Nat. Sci. Phila. 150:203–278.

Bowen, B. W., and W. S. Grant. 1997. Phylogeography of the sardines (*Sardinops* spp.): Assessing biogeographic models and population histories in temperate upwelling zones. Evolution 51:1601–1610.

Bowen, B. W., A. L. Bass, L. A. Rocha, W. S. Grant, and D. R. Robertson. 2001. Phylogeography of the trumpetfishes (*Aulostomus* spp.): Ring species complex on a global scale. Evolution 55:1029–1039.

Briggs, J. C. 1960. Fishes of worldwide (circumtropical) distribution. Copeia 1960:171–180.

———. 1961. The eastern Pacific barrier and the distribution of marine shore fishes. Evolution 15:545–554.

———. 1964. Additional transpacific shore fishes. Copeia 1964:706–708.

———. 1974. Marine zoogeography. McGraw-Hill, New York.

———. 1995. Global biogeography. Elsevier, New York.

———. 1999*a*. Coincident biogeographic patterns: Indo-West Pacific Ocean. Evolution 53:326–335.

———. 1999*b*. Modes of speciation: Marine Indo-West Pacific. Bull. Mar. Sci. 65:645–656.

———. 2003. Marine centers of origin as evolutionary engines. J. Biogeogr. 30:1–18.

Brogan, M. W. 1994. Distribution and retention of larval fishes near reefs in the Gulf of California. Mar. Ecol. Prog. Ser. 115:1–13.

Chambers, R. C. 1997. Environmental influences on egg and propagule sizes in marine fishes. Pages 63–102 *in* R. C. Chambers and E. A. Trippell, eds. Early life history and recruitment of fish populations. Chapman and Hall, London.

Chang, C. W., W. N. Tzeng, and Y. C. Lee. 2000. Recruitment and hatching dates of grey mullet (*Mugil cephalus* L.) juveniles in the Tanshui estuary of Northwest Taiwan. Zool. Stud. 39:99–106.

Chavez, F. P., and R. L. Smith. 1995. Biological and chemical consequences of open ocean upwelling. Pages 149–170 *in* C. P. Summerhays, K. C. Emeis, M. V. Angel, R. L. Smith, and B. Zeitzschel, eds. Upwelling in the ocean: Modern processes and ancient records. Wiley, New York.

Chavez, F. P., P. G. Strutton, G. E. Friederich, R. A. Feely, G. C. Feldman, D. G. Foley, and M. J. McPhaden. 1999. Biological and chemical response of the equatorial Pacific Ocean to the 1997–98 El Niño. Science (Washington, D.C.) 286:2126–2131.

Chavez, F. P., J. Ryan, S. E. Lluch-Cota, and M. C. Niquen. 2003. From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. Science (Washington, D.C.) 299:217–221.

Chen, L. 1999. Ontogenetic development in post-settlement scarids (Pisces: Scaridae): Transition in feeding modes. Ph.D. thesis, James Cook University, Townsville, Australia.

Chow, S., and H. Takeyama. 2000. Nuclear and mitochondrial DNA analyses reveal four genetically separated breeding units of the swordfish. J. Fish Biol. 56:1087–1098.

Clarke, T. A. 1995. Larvae of nearshore fishes in oceanic waters of the central equatorial Pacific. Pac. Sci. 49:134–142.

Coates, A. G., and J. A. Obando. 1996. The geologic evolution of the Central American isthmus. Pages 21–56 *in* J. B. C. Jackson, A. F. Budd, and A. G. Coates, eds. Evolution and environments in tropical America. University of Chicago Press, Chicago.

Colborn, J., R. E. Crabtree, J. B. Shaklee, E. Pfeiler, and B. W. Bowen. 2001. The evolutionary enigma of bonefishes (*Albula* spp.): Cryptic species and ancient separations in a globally distributed shorefish. Evolution 55:807–820.

Collette, B. B. 1995. Belonidae. Pages 919–926 *in* W. Fischer, F. Krupp, W. Schneider, C. Sommer, K. E. Carpenter, and V. H. Niem, eds. Guia FAO para la identificacion de especies para los fines de la pesca. Pacifico Centro-Oriental. Vol. 2. FAO, Rome.

Collette, B. B., and C. R. Aadland. 1996. Revision of the frigate tunas (Scombridae, *Auxis*), with descriptions of two new subspecies from the eastern Pacific. Fish. Bull. 94:423–441.

Collette, B. B., and H. Banford. 2001. Status of the eastern Pacific agujon needlefish *Tylosurus pacificus* (Steindachner, 1876). Rev. Biol. Trop. Suppl. 1:51–57.

Collette, B. B., and C. E. Nauen. 1983. FAO species catalogue. Vol. 2. Scombrids of the world. FAO, Rome.

Collette, B. B., C. Reeb, and B. A. Block. 2001. Systematics of the tunas and mackerels. Fish Physiol. (Tuna) 19:1–33.

Compagno, L. J. V. 1984*a*. FAO species catalogue. Vol. 4. Part I. Sharks of the world: Hexanchiformes to Lamniformes. FAO, Rome.

———. 1984*b*. FAO species catalogue. Vol. 4. Part II. Sharks of the world: Carcharhiniformes. FAO, Rome.

Compagno, L. J. V., and S. F. Cook. 1995. The exploitation and conservation of freshwater elasmobranchs: Status of taxa and prospects for the future. J. Aquaric. Aquat. Sci. 7:62–90.

Correial, A. T., C. Antunes, E. J. Isidro, and J. Coimbra. 2003. Changes in otolith microstructure and microchemistry during larval development of the European conger eel (*Conger conger*). Mar. Biol. (Berl.) 140:165–173.

Crosetti, D., W. S. Neilson, and J. C. Avise. 1994. Pronounced genetic structure of mitochondrial DNA among populations of the circumglobally distributed grey mullet (*Mugil cephalus*). J. Fish Biol. 44:47–58.

Darwin, C. 1872. The origin of species by means of natural selection. 6th ed. Random House, New York.

Dawson, C. E. 1985. Indo-Pacific pipefishes (Red Sea to the Americas). Gulf Coast Research Laboratory, Ocean Springs, Mississippi.

De Sylva, D. P., and F. Williams. 1986. Sphyraenidae. Pages 721–726 *in* M. M. Smith and P. C. Heemstra, eds. Smith's sea fishes. Springer, New York.

Doherty, P. J., S. Planes, and P. Mather. 1995. Gene flow and larval duration in seven species of fish from the Great Barrier Reef. Ecology 76:2373–2391.

Ekman, S. 1953. Zoogeography of the sea. Sidgwick and Jackson, London.

Eldin, G. 1983. Eastward flows of the south equatorial central Pacific. J. Phys. Oceanogr. 13:1461–1467.

Emerson, W. K. 1994. A zoogeographic summary of the marine molluscs of Clipperton Island (tropical eastern Pacific Ocean). Festivus 26:62–71.

Eschmeyer, W. N., E. S. Herald, and H. Hammann. 1983. A field guide to Pacific coast fishes of North America, from the Gulf of Alaska to Baja California. Houghton and Mifflin, Boston.

Fauchald, K. 1977. Polychaetes from intertidal areas in Panama, with a review of previous shallow-water records. Smithson. Contrib. Zool. 221:1–75.

Fedoryako, B. I. 1979. Triggerfishes of the genera *Canthidermis* and *Xanthichthys* (Balistidae, Tetraodontiformes) from the Indian and Pacific Oceans. J. Ichthyol. 19:19–30.

Firing, E., and R. Lukas. 1983. El Niño at the equator and at 159° W. Trop. Ocean-Atmos. Newsl. 21:9–11.

Firing, E., R. Lukas, J. Sadler, and K. Wyrtki. 1983. Equatorial undercurrent disappears during 1982–83 El Niño. Science (Washington, D.C.) 222:1121–1123.

Fischer, W., F. Krupp, W. Schneider, C. Sommer, K. E. Carpenter, and V. H. Niem, eds. 1995. Guia FAO para la identificacion de especies para los fines de la pesca. Pacifico Centro-Oriental. Vols 1–3. FAO, Rome.

Fowler, A. J. 1989. Description, interpretation and use of the microstructure of otoliths from juvenile butterflyfishes (family Chaetodontidae). Mar. Biol. (Berl.) 102:167–181.

Fowler, H. W. 1928. The fishes of Oceania. Mem. Bernice P. Bishop Mus. 10:1–540.

Fritsche, R. A. 1976. A review of the cornetfishes, genus *Fistularia* (Fistulariidae), with a discussion of intrageneric relationships and zoogeography. Bull. Mar. Sci. 26:196–204.

Garcia, M., M. Hall, A. Pares-Sierra, and P. Arenas. 1999. Simulated trajectories of floating objects entering the eastern tropical Pacific Ocean. Inter-Am. Trop. Tuna Comm. Spec. Rep. 11:346–395.

Garrison, G. 2000. Peces de la Isla del Coco (Isla del Coco Fishes). InBio, Herederia, Costa Rica.

Garth, J. S. 1974. On the occurrence in the eastern tropical Pacific of Indo-West Pacific decapod crustacean commensal with reef-building corals. Proc. 2nd Int. Coral Reef Symp. 1:397–404.

Glynn, P. W., and J. S. Ault. 2000. A biogeographic analysis and review of the far eastern Pacific coral reef region. Coral Reefs 19:1–23.

Glynn, P. W., and G. R. Wellington. 1983. Corals and coral reefs of the Galápagos Islands. University of California Press, Berkeley.

Glynn, P. W., R. H. Stewart, and J. E. McCosker. 1972. Pacific coral reefs of Panama: Structure, distribution, and predators. Geol. Rundschau 61:483–519.

Gooding, R. M., and J. J. Magnuson. 1967. Ecological significance of a drifting object to pelagic fishes. Pac. Sci. 21:486–497.

Grant, W. S., and B. W. Bowen. 1998. Shallow population histories in deep evolutionary lineages of marine fishes: Insights from the sardines and anchovies and lessons for conservation. J. Hered. 89:415–426.

Graves, J. E. 1998. Molecular insights into the population structures of cosmopolitan marine fishes. J. Hered. 89:427–437.

Graves, J. E., and A. E. Dizon. 1989. Mitochondrial DNA sequence similarity of Atlantic and Pacific albacore tuna (*Thunnus alalunga*). Can. J. Fish. Aquat. Sci. 46:870–873.

Graves, J. E., and J. R. McDowell. 1995. Inter-ocean genetic divergence of istiophorid billfishes. Mar. Biol. (Berl.) 122:193–203.

Grigg, R. W., and R. Hey. 1992. Paleoceanography of the tropical eastern Pacific Ocean. Science (Washington, D.C.) 255:172–178.

Grove, J. S. 1984. El Niño 1982–1983 and new records of Indo-West Pacific fishes at the Galapagos. West. Soc. Malacol. Annu. Rep. 21:5.

———. 1986. Some evolutionary implications of protracted El Niño events in the colonization and ecological balance of fish populations in the Galápagos Archipelago. UNESCO Intergovernmental Oceanographic Commission, Workshop Report 49:77.

Grove, J. S., and R. E. Lavenberg. 1997. Fishes of the Galápagos Islands. Stanford University Press, Stanford, California.

Hastings, P. A. 2000. Biogeography of the tropical eastern Pacific: Distribution and phylogeny of chaenopsid fishes. Zool. J. Linn. Soc. 128:319–335.

Heemstra, P. C. 1995. Lobotidae. Page 1226 *in* W. Fischer, F. Krupp, W. Schneider, C. Sommer, K. E. Carpenter, and V. H. Niem, eds. Guia FAO para la identificacion de especies para los fines de la pesca. Pacifico Centro-Oriental. Vol. 3. FAO, Rome.

Heist, E. J., J. A. Musick, and J. E. Graves. 1996. Genetic population structure of the shortfin mako (*Isurus oxyrinchus*) inferred from restriction fragment length polymorphism analysis of mitochondrial DNA. Can. J. Fish. Aquat. Sci. 53:583–588.

Hobson, E. S., and V. Walters. 1968. First eastern Pacific record of *Canthigaster amboinensis*, an Indo-West Pacific pufferfish. Copeia 1968:861–862.

Hubbs, C. L., and R. H. Rosenblatt. 1961. Effects of the equatorial currents of the Pacific on the distribution of fishes and other animals. Pages 340–341 *in* Proc. 10th Pacif. Sci. Congr. (abstract).

Hughes, T. P., D. R. Bellwood, and S. R. Connolly. 2002. Biodiversity hotspots, centres of endemicity and the conservation of coral reefs. Ecol. Lett. 5:775–784.

Humann, P., and N. Deloach. 2003. Reef fish identification: Galapagos. 2nd ed. New World Publications, Jacksonville, Florida.

Hunter, J. R., and C. T. Mitchell. 1966. Association of fishes with flotsam in the offshore waters of Central America. Fish. Bull. 66:13–29.

Jokiel, P. L. 1984. Long-distance dispersal of reef corals by rafting. Coral Reefs 3:113–116.

Jones, G. P., M. L. Caley, and P. L. Mundy. 2002. Rarity in coral reef fish communities. Pages 81–102 *in* P. F. Sale, ed. Coral reef fishes: Dynamics and diversity in a complex ecosystem. Academic Press, New York.

Jordan, D. S. 1908. The law of geminate species. Am. Nat. 62:73–80.

Kawahara, S., Y. Uozumi, and H. Yamada. 1988. First record of a carangid fish, *Trachurus murphyi* from New Zealand. Jpn. J. Ichthyol. 35:212–214.

Kokita, T. 2003. Potential latitudinal variation in egg size and number of a geographically widespread reef fish, revealed by common-environment experiments. Mar. Biol. (Berl.) 143:593–601.

Lavenberg, R. J. 1992. A new moray eel (Muraenidae: *Gymnothorax*) from Oceanic islands of the South Pacific. Pac. Sci. 46:58–67.

Leis, J. M. 1984. Larval dispersal and the East Pacific Barrier. Oceanogr. Trop. 19:181–192.

———. 1986. Ecological requirements of Indo-Pacific larval fishes: A neglected zoogeographic factor. Pages 759–766 in Proc. 2nd Int. Conf. Indo-Pacific Fish. Ichthyological Society of Japan, Tokyo.

———. 1989. Larval biology of butterflyfishes (Pisces, Chaetodontidae): What do we really know. Environ. Biol. Fishes 25:87–100.

———. 1991. The pelagic stage of reef fishes: The larval biology of coral reef fishes. Pages 183–230 *in* P. F. Sale, ed. The ecology of coral reef fishes. Academic Press, New York.

Leis, J. M., and B. M. Carson-Ewart, eds. 2000. The larvae of Indo-Pacific coastal fishes: An identification guide to marine fish larvae. Fauna Malesiana Handbooks. 2. Brill, Leiden.

Leis, J. M., and M. McCormick. 2002. The biology, behavior and ecology of the pelagic, larval stage of coral reef fishes. Pages 171–200 *in* P. F. Sale, ed. Coral reef fishes: Dynamics and diversity in a complex ecosystem. Academic Press, New York.

Lessios, H. A., B. D. Kessing, G. M. Wellington, and A. Graybeal. 1996. Indo-Pacific echinoids in the tropical eastern Pacific. Coral Reefs 15:133–142.

Lessios, H. A., B. D. Kessing, and D. R. Robertson. 1998. Massive geneflow across the world's most potent marine biogeographic barrier. Proc. R. Soc. Lond. B Biol. Sci. 265:583–588.

Lessios, H. A., B. D. Kessing, D. R. Robertson, and G. Paulay. 1999. Phylogeography of the pantropical sea urchin *Eucidaris* in relation to land barriers and ocean currents. Evolution 53:806–817.

Lessios, H. A., B. D. Kessing, and J. S. Pearse. 2001. Population structure and speciation in tropical seas: Global phylogeography of the sea urchin *Diadema*. Evolution 55:955–975.

Lessios, H. A., J. Kane, and D. R. Robertson. 2003. Phylogeography of the pantropical sea urchin *Tripneustes*: Contrasting patterns of population structure between oceans. Evolution 57:2026–2036.

Longhurst, A. 1998. Ecological geography of the sea. Academic Press, New York.

Markle, D. F., and J. E. Olney. 1990. Systematics of the pearlfishes (Pisces: Carapidae). Bull. Mar. Sci. 47:269–410.

Mayr, E. 1954. Geographic speciation in tropical echinoids. Evolution 8:1–18.

McCormick, M. I. 1994. Variability in age and size at settlement of the tropical goatfish *Upeneus tragula* (Mullidae) in the northern Great Barrier Reef lagoon. Mar. Ecol. Prog. Ser. 103:1–15.

———. 1999. Delayed metamorphosis of a tropical reef fish (*Acanthurus triostegus*): A field experiment. Mar. Ecol. Prog. Ser. 176:25–38.

McCormick, M. I., and B. W. Molony. 1995. Influence of water temperature during the larval stage on size, age and body condition of a tropical reef fish at settlement. Mar. Ecol. Prog. Ser. 118:59–68.

McCosker, J. E. 1987. The fishes of the Galapagos Islands. Oceanus 30:28–32.

———. 1998. (Review of) Fishes of the Galápagos Islands, by J. S. Grove and R. J. Lavenberg, 1997, Stanford University Press. Copeia 1998:809–812.

———. 2002. Notes on Hawaiian snake eels (Pisces: Ophichthidae), with comments on *Ophichthus bonaparti*. Pac. Sci. 56:23–34.

McCosker, J. E., and P. H. Humann. 1996. New records of Galapagos fishes. Not. Galapagos 56:18–22.

McCosker, J. E., and D. R. Robertson. 2001. *Aplatophis zorro*, a new species of eastern Pacific snake-eel, with comments on New World ophichthid distributions (Anguilliformes: Ophichthidae). Rev. Biol. Trop. Suppl. 49:13–19.

McCosker, J. E., and R. H. Rosenblatt. 1975. The moray eels (Pisces: Muraenidae) of the Galapagos Islands, with new records and synonomies of extralimital species. Proc. Calif. Acad. Sci. Ser. 4, 40:417–427.

———. 1993. A revision of the snake eel genus *Myrichthys* (Anguilliformes: Ophichthidae) with the description of a new eastern Pacific species. Proc. Calif. Acad. Sci. 48:153–169.

McCosker, J. E., L. R. Taylor, and R. R. Warner. 1978. Ichthyological studies at Galápagos. Not. Galapagos 17:13–15.

McCosker, J. E., R. H. Bustamante, and G. M. Wellington. 2003. Freshwater eels, *Anguilla marmorata*, discovered at Galápagos. Not. Galapagos 62:2–6.

Meekan, M. G., J. H. Carleton, A. D. McKinnon, K. Flynn, and M. Furnas. 2003. What determines the growth of tropical reef fish larvae in the plankton: Food or temperature? Mar. Ecol. Prog. Ser. 256:193–204.

Merlen, G. 1988. Two new butterflyfish records from Wenmen Island. Not. Galapagos 46:8–10.

Mora, C., and A. F. Ospina. 2001. Tolerance to high temperatures and potential impact of sea warming on reef fishes of Gorgona Island (tropical eastern Pacific). Mar. Biol. (Berl.) 139:765–769.

Mora, C., V. Francisco, and F. A. Zapata. 2001. Dispersal of juvenile and adult reef fishes associated with floating objects and their recruitment into Gorgona Island reefs, Colombia. Bull. Mar. Sci. 68:557–561.

Mora, C., P. M. Chittaro, P. F. Sale, J. P. Kritzer, and S. A. Ludsin. 2003. Patterns and processes in reef fish diversity. Nature (Lond.) 421:933–936.

Mundy, B. C. In press. A checklist of the fishes of the Hawaiian Archipelago. Bishop Mus. Bull. Zool.

Myers, R. F. 1999. Micronesian reef fishes. 3rd ed. Coral Graphics, Guam.

Nakamura, I. 1985. FAO species catalogue. Vol. 5. Billfishes of the world. FAO, Rome.

Nilsson, G. E., and S. Ostlund-Nilsson. 2004. Hypoxia in paradise: Widespread hypoxia tolerance in coral reef fishes. Biol. Lett. 271:S30–S33.

Oda, D. K., and J. D. Parrish. 1981. Ecology of commercial snappers and groupers introduced to Hawaiian reefs. Proc. 4th Int. Coral Reef Symp., Manila 1:59–67.

Paulay, G. 1997. Diversity and distribution of reef organisms. Pages 298–353 *in* C. Birkeland, ed. The life and death of coral reefs. Chapman and Hall, New York.

Pfeiler, E., M. A. Mendoza, and F. A. Manrique. 1988. Premetamorphic bonefish (*Albula* sp.) leptocephali from the Gulf of California with comments on life history. Environ. Biol. Fishes 21:241–249.

Pietsch, T. W., and D. B. Grobeker. 1987. Frogfishes of the world: Systematics, zoogeography and behavioral ecology. Stanford University Press, Stanford, California.

Planes, S. 1993. Genetic differentiation in relation to restricted larval dispersal of the convict surgeonfish *Acanthurus triostegus* in French Polynesia. Mar. Ecol. Prog. Ser. 98:237–246.

———. 1998. Genetic diversity and dispersal capabilities in marine fish. Evol. Biol. 30:253–298.

———. 2002. Biogeography and larval dispersal inferred from population genetic analysis. Pages 201–220 *in* P. F. Sale, ed. Coral reef fishes: Dynamics and diversity in a complex ecosystem. Academic Press, New York.

Planes, S., and C. Fauvelot. 2002. Isolation by distance and vicariance drive genetic structure of a coral reef fish in the Pacific Ocean. Evolution 56:378–399.

Planes, S., M. Parroni, and C. Chauvet. 1998. Evidence of limited gene flow in three species of coral reef fishes in the lagoon of New Caledonia. Mar. Biol. (Berl.) 130:361–368.

Planes, S., G. Lecaillon, P. Lenfant, and M. Meekan. 2002. Genetic and demographic variation in new recruits of *Naso unicornis*. J. Fish Biol. 61:1033–1049.

Pyle, R. L. 1999. Patterns of Pacific reef and shore fish biodiversity. Pages 157–175 *in* L. G. Eldredge, J. E. Maragos, P. F. Holthus, and H. F. Takeuchi, eds. Marine and coastal biodiversity in the tropical island Pacific region. Vol. 2. Population, development, and conservation priorities. Pacific Science Association, Honolulu.

Randall, J. E. 1956. A revision of the surgeonfish genus *Acanthurus*. Pac. Sci. 10:159–235.

———. 1963. Review of the hawkfishes (family Cirrhitidae). Proc. U.S. Natl. Mus. 3472:389–451.

———. 1972. The Hawaiian trunkfishes of the genus *Ostracion*. Copeia 1972:767–768.

———. 1985. Fishes. Pages 462–481 *in* B. Delesalle, R. Galzin, and B. Salvat, eds. French Polynesian coral reefs. Vol. 1. Proc. 5th Int. Coral Reef Congress, Tahiti, 1985. Antenne Museum-EPHE, Moorea.

———. 1997. The hawkfish *Cirritichthys serratus* Randall, a junior synonym of *C. falco*. Micronesica 30:199–203.

———. 2000. Revision of the Indo-Pacific labrid fishes of the genus *Stethojulis*, with descriptions of two new species. Indo-Pac. Fishes 31:1–42.

Randall, J. E., and M. L. Bauchot. 1999. Clarification of the two Indo-Pacific species of bonefishes, *Albula glossodonta* and *A forsteri*. Cybium 23:79–83.

Randall, J. E., and B. A. Carlson. 1999. *Caranx caballus*, a new immigrant carangid fish to the Hawaiian Islands from the tropical eastern Pacific. Pac. Sci. 53:357–360.

Randall, J. E., and J. L. Earle. 2000. Annotated checklist of the shore fishes of the Marquesas Islands. Bishop Mus. Occas. Pap. 66:1–39.

Randall, J. E., and J. E. McCosker. 1975. The eels of Easter Island with a description of a new moray. Contrib. Sci. (Los Angel.) 264:1–32.

Randall, J. E., and B. C. Mundy. 1998. *Balistes polylepis* and *Xanthichthys caeruleolineatus*, two large triggerfishes (Tetraodontiformes: Balistidae) from the Hawaiian Islands, with a key to the Hawaiian species. Pac. Sci. 52:322–333.

Randall, J. E., and H. A. Randall. 2001. Review of the fishes of the genus *Kuhlia* (Perciformes: Kuhliidae) of the central Pacific. Pac. Sci. 55:227–256.

Randall, J. E., K. Matsuura, and A. Zama. 1978. A revision of the triggerfish genus *Xanthichthys*, with a description of a new species. Bull. Mar. Sci. 28:688–706.

Randall, J. E., G. R. Allen, and D. R. Robertson. 2003. *Myripristis earlei*, a new soldierfish (Beryciformes: Holocentridae) from the Marquesas and Phoenix Islands. Zool. Stud. 42:405–410.

Richmond, R. H. 1990. The effects of El Niño/Southern Oscillation on the dispersal of corals and other marine organisms. Pages 153–190 *in* P. W. G. Glynn, ed. Global ecological consequences of the 1982–83 El Niño Southern Oscillation. Elsevier, Amsterdam.

Riginos, C., and B. C. Victor. 2001. Larval spatial distributions and other early life-history characteristics predict genetic differentiation in eastern Pacific blennioid fishes. Proc. R. Soc. Lond. B Biol. Sci. 268:1–6.

Robertson, D. R. 1998. Do coral-reef fish faunas have a distinctive taxonomic structure? Coral Reefs 17:179–186.

Robertson, D. R., and G. R. Allen. 1996. Zoogeography of the shorefish fauna of Clipperton Atoll. Coral Reefs 15:121–131.

———. 2002. Shorefishes of the tropical eastern Pacific: An information system. CD-ROM, Smithsonian Tropical Research Institute, Balboa.

Robinet, T., R. Lecomte-Finiger, K. Escoubeyrou, and E. Feunteun. 2003. Tropical eels *Anguilla* spp. recruiting to Réunion Island in the Indian Ocean: Taxonomy, patterns of recruitment and early life histories. Mar. Ecol. Prog. Ser. 259:263–272.

Rosenblatt, R. H. 1967. The zoogeographic relationships of the marine shore fishes of tropical America. Stud. Trop. Oceanogr. (Miami) 5:579–592.

Rosenblatt, R. H., and B. W. Walker. 1963. The marine shore fishes of the Galapagos Islands. Occas. Pap. Calif. Acad. Sci. 44:97–106.

Rosenblatt, R. H., and R. S. Waples. 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.

Rosenblatt, R. H., J. E. McCosker, and I. Rubinoff. 1972. Indo-West Pacific fishes in the Gulf of Chiriqui, Panama. Contrib. Sci. (Los Angel.) 234:1–18.

Rubio, E. A., A. Suarez, F. Estupian, W. Henao, and B. Vargas. 1992. Los recursos ictiologicos de la Isla Malpelo (Colombia). I. Una revision de su conocimiento y nuevos reportes para la ictiofauna de la Isla. Pages 642–658 *in* VIII Seminario Nacional de las Ciencia y las Tecnologias del Mar y Congreso Centroamericano y del Caribe en Ciencias del Mar. Memorias Tomo 2.

Ruttenberg, B. I. 2000. An unusual pulse of recruitment of two coral reef fishes in the Galapagos Islands coincident with the 1997–98 El Niño. Bull. Mar. Sci. 67:869–874.

Scheltema, F. S. 1988. Initial evidence for the transport of teleplanic larvae of benthic invertebrates across the East Pacific barrier. Biol. Bull. (Woods Hole) 174:145–152.

Scoles, D. R., B. B. Collette, and J. E. Graves. 1998. Global phylogeography of the mackerels of the genus *Scomber*. Fish. Bull. 96:823–842.

Shasky, D. R. 1985. Update on mollusks with Indo-Pacific faunal affinities in the tropical East Pacific. West. Soc. Malacol. Annu. Rep. 18:27.

Smith, C. L. 1997. National Audubon guide to the tropical marine fishes of the Caribbean, the Gulf of Mexico, Florida, the Bahamas, and Bermuda. Knopf, New York.

Smith-Vaniz, W. 1995. Carangidae. Pages 940–986 *in* W. Fischer, F. Krupp, W. Schneider, C. Sommer, K. E. Carpenter, and V. H. Niem, eds. Guia FAO para la identificacion de especies para los fines de la pesca. Pacifico Centro-Oriental. Vol. 2. FAO, Rome.

Sponaugle, S., and R. K. Cowen. 1994. Larval duration and recruitment patterns of two Caribbean gobies (Gobiidae): Contrasting early life histories in demersal spawners. Mar. Biol. (Berl.) 120:133–143.

Springer, V. G. 1982. Pacific Plate biogeography with special reference to the shore fishes. Smithson. Contrib. Zool. 367:1–182.

Starnes, W. C. 1988. Revision, phylogeny and biogeographic comments on the circumtropical marine percoid fish family Priacanthidae. Bull. Mar. Sci. 43:117–203.

Stepien, C. A., and R. H. Rosenblatt. 1996. Genetic divergence in antitropical marine fishes (*Trachurus*, *Merluccius*, and *Scomber*) between North and South America. Copeia 1996:586–598.

Stepien, C. A., J. E. Randall, and R. H. Rosenblatt. 1994. Genetic and morphological divergence of a circumtropical complex of goatfishes: *Mulloidichthys vanicolensis*, *M. dentatus*, and *M. martinicus*. Pac. Sci. 48:44–56.

Streelman, J. T., M. Alfaro, M. W. Westneat, D. R. Bellwood, and S. A. Karl. 2002. Evolutionary history of the parrotfishes: Biogeography, ecomorphology, and comparative diversity. Evolution 56:961–971.

Stroud, G., B. Goldman, and W. Gladstone. 1989. Larval development, growth and age determination in the sharpnose puffer *Canthigaster valentini* (Teleostei: Tetraodontidae). Jpn. J. Ichthyol. 36:327–337.

Teske, P. R., M. I. Cherry, and C. A. Matthee. 2003. The evolutionary history of seahorses (Syngnathidae: *Hippocampus*): Molecular data suggest a West Pacific origin and two invasions of the Atlantic Ocean. Mol. Phylogenet. Evol. In Press.

Thompson, D. A., L. T. Findley, and A. N.

Kerstitch. 1979. Reef fishes of the Sea of Cortez. Wiley, New York.

Thomson, J. M. 1997. The Mugilidae of the world. Mem. Queensl. Mus. 41:457–562.

Thresher, R. E. 1991. Geographic variation in the ecology of coral reef fishes: Evidence, evolution and possible implications. Pages 401–436 *in* P. F. Sale, ed. The ecology of coral reef fishes. Academic Press, New York.

Thresher, R. E., and E. B. Brothers. 1985. Reproductive ecology and biogeography of Indo-West Pacific angelfishes (Pisces: Pomacanthidae). Evolution 39:878–887.

———. 1989. Evidence of intra- and interoceanic regional differences in the early life history of reef-associated fishes. Mar. Ecol. Prog. Ser. 57:187–205.

Thresher, R. E., P. L. Colin, and L. J. Bell. 1989. Planktonic duration, distribution and population structure of western and central Pacific damselfishes (Pomacentridae). Copeia 1989:420–434.

Vermeij, G. J. 1978. Biogeography and adaptation: Patterns of marine life. Harvard University Press, Cambridge, Massachusetts.

———. 1987. The dispersal barrier in the tropical Pacific: Implication for molluscan speciation and extinction. Evolution 41:1046–1058.

———. 1991. When biotas meet: Understanding biotic interchange. Science (Washington, D.C.) 253:1099–1104.

Vermeij, G. J., and G. Rosenberg. 1993. Giving and receiving: The tropical Atlantic as donor and recipient region for invading species. Am. Malacol. Bull. 10:181–194.

Victor, B. C. 1986. Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (Family Labridae). Mar. Biol. (Berl.) 90:317–326.

———. 1987. Growth, dispersal, and identification of planktonic labrid and pomacentrid reef-fish larvae in the eastern Pacific Ocean. Mar. Biol. (Berl.) 95:145–152.

Victor, B. C., and G. M. Wellington. 2000. Endemism and the pelagic larval duration of reef fishes in the eastern Pacific Ocean. Mar. Ecol. Prog. Ser. 205:241–248.

Victor, B. C., G. M. Wellington, D. R. Robertson, and B. Ruttenberg. 2001. The effects of the El Niño–Southern Oscillation event on the distribution of reef associated labrid fishes in the eastern Pacific Ocean. Bull. Mar. Sci. 69:279–288.

Ward, R. D., N. G. Elliott, B. H. Innes, A. J. Smolenski, and P. M. Grewe. 1997. Global population structure of yellowfin tuna, *Thunnus albacares*, inferred from allozyme and mitochondrial DNA variation. Fish. Bull. 95:566–575.

Wellington, G. M., and D. R. Robertson. 2001. Variation in larval life-history traits among reef fishes across the Isthmus of Panama. Mar. Biol. (Berl.) 138:11–22.

Wellington, G. M., and B. C. Victor. 1989. Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). Mar. Biol. (Berl.) 101:557–567.

———. 1992. Regional differences in duration of the planktonic larval stage of reef fishes in the eastern Pacific Ocean. Mar. Biol. (Berl.) 113:491–498.

Whitehead, P. J. P. 1985. Clupeoid fishes of the world: An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, anchovies and wolfherrings. FAO species catalogue. Vol. 7. Pts 1 and 2. FAO, Rome.

Whitehead, P. J. P., and R. Rodriguez-Sanchez. 1995. Albulidae. Pages 851–853 *in* W. Fischer, F. Krupp, W. Schneider, C. Sommer, K. E. Carpenter, and V. H. Niem, eds. Guia FAO para la identificacion de especies para los fines de la pesca. Pacifico Centro-Oriental. Vol. 2. FAO, Rome.

Williams, D. McB. 1991. Patterns and processes in the distribution of coral reef fishes. Pages 437–474 *in* P. F. Sale, ed. The ecology of coral reef fishes. Academic Press, New York.

Wilson, D. T., and M. I. McCormick. 1999. Microstructure of settlement-marks in the otoliths of tropical reef fishes. Mar. Biol. (Berl.) 134:29–41.

Wilson, D. T., and M. G. Meekan. 2002. Growth-related advantages for survival to the point of replenishment in the coral reef fish *Stegastes partitus* (Pomacentridae). Mar. Ecol. Prog. Ser. 231:247–260.

Wilson, G. 2001. Early post-settlement life history in *Lethrinus* species (Pisces: Lethrinidae): Systematics, distribution and development. Ph.D. thesis, James Cook University, Townsville, Australia.

Wyrtki, K. 1965. Surface currents of the eastern tropical Pacific Ocean. Inter-Am. Trop. Tuna Comm. Bull. 9:296–304.

———. 1967. Circulation and water masses in the eastern equatorial Pacific Ocean. Int. J. Oceanol. Limnol. 1:117–147.

———. 1985. Sea level fluctuations in the Pacific during the 1982–83 El Niño. Geophys. Res. Lett. 12:125–128.

Wyrtki, K., E. Firing, D. Halpern, R. Knox, G. J. McNally, W. C. Patzert, E. D. Stroup, B. A. Taft, and R. Williams. 1981. The Hawaii to Tahiti shuttle experiment. Science (Washington, D.C.) 211:22–28.

Zapata, F. A., and P. A. Herron. 2002. Pelagic larval duration and geographic distribution of tropical eastern Pacific snappers (Pisces: Lutjanidae). Mar. Ecol. Prog. Ser. 230:295–300.

Appendix 1

Additional Information on Transpacific Fishes Listed in Table 1

Notorynchus cepedianus: occurs on the northwestern and southwestern edges of the Pacific but not the Pacific Plate. *Carcharhinus albimarginatus:* occurs in the northwestern Pacific and scattered central Pacific sites, including to the west of the Line Islands; possibly vagrant in Hawai'i. *Carcharhinus brachyurus:* known from the northern and southern temperate parts of the eastern Pacific (extending into the fringes of the TEP) and the continental northwestern and southwestern Pacific. *Carcharhinus galapagensis:* found at scattered locations in the central (but not western) Pacific, including the Phoenix Islands to the west of the Line Islands, and southern French Polynesia. *Carcharhinus leucas:* occurs along the western edge of the Pacific, known in the South-central Pacific from a single record at the Tuamotus. *Carcharhinus limbatus:* found along the western edge of the Pacific but at few locations in the central Pacific, not including the Line Islands. *Carcharhinus obscurus:* unconfirmed reports from Hawai'i; no records from elsewhere on the Pacific Plate. *Triaenodon obesus:* at Cocos Island in the TEP it is ubiquitous and can readily be observed in aggregations of dozens of individuals; also reaches moderate densities on the coast of Panama and occurs as far north as the tip of Baja California and at the Revillagigedos Islands (E. Ochoa, pers. comm., 2003). *Sphyrna lewini:* occurs along the western edge of the Pacific, in Oceania restricted to the easternmost islands: Hawai'i (as a resident), the Line Islands, and French Polynesia. *Sphyrna mokarran:* occurs in the western Pacific, but in Oceania is known only from one sight record at Hawai'i by R. Pyle (pers. comm., 2000). *Sphyrna zygaena:* occurs in the northwestern and southwestern corners of the Pacific; on the Pacific Plate only at the Hawaiian Islands. *Odontaspis ferox:* in the northwestern and southwestern Pacific; known in the central Pacific only from Hawai'i, where it probably is a resident (B. C. Mundy, pers. comm., 2003). *Dasyatis dipterura:* known outside the TEP from a single juvenile specimen collected in Hawai'i (J. E. Randall, pers. comm., 2002). *Taeniura meyeni:* in the TEP common at Cocos Island (Garrison 2000) and the Galápagos (Grove and Lavenberg 1997; J. Earle, pers. comm., 2003). *Anguilla marmorata:* McCosker et al. (2003) discussed a specimen of what likely is this species collected in the Galápagos in 1997, although there are indications of previous arrivals. McCosker et al. (2003) considered these to be vagrants that crossed the EPB. No other anguillids are known from the TEP. From a reproductive perspective this species may effectively be disjunct because the only known spawning area in the Pacific is in the western Pacific. *Enchelychore lichenosa:* known only from Japan/Taiwan and the Galápagos; two specimens collected at the Galápagos in 1964 and two in 1966 (McCosker and Rosenblatt 1975), three different individuals photographed between 1990 and 1992 (Robertson and Allen 2002, Humann and Deloach 2003); not known elsewhere despite extensive collecting at intervening locations. *Enchelynassa canina:* in the TEP known only from Clipperton, where it is not uncommon, and western Panama. *Gymnothorax buroensis:* not uncommon in rotenone collections at Clipperton and at islands in the Gulf of Chiriquí, Panama; known in Hawai'i (where it is replaced by *G. eurostus*, see Bohlke and Randall [2000]) from a single specimen, perhaps of TEP origin? *Gymnothorax flavimarginatus:* moderately common at the offshore islands of the TEP and in western Panama. *Gymnothorax javanicus:* one large adult photographed by D.R.R. at Cocos Island in 1997 (Robertson and Allen 2002, and see Garrison 2000), one by P. Humann in the Galápagos after 2000 (J.E.M., unpubl data), and two 1.5- to 2-m individuals observed by D.R.R. (and photographed by J. Earle) at Coiba Island, Panama, in May 2003. *Gymnothorax meleagris:* photographed by Humann and Deloach (2003) at the Galápagos; one adult observed at Cocos Island in 1997 by J. Earle (pers. comm., 1997). *Gymnothorax pictus:* not uncommon in the intertidal reef flat (its typical habitat) at Clipperton. *Gymnothorax undulatus:* first recorded in western Panama in the early 1970s (Rosenblatt et al. 1972); often seen by D.R.R. there in 1999 and 2003 and in the Pearl Islands (Gulf of Panama) in 2002; one individual seen in the Revillagigedos by A. Kerstitch (pers. comm., 1995); not currently known from the Marquesas but present in the Society and Tuamotu Islands. *Uropterygius supraforatus:* several adults of various sizes collected by D.R.R. with rotenone at 5 m depth in the groove-and-spur zone of the Clipperton reef in April 1998. *Etrumeus teres:* in the Pacific there are disjunct populations in the eastern Pacific (including the TEP), Hawai'i, Japan, and southeastern Australia. Whitehead (1985) treated these as a single species but noted that they could be separate. *Encheliophis dubius:* outside the TEP known only from Hawai'i, from a single confirmed record (B. C. Mundy and J. E. Randall, pers. comms., 2003). *Encheliophis vermicularis:* only found at the western and eastern fringes of the Pacific. Randall's (1985) record from the Society Islands appears to be an error (J. E. Randall, pers. comm., 2000). *Brotula multibarbata:* in the TEP known from two small juveniles (identified by J. Neilsen) collected by D.R.R. in a rotenone station at 40 m depth at Clipperton in April 1998. *Antennarius coccineus:* replaced in the Hawaiian Islands by its sister species, *A. drombus*. *Antennarius commerson:* scattered records at widely distributed TEP sites over a quarter century (Pietsch and Grobeker 1987, Garrison 2000, Robertson and Allen 2002, Humann and Deloach 2003; A. Kerstitch, pers. comm., 1995); this large, cryptic, typically uncommon species occurs to depths of 70 m, and its apparent absence from the Line and Marquesas Islands may reflect inadequate sampling. *Myripristis berndti:* abundant at the offshore islands of the TEP and moderately common at islands in the Gulf of Chiriquí, western Panama. *Plectrypops lima:* its absence from the Line Islands may be a sampling artifact because *P. lima* is a small, highly cryptic fish that typically is collected by poison from deep caves. *Doryrhamphus excisus excisus:* two subspecies occur in the TEP, *D. excisus paulus* (endemic to the Revillagigedos Islands) and *D. e. excisus*, which occurs throughout the remainder of the TEP (Dawson 1985), where it is common (D.R.R., pers. obs.). *Aulostomus chinensis:* common at the oceanic islands of the TEP but rare on the mainland. *Taenianotus triacanthus:* known in the TEP from one specimen photographed in the Galápagos (McCosker 1987). *Cookeolus japonicus:* the lack of a Marquesan record may reflect a sampling bias, because it usually occurs in deep water (to 400 m). *Priacanthus alalaua:* known only from Hawai'i and, in the TEP, at the Revillagigedos Islands and Baja California. *Carangoides caballus:* abundant on the mainland of the TEP but uncommon at the oceanic islands. *Caranx lugubris:* in the TEP most common around the offshore islands. *Caranx melampygus:* in the TEP most common at the oceanic islands; also common at islands in western Panama. *Caranx sexfasciatus:* in the TEP is most common around the offshore islands and islands of western Panama. *Decapterus macrosoma:* not known from the Marquesas, but occurs in the Society Islands and westward from there. *Decapterus muroadsi:* besides the TEP, populations occur in the northwestern and southwestern Pacific and in the central Pacific only at Hawai'i. *Elegatis bipinnulata:* often found associated with flotsam far offshore. *Gnathanodon speciosus:* common on most of the mainland of the TEP and found at all the offshore islands (although only as juveniles at the Galápagos [J.E.M., unpubl. data]) except Clipperton. *Seriola lalandi:* antitropical, rare in the Hawaiian Islands; not known from Micronesia, the Line Islands, and Marquesas Islands; occurs in the southwestern to southeastern Pacific and Japan. *Seriola rivoliana:* absent from French Polynesia and the Line Islands; present throughout Micronesia and the West Pacific; rare in Hawai'i. *Trachurus murphyi:* in the eastern Pacific extends from the southern fringe of the TEP to Chile, and between there and New Zealand (Kawahara et al. 1988). *Uraspis helvola:* taxonomy of this genus needs revision; we follow Smith-Vaniz (1995), use the older of the two available names, and assume there is one circumtropical species; in the central Pacific known only from Hawai'i and the Marquesas Islands; not common in Hawai'i and records are sporadic (B. C. Mundy, pers. comm., 2001) and may be a vagrant there. *Aphareus furca:* first collected at Cocos Island in 1925 (AMNH lot 8554); adults of various sizes not uncommonly observed by D.R.R. there in 1997 (see also Garrison 2000); resembles and shares habitat with *Paranthias colonus*, which is abundant at Cocos; hence it could easily be missed in dense aggregations of that serranid and be common at Cocos. *Pristipomoides zonatus:* this widespread Indo-central Pacific species is known from a single specimen collected in the Galápagos (J.E.M., unpubl. data). *Mulloidicthys vanicolensis:* part of a pantropical species complex with four members that occurs throughout the Indo-central Pacific; genetic data (see section on Genetic Studies in Discussion) show that it co-occurs with the TEP endemic *M. dentatus* at Clipperton, Baja California, and Panama (H. A. Lessios, D.R.R., and B. Kessing, unpubl. data). *Chaetodon auriga:* the only TEP records are several specimens noted in the Galápagos between 1984 and 1986 (Grove 1984, 1986, Merlen 1988). *Chaetodon kleinii:* in the TEP known from a single individual photographed in the Galápagos (Grove and Lavenberg 1997); does not occur in French Polynesia (where it is replaced by its sister species, *C. trichrous*). *Chaetodon lunula:* known in the TEP from one fish observed at Cocos Island (Garrison 2000) and another at the Galápagos (Merlen 1988). *Chaetodon meyeri:* in the TEP single individuals have been seen at the Revillagigedos (A. Kerstitch, pers. comm., 1995) and the Galápagos. *Chaetodon unimaculatus:* the only TEP record is one individual photographed in the Galápagos (Humann and Deloach 2003). *Forcipiger flavissimus:* notably common at Clipperton in the TEP, uncommon on most of the mainland (Allen and Robertson 1996; D.R.R., pers. obs.), except common at the tip of Baja California (J. Earle, pers. comm., 2003). *Sectator ocyurus:* common throughout the TEP; isolated individuals at Moorea, Hawai'i (repeatedly), and Japan; recently at Baker Island, ~500 km west of the Line Islands (E. DeMartini, pers. comm., 2000); common at the Marquesas (Randall and Earle 2000; D.R.R., pers. obs.); small groups of adults observed at Rangiroa in the Tuamotus in 2004 (J. Earle, pers.

comm.). *Kuhlia mugil:* absent from the Hawaiian and Marquesas groups, each of which has an endemic congener (Randall and Randall 2001). *Cirrhitichthys oxycephalus:* abundant throughout the TEP. *Oxycirrhitus typus:* no published records from French Polynesia but recently photographed in the Marquesas (J. Earle, pers. comm., 2003). *Mugil cephalus:* circumglobal, subtropical to warm temperate, with populations in the western Pacific, the TEP, and, in the central Pacific, only at Hawai'i; known from Rapa in southeastern Polynesia (Randall 1985); several TEP populations synonymized with *M. cephalus* by Thomson (1997). *Iniistius pavo:* common at western Panama and Cocos Island (D.R.R., pers. obs.); not known from the Line Islands but is widespread in the central Pacific and seems likely to be there. *Novaculichthys taeniourus:* common throughout the TEP (D.R.R., pers. obs.). *Stethojulis bandanensis:* common at several offshore islands in the TEP; in 1999 either arrived at or increased in abundance at the Galápagos (Victor et al. 2001); replaced in the Hawaiian and Marquesas Islands by endemic congeners (Randall 2000). *Thalassoma purpureum:* common at Clipperton in 1994 (Robertson and Allen 1996), less so elsewhere in the TEP; observed by D.R.R. at the Galápagos (1990) (and see also Humann and Deloach 2003), Cocos Island (1992 and 1997), and Isla Montuosa (western Panama) in 1998, where spawning was seen. *Calotomus carolinus:* common in the Revillagigedos Islands (D.R.R., pers. obs., 1992, 1994); not recorded in the Galápagos before 1977 (McCosker et al. 1978). *Scarus ghobban:* common on much of the mainland of the TEP. *Scarus rubroviolaceus:* common throughout much of the TEP, on the mainland and offshore islands. *Acanthurus achilles:* known in the TEP from two pelagic juveniles, one collected near Clipperton and the other near the tip of Baja California. *Acanthurus nigricans:* abundant at Clipperton, Cocos Island, and the Galápagos, less common on mainland reefs; relatively uncommon in the Hawaiian Islands (most common on the island of Hawai'i [D.R.R., pers. obs., 2003]). *Acanthurus triostegus triostegus:* there are three subspecies: *A. t. sandvicensis* from Hawai'i, *A. t. marquesensis* from the Marquesas, and *A. t. triostegus* from the remainder of its range, including the Line Islands and the TEP (Randall 1956); in the TEP is particularly abundant at the offshore islands and in western Panama. *Acanthurus xanthopterus:* common on the TEP mainland and some of the oceanic islands (e.g., Cocos Island). *Ctenochaetus marginatus:* abundant at several offshore islands in the TEP (D.R.R., pers. obs.). *Naso annulatus:* only two records for the TEP: Allen and Robertson (1996) observed one adult at Clipperton in 1994, as did D.R.R. at Cocos Island in November 1997. *Naso brevirostris:* McCosker and Humann (1996) recorded one individual in the Galápagos (see also Humann and Deloach 2003). *Naso hexacanthus:* Robertson and Allen (1996) observed a pair of adults at Clipperton in 1994, and D.R.R. observed a group of three same-sized adults at Cocos Island in 1997. *Naso lituratus:* known in the TEP only from about a dozen same-sized adults observed at Clipperton in 1994 (Robertson and Allen 1996) and 1998 (by D.R.R.). *Naso vlamingii:* McCosker and Humann (1996) recorded one individual at the northern Galápagos (see also Humann and Deloach 2003); one subadult was photographed in the Galápagos in 1990 by R. Steene (see Robertson and Allen 2002). *Sphyraena barracuda:* known in the TEP from one specimen caught in western Panama and two caught in the Galápagos (see Robertson and Allen 2002; J.E.M., unpubl. data). We classify this as circumtropical because the taxonomic status of Indo-Pacific and Atlantic populations (which differ in color and behavior [J. E. Randall, pers. comm., 2003]) has not been formally resolved. *Sphyraena qenie:* recorded from Mexico by De Sylva and Williams (1986) and observed at Isla Isabela, SE Gulf of California by DRR in October 2003; common at the islands of western Panama between 1977 and 2003, and at Clipperton in 1998 (D.R.R., pers. obs.). *Trichiurus lepturus:* common in most of the TEP; absent from the Pacific Plate, present in the western Pacific. *Scomber australasicus:* known in the TEP only from the Revillagigedo Islands, where it is a resident (see section on Genetic Studies in Discussion). *Scomber japonicus:* no confirmed records anywhere in the central Pacific. *Balistes polylepis:* low numbers observed and collected in the main Hawaiian Islands over the past 20 yr; D.R.R. and John Earle found this species to be not uncommon at sites scattered along much of the western coast of Hawai'i Island in July 2003; hence is a resident at Hawai'i (see also Randall and Mundy 1998); known from one individual in the Marquesas (Randall and Earle 2000). *Canthidermis maculatus:* the taxonomy of this species is problematic, with between one and five species, including a TEP endemic (Fedoryako 1979); treated here as a single circumtropical species; not recorded from the Line or Marquesas Islands but likely occurs there because juveniles and adults are semioceanic. *Melichthys niger:* known from all the offshore islands in the TEP, particularly abundant at Clipperton (Robertson and Allen 1996); uncommon on the mainland. *Melichthys vidua:* not uncommon at Cocos Island (D.R.R., pers. obs., 1997, and see Garrison 2000); D.R.R. observed one adult at Clipperton in 1998 and various adults around Isla Montuosa in western Panama in the same year; rare at the Galápagos (Humann and Deloach 2003). *Xanthichthys caeruleolineatus:* known only from Cocos Island and the Galápagos in the TEP; relatively deep-living (to 200 m) and uncommon within usual scuba limits (Randall et al. 1978), hence its range and population status within the TEP are unclear. *Xanthichthys mento:* in the TEP known mainly from the offshore islands; antitropical in the central and West Pacific; occurs at Japan; common at Easter Island (D.R.R., pers. obs., 1997). *Aluterus monocerus:* contrary to assertions by Grove and Lavenberg (1997), this species is widely distributed, although not common, in the TEP (see Robertson and Allen 2002). *Cantherines dumerilii:* notably abundant at Clipperton and Cocos Island in the TEP. *Ostracion meleagris meleagris:* Randall (1972) classified the Hawaiian population of *O. meleagris* as an endemic subspecies, *O. m. camurum*, and suggested (J. E. Randall, pers. comm., 2003) that the TEP form might also belong to that subspecies. Until this matter has been formally resolved we treat the TEP form as *O. meleagris meleagris*. *Lactoria diaphana:* only pelagic-phase individuals found in TEP, in offshore waters; these may represent an undescribed oceanic species (J. Leis, pers. comm., 2000); hence we class TEP individuals as oceanic. *Canthigaster amboinensis:* a single record from the TEP, in the northern Galápagos in 1967 (Hobson and Walters 1968). *Canthigaster janthinoptera:* known in the TEP from one specimen at the Galápagos and another in western Panama (see Robertson and Allen 2002); replaced in Hawai'i by an endemic sister species. *Canthigaster valentini:* in the TEP known from two individuals collected at the Galápagos; absent from western edge of the EPB and the Phoenix Islands to the southwest of the Line Islands (G. R. Allen, pers. comm., 2002); occurs in the Tuamotus (~500 km southwest of the Marquesas) and the Caroline Islands (~1,000 km west of the Marquesas); absent from the Gilbert Islands (west of the Line Islands [G. R. Allen, pers. comm., 2002]); present at the southern Marshall Islands between 5 and 10° N (Allen and Randall 1977, Randall 1985, Myers 1999, Mundy in press), ~2,000 km west of the Line Islands, which are at 2–7° N. *Chilomycterus reticulatus:* common at the Revillagigedo Islands in 1994 (D.R.R., pers. obs.); in the central Pacific resident only at Hawai'i and perhaps Easter Island; pelagic juveniles collected at the Tuamotus, the Line Islands, and near the Marquesas; pelagic juveniles are large (to 20 cm SL [J. Leis, pers. comm., 2000]) and probably have great powers of dispersal. *Cyclichthys spilostylus:* only two specimens known from the TEP, which were photographed at different sites and 16 yr apart in the Galápagos (Humann and Deloach 2003); elsewhere in the Pacific not known eastward of New Caledonia (>10,000 km in a direct line from the Galápagos); not known to have a large, probably long-lived pelagic juvenile (J. Leis, pers. comm., 2000). *Diodon holocanthus:* largely absent from the central Pacific (common only at Hawai'i); a record from the Society Islands (Randall 1985) likely is of *D. liturosus* (J. Leis, pers. comm., 2000); common throughout the TEP but antiequatorial in the central and western Pacific.