

Review Article

Zoogeography of Shore Fishes of the Indo-Pacific Region

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ABSTRACT

John E. Randall (1998) Zoogeography of shore fishes of the Indo-Pacific region. *Zoological Studies* 37(4): 227-268. The East Indian region (Indonesia, New Guinea, and the Philippines), with perhaps as many as 2800 species of shore fishes, has the richest marine fish fauna of the world. The numbers of species of fishes decline, in general, with distance to the east of the East Indies, ending with 566 species in Hawaii and 126 at Easter Island. The richness of the marine fauna of the East Indies is explained in terms of its relatively stable sea temperature during ice ages, its large size and high diversity of habitat, in having many families of shore fishes adapted to the nutrient-rich waters of continental and large island shelves that are lacking around oceanic islands, in having many species with larvae unable to survive in plankton-poor oceanic seas or having too short a life span in the pelagic realm for long transport in ocean currents, and in being the recipient of immigrating larvae of species that evolved peripherally. It is also a place where speciation may have occurred because of a barrier to east-west dispersal of marine fishes resulting from sea-level lowering during glacial periods (of which there have been at least 3 and perhaps as many as 6 during the last 700 000 years), combined with low salinity in the area from river discharge and cooling from upwelling. There could also have been speciation in embayments or small seas isolated in the East Indian region from sea-level lowering. Sixty-five examples are given of possible geminate pairs of fishes from such a barrier, judging from their similarity in color and morphology. Undoubtedly many more remain to be elucidated, some so similar that they remain undetected today. Fifteen examples are listed of possible geminate species of the western Indian Ocean and western Pacific that are not known to overlap in the East Indies, and 8 examples of color variants in the 2 oceans that are not currently regarded as different enough to be treated as species. Five examples of species pairs are cited for the Andaman Sea and western Indonesia that may be the result of near-isolation of the Andaman Sea during the Neogene. Explanation is given for distributions of fishes occurring only to the east and west of the East Indies in terms of extinction there during sea-level lows. The causes of antitropical distributions are discussed. The level of endemism of fishes for islands in the Pacific has been diminishing as a result of endemics being found extralimittally, as well as the discovery of new records of Indo-Pacific fishes for the areas. Hawaii still has the highest, with 23.1% endemism, and Easter Island is a close second with

22.2%. The use of subspecies is encouraged for geographically isolated populations that exhibit consistent differences but at a level notably less than that of similar sympatric species of the genus. In order to ensure continuing stability in our classification of fishes, a plea is given not to rank characters obtained from molecular and biochemical analyses higher than the basic morphological characters that are fundamental to systematics.

Key words: Indo-Pacific, East Indies, Speciation, Endemism, Subspecies.

INTRODUCTION

The following discussion of zoogeography pertains to reef and shore fishes, defined as those occurring from the shore to a depth of 200 m, and those which are dependent for their distribution across zones of deep open ocean by the transport of their eggs and larvae in ocean currents. Sharks and rays that are primarily shallow coastal species are also regarded as shore fishes (though of course their distributions are attained by movements of juveniles or adults). Brackish water species are included as shore fishes but not purely freshwater species, even though some gobioids have larval stages that develop in the sea. Some families of fishes are not considered as shore fishes in the present paper even though they may at times be found in coastal waters. Examples are the flyingfishes (Exocoetidae), drifffishes (Nomeidae), billfishes (Istiophoridae and Xiphiidae), snake mackerels (Gempylidae), and lanternfishes (Myctophidae). A few families contain species that are offshore epipelagic and others that are pelagic coastal species. Species of the latter category include the following genera of tunas and mackerels (Scombridae): *Grammatorcynus*, *Gymnosarda*, *Rastrelliger*, *Scomber*, and *Scomberomorus*. Of the halfbeaks (Hemiramphidae), the flying halfbeak (*Euleptorhampus viridis*) is regarded as offshore pelagic; so also is the sargassumfish (*Histrio histrio*) of the frogfish family Antennariidae and the pelagic porcupinefish *Diodon eydouxii*. The patterns of distribution of pelagic fishes are usually very different from those of shore fishes. The same is true of the deeper-water benthic fishes living where current patterns may differ from those of the surface, and the undersea topography of seamounts and undersea ridges provides avenues for dispersal not found in shoal waters. Furthermore, our knowledge of the deeper-dwelling fishes is more limited and too unequal from area to area for proper comparisons.

The tropical and subtropical Indo-Pacific region extends from the Red Sea and east coast of Africa to the Hawaiian Islands and Easter Island. Only 12 species of fishes are common to the 3

most peripheral localities, the Red Sea, Hawaii, and Easter Island. This is because the fish faunas of these areas are impoverished, especially that of Easter Island with only 126 species of shore fishes, and the level of endemism is high. If, however, we consider a distribution from the western Indian Ocean (west of the southern tip of India) to either the Hawaiian Islands, Line Islands or the islands of French Polynesia (all to the east of West Longitude 160°), we find that a surprising 492 species of fishes range over this vast distance. The 3 largest families of these truly Indo-Pacific species of fishes are the wrasses (Labridae) with 39 species, the morays eels with 35 species, and the groupers and sea basses (Serranidae) with 30 species.

There is a striking difference between the Indo-Pacific shore-fish fauna and that of the tropical eastern Pacific. The 2 faunas are separated by a 5000-km expanse of open ocean known as the East Pacific Barrier. Briggs (1961) listed 52 Indo-Pacific species of fishes that have been found in the eastern Pacific, principally on offshore islands. D. Ross Robertson (pers. comm.) has raised this total to 106 species. Herre (1940) proposed the obvious route whereby these fishes crossed the East Pacific Barrier, namely the Equatorial Countercurrent. Brothers and Thresher (1985) concluded that such colonization probably took place when the Countercurrent was unusually strong, as during an El Niño event. Rosenblatt and Waples (1986) have shown from genetic evidence that such dispersal has been relatively recent (by comparing the genetic differences of western Atlantic and eastern Pacific species of fishes separated by the isthmus of Panama for about 3 million years).

Springer (1982) estimated the total number of shore fishes for the Indo-Pacific region at 4000, but added that it might be too low. One reason we cannot make a more definitive estimate of the number of species of Indo-Pacific shore fishes is the lack of up-to-date checklists from many of the subprovinces within the region. Another is the difficulty of integrating the existing checklists. Also there is a need for systematic revisions of several large families of marine fishes, especially the largest, the Gobiidae. Nelson (1994) stated that there

are about 212 genera and roughly 1875 species of gobiid fishes in the world. It would be conservative to estimate that the total number of goby species will one day reach 2000.

NUMBERS OF SHORE FISHES BY REGION

It has long been known that the islands of the East Indies have the richest marine fauna and flora in the world. The East Indies consist of over 13 000 Indonesian islands, the huge islands of Sumatra, Borneo, and New Guinea (major parts of the last two are Indonesian), the islands of the South China Sea, and the Philippines with over 7000 islands. Some persons may wish to add peripherally the Solomon Islands to the east and the Nicobar and Andaman Islands to the west. Herre (1953) compiled a checklist of 2145 species of fishes for the Philippines. Much taxonomic research on Philippine fishes has taken place since 1953, so this list is in need of considerable correction and updating. Myers (1989: fig. 7) has estimated that these islands have 2500 species of marine fishes. Kailola (1987-1991) recorded 2146 species from Papua New Guinea; she estimated that 200 more species should be expected. Froese et al. (1996) prepared a preliminary list of 2151 marine and brackishwater fishes for Indonesia. They did not rely on the largely outdated 11-volume *The Fishes of the Indo-Australian Archipelago* by Weber and de Beaufort (1911-1962) which covers 2778 marine and freshwater fishes of Indonesia. It is clear from examining groups within the list of Froese et al. with which the author is familiar that there are many omissions. For example, among the holocentrid fishes, 7 species are left out, and another 5 are probable (meaning that a species such as *Myripristis robusta*, known from Papua New Guinea and the Philippines, very likely occurs in Indonesia) (revisions of *Myripristis* by Randall and Greenfield 1997 and *Sargocentron* by Randall 1998 were not available to Froese et al.). Of the Apogonidae, 30 species are not listed that are known from the area (not counting 4 currently being described by Gerald R. Allen and the author). The number of goby omissions will be even greater, judging from *Pleurosicya* of which 5 are omitted (2 others being probable), and *Priolepis* for which 9 are not listed. Only 1 species of *Trimma* is on the list, but 30 are known (though most are undescribed; Richard Winterbottom pers. comm.). Undoubtedly, the number of fishes for Indonesia will greatly increase as more collecting is carried

out and when unidentified or misidentified specimens on museum shelves are studied. An indication that collecting is incomplete is the author's finding 7 new records and 8 new species of reef fishes for Indonesia from 5 days of diving in less than 35 m off Padang, Sumatra and the Mentawai Islands in April 1997 (Randall and Kunzmann 1998). Also deep diving with mixed gas rebreather gear by Richard L. Pyle and John L. Earle in Papua New Guinea and Palau to depths as great as 130 m has resulted in the sighting and collection of many undescribed reef fishes. I believe that the definitive count of shore fishes for Indonesia may reach 2600. If all of the East Indies are regarded as an entity, perhaps as many as 2800 species of shore fishes will ultimately be found there.

The geological history of southeast Asia and the East Indies is complex. The reader is referred to Hall (1996), Springer (1988), Springer and Williams (1994), and Springer and Randall (in press) concerning tectonic movements in the region and how they relate to fish distributions.

Turning now to island groups in the Pacific that lie to the east of the East Indies, we can see that the number of species of shore fishes drops progressively, in general, with increasing distance. These numbers as given by Myers (1989: fig. 7) for the various island groups show this trend well, as does Fig. 3 of Randall et al. (1997), but some of the totals need updating. Also, it must be stressed that some areas have been more intensively collected and the fishes more thoroughly classified than in others.

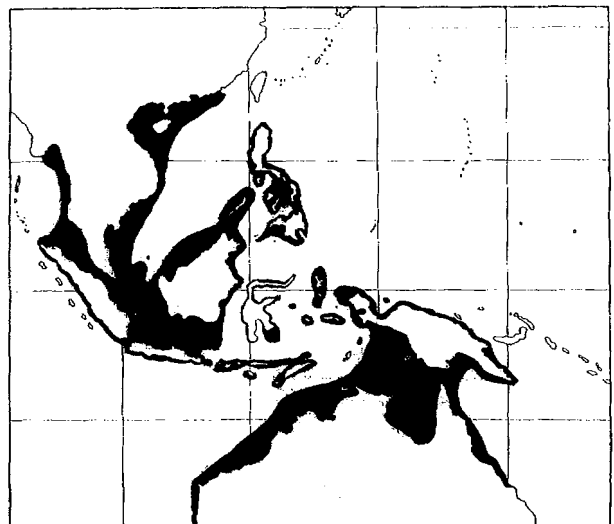


Fig. 1. Emergent land (in black) of southeast Asia and Australia during the Pleistocene (after Greenfield 1968 and Allen 1972).

The islands of Palau, lying only 850 km east of Mindanao and about the same distance north of the western end of New Guinea (but linked to the latter with reefs and small islands) would be expected to have the richest fish fauna of Micronesia, and they do, with 1374 species of shore fishes (R.F. Myers pers. comm.). Myers expects the definitive number to be about 1575. He has revised his list of shore fishes for the Caroline Islands east of Yap downward from 1149 to 1118 species. Myers and Donaldson (1996) raised the total number of shore and epipelagic species for the Mariana Islands to 943; if we eliminate the 24 offshore pelagic species, the shore-fish total is 919. The higher number of fish species for the eastern Carolines than the Marianas that lie closer to the East Indies is easily explained by noting the broad expanse of the Philippine Sea that separates the Marianas from the Philippines and comparing this to the proximity of Palau and the Caroline Islands to the islands of the East Indies. Furthermore, there is the eastward flow of the Equatorial Countercurrent in the Carolines region, in contrast to the westward-flowing Northern Equatorial Current that bathes the Marianas. Springer (1982) has termed the route whereby East Indian shore fishes could colonize oceanic islands to the east as the Caroline Islands conduit. Randall and Randall (1987) listed 817 species of fishes from the Marshall Islands, and Myers (1989) added 10 more from Thresher and Colin (1986). If pelagic species are eliminated, the number is reduced to 814. Thirty-one additional new records of shore fishes have been found in the Marshalls, principally from the atolls of Majuro and Kwajalein (Randall et al., MS), thus the revised number for the Marshalls is 845. Myers (1989) listed 460 shore fishes for the Hawaiian Islands; this is now raised to 566 species (not including introduced fishes).

Moving southward from the East Indies, there is also a diminution in the number of tropical-subtropical species of fishes. Myers (1989: fig. 7) provided an estimate of 1300 species of fishes for the Great Barrier Reef, with the number dropping to 859 for the Capricorn Group near the southern end of the Reef. Randall et al. (1990) published a semipopular book with illustrations and accounts of 1111 species of fishes for the Great Barrier Reef and Coral Sea, of which 20 are pelagic fishes. In a 2nd edition (1998), 143 species were added, bringing the total to 1244 species of shore fishes; the final number may exceed 1500 species. Myers (1989) listed "ca. 1000" shore fishes for New Caledonia, and Randall et al. (1997) recorded

1529; the species count now stands at 1610 (Kulbicki and Rivaton 1997). Kulbicki and Williams (1997) recorded 653 species of shore fishes from Ouvéa Atoll in the nearby Loyalty Islands, remarking that the low number relative to New Caledonia is due to these islands being atolls, hence lacking some important habitats of high islands. Lord Howe Island at 31°33'S was reported as having 390 inshore species by Myers (1989), but the number has been raised to 433 by Francis (1993). Francis also provided a checklist of 254 species from Norfolk Island and 145 from the Kermadec Islands. Analysis of the tropical and subtropical shore-fish fauna of Australia must wait the completion of the well-documented checklist that is in progress. The 1st volume includes the fishes from the families Petromyzontidae to Carangidae (Paxton et al. 1989).

To the east of New Caledonia the numbers of shore fishes drop to 915 for Samoa, 633 for the Society Islands, 256 for Rapa, and 126 for Easter Island. All of these totals can be expected to increase with further collecting and study.

North of the Philippines the number of species of shore fishes is reduced slightly to 2189 in Taiwan (Shao 1994, Kwang-Tsao Shao pers. comm.). Of these, 306 are from the northern and western part of the island, most of which are not believed to range south to the Philippines. Myers (1989) listed 1209 shore fishes for the Ryukyu Islands, and Randall et al. (1997) raised this to 1710; at least 2000 should be expected (Tetsuo Yoshino pers. comm.). Randall et al. (1997) recorded 801 shore fishes for the Ogasawara (Bonin) Islands. This number is also low due to insufficient collecting. However, these small islands cannot be expected to have nearly as rich a fauna as the Ryukyus which lie in the path of the Kuroshio Current bringing larvae from the rich Philippine and Taiwan faunas.

Moving to the west of the East Indies, there is again a diminution of species of shore fishes, but there are few areas in the Indian Ocean for which comprehensive checklists of fishes have been published. There is no current list of fishes for Sri Lanka or India. Randall and Anderson (1993) prepared a checklist of 899 species of shore and epipelagic fishes from the Maldivé Islands, 35 of which are offshore pelagic. Anderson et al. (1998) added 86 records of shore fishes, thus bringing the total to 949 species. Winterbottom et al. (1989) prepared a checklist of 703 species of fishes for the Chagos Archipelago. Winterbottom and Anderson (1997) added 80 new records and revised the earlier list to

a total of 773 species, of which 32 are pelagic. The fish fauna, however, could be expected to more nearly approach that of the Maldives lying just to the north on the Chagos-Laccadives Plateau. Smith and Smith (1963) recorded 775 species of fishes from the northern Seychelles, including pelagic species and some deep sea fishes. Randall and Egmond (1994) added 108 new records of fishes for these islands. They pointed out the need for revising the list of Smith and Smith from systematic research on Indo-Pacific fishes since 1963. Baissac (1990) prepared a checklist of 724 species of fishes for Mauritius, of which 663 are shore fishes. That this list is far from complete can readily be determined from noting that he included only 12 cardinalfishes, 19 blennies, and 14 gobies.

Randall (1995a) documented 930 species of fishes from Oman, of which 25 are pelagic, but this publication includes fishes from the Arabian Sea, Gulf of Oman, and the Persian Gulf (since Oman borders all 3 of these bodies of water).

Goren and Dor (1994) updated the checklist of the fishes of the Red Sea by Dor (1984) to 1248 species, but at least 100 of these are expected to be eliminated as pelagic, occurring deeper than 200 m, or as invalid taxa due to being synonyms or erroneous records for the Red Sea.

No checklist has been prepared for fishes of the east coast of Africa except for Natal. Phillip C. Heemstra and Joan E. Wright (pers. comm.) have compiled a list of 1168 species of shore fishes for Natal, of which 34 (2.9%) are endemic. About 13% of the total fish fauna of southern Africa is endemic (Smith and Heemstra 1986), but most of these fishes reside in the sea south of Natal.

WHY IS THE EAST INDIAN REGION SO RICH?

The above numbers to the east and west of the East Indian region clearly show why it has been regarded as the center of diversity of the Indo-Pacific marine life. To some such as Ekman (1953) and Briggs (1974 1984 1992), it meant that species evolved there and radiated peripherally. To others such as Ladd (1960), Woodland (1983), Donaldson (1986), and Jokiel and Marinelli (1992) it is the place where species that evolved peripherally have accumulated. In my view, it is both.

Five explanations are offered to collectively account for the rich diversity of marine life of the East Indian region compared to peripheral areas. One is its stability with respect to sea temperature during glacial periods. Extinction rates of tropical

biota were high in the higher latitudes and on the eastern side of the 3 oceans where cold currents today compress the tropical zone toward the equator. By contrast, the west side of the oceans, with a broader tropical zone, was affected less by ice-age temperature drop.

The 2nd explanation is the large size of the East Indian region, from about latitude 20°N to 10°S and longitude 95°E to 160°W — a longitudinal span covering over 7000 km. The size is enhanced by the profusion of islands, each with its insular shelf. Furthermore, it includes some very large shelf areas, such as the Sunda Shelf. Obviously, the larger the area, and hence the larger the populations of animals and plants therein, the lower the possibility of extinctions. The large size is coupled with incredible environmental diversity. Woodland (1990: 10) wrote, "The Indo-Malayan area is a confluence of major habitat types. It is the meeting place of the shelves of two continents, each with a different geological history. Nowhere else is such a variety of marine habitats found in such abundance: large estuaries and coastal lagoons; offshore rock reefs and rocky headlands; extensive mangrove forests; bottoms of mud and silica and coral sand in various proportions; sand flats covered with seagrass; waters with a combination of low salinity and high turbidity supporting impoverished coral communities; flourishing barrier reefs; and so on. It is the author's view that it is this habitat diversity which enables so many species to occur in the Indo-Malayan area." Localities peripheral to the East Indies, in particular oceanic islands, do not provide such a variety of habitats. Several large fish families, such as the Clupeidae, Engraulidae, Ariidae, Ambassidae, Leiognathidae, Mugilidae, Sciaenidae, and Sparidae are poorly represented at oceanic islands. These are families with a preponderance of species that are adapted to the nutrient-rich coastal seas of continents and large islands.

The 3rd explanation involves larval development. The larval stage of many fishes of the Asian continental shelf or the insular shelf of large islands undergo their development in plankton-rich inshore seas. They are not apt to survive transport over long stretches of blue open-ocean water of low plankton productivity. The species of other large families that lay demersal eggs, such as the Pseudochromidae, Pomacentridae, Gobiidae, and Blenniidae, are also not as numerous at distant archipelagoes as one would expect from their total number of species. The same is true of fishes of the families Apogonidae and Opistognathidae with

oral incubation of the ova, and the Syngnathidae wherein the males incubate the ova on the abdomen. The duration of larval life of these fishes is short, in general, hence there is less time for broad dispersal. Other fishes that lay pelagic eggs but exist for a short span of time as larvae also face restricted opportunity for long transport in ocean currents. However, some of these fishes with a short larval life have exceptionally broad Indo-Pacific distributions. One example is the cardinalfish *Apogon kallopterus* that ranges from the Red Sea and East Africa to Hawaii and Pitcairn Island. The explanation for its success appears to lie in the ability to survive as a juvenile in the pelagic realm. One cardinalfish of this species was caught as a juvenile in a Cobb-anchovy trawl 5-15 nautical miles from the nearest land of the Hawaiian Islands (Bruce C. Mundy pers. comm.). Woodland (1983) noted that the most wide-ranging species of rabbitfish, *Siganus argenteus*, "is unique among the siganids in having distinct pre-juvenile stage which is adapted for a pelagic existence". The damselfish *Abudefduf vaigiensis* (the Indo-Pacific counterpart of the Atlantic *A. saxatilis*) may be found far from shoal water, rafting with floating debris or masses of algae. The tripletail *Lobotes surinamensis* and the species of *Kyphosus* are also known for rafting as juveniles. A useful discussion of larval life and distribution of coral-reef fishes may be found in Brothers and Thresher (1985).

The 4th reason for the abundance of species in the East Indies is the capacity to receive larvae

of fishes that have evolved extralimally. Woodland (1990) wrote, "the coral islands of the Pacific impose their influence by disseminating propagules of their unique species into the (East Indian) area on the equatorial currents." Certainly the current pattern is favorable for such transport, but establishing a breeding population in the high species diversity of the East Indies entails more than just the arrival of larvae. Not only is there a problem of competing species for every niche and a full complement of predators, but environmental conditions of the East Indies differ from those of oceanic islands. However, there are times when the East Indian region is one of low diversity for marine species, as noted in the 5th point below. So, it seems likely that some species that evolved peripheral to the East Indies have colonized the region.

The 5th explanation is the opportunity for allopatric speciation within the East Indian region as the result of a barrier to east-west dispersal of marine fishes during ice ages. Over the last 700 000 years there have been at least 3 (and perhaps as many as 6) glacial periods that have lowered the sea level enough to close the Torres Strait, the Malacca Strait, and the Sunda Strait (between Sumatra and Java) (Allen 1975, Chappell 1981, Potts 1983) (Fig. 2). Although there was not a total east-west land barrier, there was a barrier to the east-west dispersal of purely marine species due to the low salinity and high turbidity resulting from the discharge of large rivers to the area. The barrier was also enhanced by the upwelling of cool

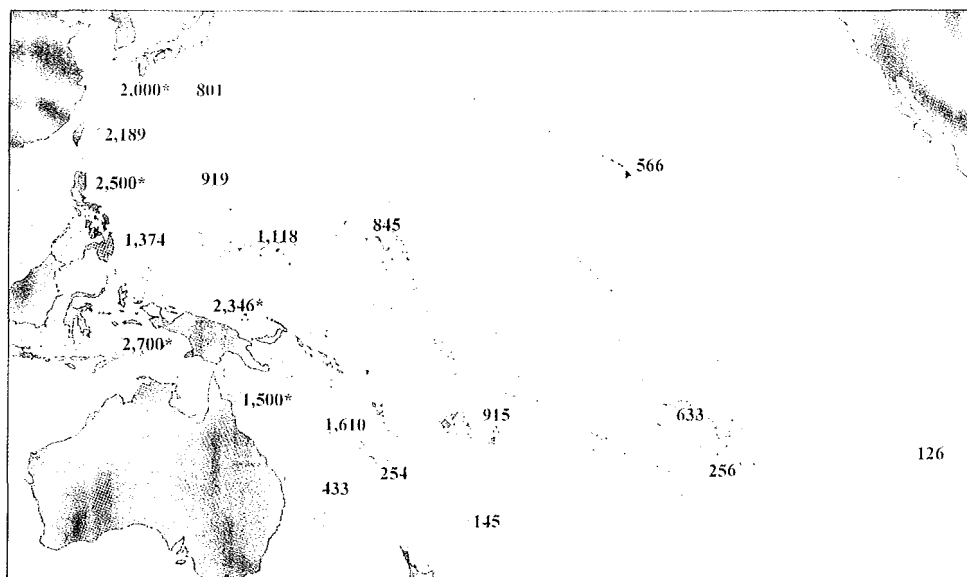


Fig. 2. Numbers of species of shore fishes for various Pacific Ocean localities. Numbers with an asterisk represent estimates.

water from the increased land masses in the area, as postulated by Fleminger (1986). Theoretically, there is the potential, with each ice age, to double the number of species in the area. In the New World in the late Pliocene a seaway broadly connecting the western Atlantic and eastern Pacific was closed by uplifting of the land at Panama. Jordan (1885 1908) noted that there are many closely related species pairs, 1 on the Atlantic and 1 on the Pacific side of Panama which he termed geminate species. Presumably these have evolved as different species since the late Pliocene when the 2 oceans were separated.

INDO-PACIFIC GEMINATE SPECIES OF FISHES

Lowered sea levels could also have isolated small seas or embayments in the East Indian region where surviving species of smaller population size, undergoing habitat change, might have evolved more rapidly.

The last glacial period was 18 000 years ago. With the interglacial period that followed, the sea level rose and the fish populations in the Indo-Malayan region that had been separated from east to west or in isolated embayments were able to intermix. It seems likely that most of these populations had not differentiated enough to avoid interbreeding freely. Or if they did differentiate enough to remain as distinct sympatric species, then one might replace the other over time. However, we now have a number of what appear to be very closely related species pairs that might be the result of the barrier described above, or of 1 of the previous barriers from older glacial periods. These are pairs which are either sympatric or are allopatric, east to west. That they are candidates as sister or geminate species is best appreciated when they are seen in life color. For that reason, selected pairs are here illustrated in color.

Allen (1975) proposed 4 such pairs of geminate species of anemonefishes of the genus *Amphiprion*: 2 of which have overlapping distributions, *A. akallopisos* - *A. sandarinos* (Figs. 3, 4) and *A. polymnus* - *A. sebae*; and 2 pairs which are allopatric: *A. frenatus* - *A. rubrocinctus* and *A. ocellaris* - *A. percula* (Figs. 5, 6). The last pair are nearly identical in color but differ in *ocellaris* having modally 1 more dorsal spine and a higher spinous portion of the dorsal fin than does *percula*.

Smith-Vaniz (1987) suggested 2 "geminate species-pairs" of the blennioid genus *Meiacanthus*:

M. geminatus - *M. vicinus*, the former from Sabah and Palawan Province of the Philippines, and the latter from southern Sulawesi; and *M. luteus* - *M. vittatus*, the former broadly distributed over the northern part of Australia, and the latter from eastern Papua New Guinea.

Blum (1989) provided an analysis of the butterflyfish family Chaetodontidae. He discussed sister species and barriers that were inferred from the distribution of species within complexes.

Woodland (1990) documented 4 such sibling species pairs of the rabbitfish genus *Siganus*: *S. guttatus* - *S. lineatus* (Figs. 7, 8) that overlap broadly (Woodland 1990: fig. 19); *S. doliatus* - *S. virgatus* (Figs. 9, 10) and *S. punctatus* - *S. stellatus* that overlap slightly (Woodland 1990: figs. 18, 16); and *S. puellus* - *S. puelloides* that are allopatric (Woodland 1990: fig. 13).

Springer and Williams (1994) provided 2 examples of sister species of their newly described blenny genus *Blenniella* which could be the result of glacial sea-level lowering: *B. caudolineata* - *B. cyanostigma* and *B. interrupta* - *B. leopardus*. They also listed species of marine fishes with localized distributions in the Philippines-Sulu Sea area which might be the result of populations isolated in bays during a glacial period. Some of these have since been shown to have broader distributions. *Meiacanthus abditus*, described from the Sulu Archipelago, has been photographed underwater by the author at Sipadan Island off Sabah, and Moyo Island and Batang Island, Indonesia. *Stonogobiops nematodes* was noted by Kuitert and Debelius (1994) as "widespread Indonesia, Malaysia, and the Philippines".

Pterois miles - *P. volitans* is an east-west species pair in the Scorpaenidae with a species vs. subspecies classification problem. Schultz (1986: fig. 3) shows the Pacific *volitans* ranging west to Viet Nam, Sulawesi, and Western Australia, and the Indian Ocean *miles* east to Sumatra. Somewhere in Indonesia between Sulawesi and Sumatra the 2 species can be expected to meet. It will be of interest to see if they merge as 1 species or coexist as 2.

Randall and Heemstra (1991) faced a difficult taxonomic decision with respect to the Pacific serranid fish *Cephalopholis urodeta* and the Indian Ocean *C. nigripinnis*. These 2 small groupers seem very distinct, the latter with uniformly dark pectoral and caudal fins, the former with pale pectorals and 2 white converging bands on the caudal fin. However, when no morphological differences could be found and intermediate specimens were

discovered from Christmas Island in the Indian Ocean, *nigripinnis* was placed in the synonymy of *urodeta*.

The following is an additional list of what appear to be closely related pairs of species of fishes that may have resulted from a barrier in the East Indies during a glacial period. These geminate pairs are all ones that occur in the East Indies (though not all with overlapping ranges). Surely not all are valid geminate species resulting from isolation of populations from the lowering of sea level during an ice age. They are listed here because they seem to have evolved relatively recently, judging from their similarity, especially in color pattern. The Indo-Pacific gobies *Gnatholepis anjerensis* and *G. cauerensis* (clarification of these formerly confused taxa by Randall and Greenfield, MS) would seem to be an obvious geminate pair, in view of their great similarity in color and morphology. However, *G. thompsoni* from the Atlantic would be an even closer species to link with *G. cauerensis*.

Scorpaenidae (scorpionfishes)

Inimicus cuvieri - *I. sinensis* (see Eschmeyer and Rama-Rao 1979)

Plesiopidae (longfins)

Plesiops cephalotaenia - *P. gracilis* (see Mooi 1995)

Pseudochromidae (dottybacks)

Pseudochromis moorei - *P. steenei* (Figs. 11, 12) (see Gill and Randall 1992)

Apogonidae (cardinalfishes)

Apogon abrogramma - *A. exostigma* (see Fraser and Lachner 1985) (Figs. 13, 14)

Apogon aureus - *A. fleurieu* (see Randall et al. 1990) (Figs. 15, 16)

Apogon chrysopomus - *A. sealei* (see Kuitert 1992) (Figs. 17, 18)

Apogon cyanosoma - *A. rubrimacula* (Randall and Kulbicki 1998) (Figs. 19, 20)

Apogon dispar - *A. melanoproctus* (see Fraser and Randall 1976) (Figs. 21, 22)

Apogon fragilis - *A. gilberti* (see Fraser and Lachner 1985)

Apogon neotes - *A. parvulus* (see Masuda et al. 1984, Allen et al. 1994) (Figs. 23, 24)

Apogon rhodopterus - *A. trimaculatus* (Randall and Fraser MS).

Archamia biguttata - *A. dispilus* (see Lachner 1951, Chen and Shao 1993)

Cheilodipterus alleni - *C. macrodon* (see Gon 1993) (Figs. 25, 26)

Cheilodipterus artus - *C. intermedius* (see Gon

1993)

Lutjanidae (snappers)

Lutjanus lutjanus - *L. madras* (See Allen and Talbot 1985)

Caesionidae (fusiliers)

Caesio teres - *C. xanthonota* (see Carpenter 1987) (Figs. 27, 28)

Chaetodontidae (butterflyfishes)

Chaetodon baronessa - *C. triangulum* (see Burgess 1978, Allen 1979) (Figs. 29, 30)

Chaetodon decussatus - *C. vagabundus* (see Burgess 1978, Allen 1979) (Figs. 31, 32)

Chaetodon falcula - *C. ulietensis* (see Burgess 1978, Kuitert and Debelius 1994) (Figs. 33, 34)

Chaetodon lineolatus - *C. oxycephalus* (see Burgess 1978, Allen 1979) (Figs. 35, 36)

Chaetodon lunulatus - *C. trifasciatus* (see Kuitert 1995) (Figs. 37, 38)

Chaetodon melannotus - *C. ocellicaudus* (see Burgess 1978, Allen 1979) (Figs. 39, 40)

Chaetodon pelewensis - *C. punctatofasciatus* (hybrids observed; see Steene 1978)

Heniochus pleurotaenia - *H. varius* (see Burgess 1978, Allen 1979)

Pomacanthidae (angelfishes)

Centropyge eibli - *C. vroliki* (see Pyle and Randall 1994)

Chaetodontoplus mesoleucos - *C. sp.* (see Kuitert and Debelius 1994) (Figs. 41, 42)

Pomacentridae (damsel-fishes)

Chrysiptera sinclairi - *C. springeri* (see Allen 1991) (Figs. 43, 44)

Dascyllus carneus - *D. reticulatus* (see H. Randall and Allen 1977) (Figs. 45, 46)

Pomacentrus auriventris - *P. coelestis* (see Allen 1991)

Labridae (wrasses)

Anampses lineatus - *A. melanurus* (see Kuitert and Debelius 1994) (Figs. 47, 48)

Bodianus diana - *Bodianus sp.* (see Kuitert and Debelius 1994)

Bodianus axillaris - *B. mesothorax* (see Randall et al. 1990)

Epibulus insidiator - *Epibulus sp.* (Randall and Carlson MS)

Halichoeres binotopsis - *H. timorensis* (see Kuitert and Debelius 1994)

Halichoeres chrysus - *H. leucoxanthus* (see Randall 1980b, Randall and Smith 1982) (Figs. 49, 50)

Halichoeres hartzfeldii - *H. zeylonicus* (Kuitert pers. comm., reported observing both species in Bali; see Randall and Smith 1982,

Kuiter 1995)

Halichoeres margaritaceus - *H. nebulosus*
(see Kuiter and Randall 1981) (Figs. 51-54)

Halichoeres melanurus - *H. vrolikii* (see Kuiter 1992) (Figs. 55, 56).

Pseudojuloides cerasinus - *P. kaleidos* (see Kuiter and Randall 1995) (Figs. 57, 58)

Scaridae (parrotfishes)

Chlorurus bleekeri - *C. troschellii* (see Randall and Choat 1980) (Figs. 59, 60)

Scarus spinus - *S. viridifucatus* (see Satapoomin et al. 1994) (Figs. 61, 62)

Blenniidae (blennies)

Ecsenius axelrodi - *E. bathi* (see Springer 1988) (Figs. 63, 64)

Ecsenius monoculus - *E. paroculus* (see Springer 1988)

Salarias ceramensis - *S. fasciatus* (see Bath and Randall 1991, Eichler and Myers 1997) (Figs. 65, 66)

Gobiesocidae (clingfishes)

Discotrema crinophila - *D.* sp. (Briggs and Randall MS) (Figs. 67, 68)

Gobiidae (gobies)

Cryptocentrus cinctus - *C. fasciatus* (see Randall et al. 1990) (Figs. 69, 70)

Ctenogobius feroculus - *C. pomastictus* (see Myers 1989) (Figs. 71, 72)

Istigobius goldmanni - *I. nigroocellatus* (see Murdy and Hoese 1985) (Figs. 73, 74)

Trimma naudei - *T.* sp. (Winterbottom MS) (Figs. 75, 76)

Valenciennesa bella - *V. randalli* (see Hoese and Larson 1994)

Acanthuridae (surgeonfishes)

Acanthurus pyroferus - *A. tristis* (see Randall 1993)

Tetraodontidae (puffers)

Arothron immaculatus - *A. manilensis* (see Randall 1985) (Figs. 77, 78)

Undoubtedly there are more closely related species pairs like the above, particularly in the Pinguipedidae, Tripterygiidae, and Gobiidae; these are families for which much systematic research needs to be done. More pairs will probably be elucidated in the Apogonidae when the study of the species of the *Apogon bandanensis* complex is completed by Thomas H. Fraser and that of the complex of small transparent red species currently identified as *A. coccineus*, *A. crassiceps*, and *A. erythrinus* by David W. Greenfield.

Most of the above geminate species have

been discovered by differences in their color patterns. What of those pairs that now look the same or are so close in color that they have not yet been detected? Differences in ecology or behavior might provide clues of the existence of geminate species. An undescribed drab species of *Epibulus* from the East Indies and Palau was discovered by noting that it occurs in turbid protected reef areas where the more colorful terminal male of *E. insidiator* was not seen. Independently, D. Ross Robertson (pers. comm.) concluded that there are 2 species of *Epibulus* in Palau because he noticed 2 different spawning patterns. Specimens of both species have failed to show any morphological differences, and molecular analysis is now being undertaken.

There are other species pairs of fishes with similar color patterns that coexist in the East Indian region that were not listed above because they are more differentiated, and most are more widely distributed. Such pairs have probably been distinct from one another for a longer period than the recent ice ages. Examples of these are the serranids *Plectranthias longimanus* - *P. nanus* (see Randall 1980a); the apogonids *Apogon cookii* - *A. taeniophorus* (see Randall and Lachner 1986); the lutjanids *Lutjanus bengalensis* - *L. kasmira* (see Allen and Talbot 1985) and *Macolor macularis* - *M. niger* (not convincingly separated as species until the study of Kishimoto et al. 1987); the chaetodontids *Coradion chrysozonus* - *C. melanopus*, *Heniochus acuminatus* - *H. diphreutes* (see Allen and Kuiter 1978), and *Forcipiger flavissimus* - *F. longirostris*; the pomacentrids *Chromis atripectoralis* - *C. viridis*; the labrids *Oxycheilinus digrammus* - *O. unifasciatus* (see Eichler and Myers 1997), and *Thalassoma purpureum* - *T. trilobatum*; and the gobiids *Amblygobius decussatus* - *A. nocturnus*.

During the Neogene, the Andaman Sea was a nearly enclosed basin (McManus 1985). This may have been the basis for the following geminate species pairs from the Andaman Sea that overlap in range in Sumatra or the Mentawai Islands.

Serranidae

Cephalopholis microprion - *C.* sp. (Randall MS) (Figs. 79, 80)

Apogonidae

Archamia zosterophora - *Archamia* sp. (Randall and Satapoomin, in press) (Figs. 81, 82)

Labridae

Halichoeres kallochroma - *H. leucurus* (*H. purpurascens* is a junior synonym of *H.*

leucurus) (Figs. 83, 84)

Scaridae

Scarus flavipectoralis - *S.* sp. (Westneat, Satapoomin and Randall MS) (Figs. 85, 86)

Blenniidae

Blenniella interrupta - *B. leopardus* (see Springer and Williams 1994)

There are species of fishes in the western Indian Ocean with a sister species in the western Pacific which as yet are not known to overlap in their distributions in the East Indies. Examples are *Pseudanthias dispar* - *P. ignitus* (Figs. 87, 88), *Pseudanthias pulcherrimus* - *P. randalli* (Figs. 89, 90), *Chaetodon madagaskariensis* - *C. mertensii* (Figs. 91, 92), *Chromis alpha* - *C. nigroanalis* (Figs. 93, 94), *Chromis analis* - *C. pembae*, *Chromis atripes* - *C. xutha* (Figs. 95, 96), *Chromis dimidiata* - *C. iomelas* (Figs. 97, 98), *Coris cuvieri* (*C. africana* is a junior synonym) - *C. gaimard* (Figs. 99, 100), *Halichoeres cosmetus* - *H. ornatissimus* (Figs. 101, 102), *Halichoeres pallidus* - *H. trispilus* (Figs. 103-104), *Chlorurus microrhinos* - *C. strongylocephalus* (Figs. 105, 106), *Scarus caudofasciatus* - *S. xanthopleura* (*S. atropectoralis* is a junior synonym), *Zebрасoma desjardini* - *Z. veliferum* (Figs. 107, 108), *Cirripectes fuscoguttatus* - *C. gilberti*, and *Synchiropus ocellatus* - *S. stellatus*. Some of these siblings are clearly different species, but others like the first 3 pairs listed above differ so slightly that one might question calling them separate species.

On the other hand, we have species in the western Indian Ocean that exhibit slight differences from what are regarded as the same species in the western Pacific by most authors. Examples are *Pogonoperca punctata* (Figs. 109, 110), *Chaetodon unimaculatus* (Figs. 111, 112), *Pygoplites diacanthus* (Figs. 113, 114), *Halichoeres hortulanus*, *Labroides dimidiatus* (the different caudal-fin coloration is the same in its mimic, *Aspidontus taeniatus*) (Figs. 115, 116), *Ctenochaetus strigosus*, *Naso lituratus* (Figs. 117, 118), and *Balistapus undulatus* (Figs. 119, 120). Some of these, such as *Ctenochaetus strigosus* might best be differentiated into east-west species pairs. As noted by Anderson et al. (in press), *Pogonoperca punctata* in the western Indian Ocean seems different enough in color to warrant consideration as a species, *P. ocellata* Günther. *Chaetodon unimaculatus* was divided into 2 subspecies by Ahl (1923): *C. u. interruptus* in the Indian Ocean and *C. u. unimaculatus* in the Pacific. He was followed by Burgess (1978) and Kuitert and Debelius (1994).

Burgess stated that the 2 are apparently not sympatric, but he added that they might "come together in the vicinity of the western part of the East Indies". Again, the differences as given by Burgess may be significant enough to regard *interruptus* as a species.

It is obvious that we systematists have not been consistent in naming these allopatric populations. As will be discussed further below, more consideration should be given to the use of subspecies for such populations with clear but slight color differences, as Randall and Lubbock (1982) did for the microdesmid *Ptereleotris grammica*.

DISJUNCT DISTRIBUTIONS

Springer and Williams (1990: figs. 3, 4) called attention to the east-west disjunct distributions of the wide-ranging *Istiblennius gibbifrons* (now reclassified in *Blenniella*) and *I. bellus*. They also listed 7 mollusks and the following fishes with similar distributions: *Stegastes albifasciatus*, *Pervagor aspricaudus*, *Liopropoma lunulatum*, *L. tonstrinum*, and *Cirripectes perustus*. Allen (1991: table 8), however, has recorded *S. albifasciatus* from Malaysia, Indonesia, and the Philippines. Springer and Williams (1994) added still more examples of east-west species with disjunct distributions: *Synodus binotatus*, *Apogon taeniopterus*, *Eviota distigma*, *Calotomus carolinus*, *Cephalopholis sexmaculata*, *Epinephelus chlorostigma*, *E. hexagonatus*, *E. tauvina*, and *Plectropomus laevis*. Three of these species, however, have Indonesian records: Lachner and Karnella (1980) recorded 3 lots of *Eviota distigma* from Indonesia; Bruce and Randall (1985) recorded 17 lots of *Calotomus carolinus* from the East Indies; and Randall and Heemstra (1991) listed *Cephalopholis sexmaculata* from Bali. *Plectropomus laevis* remains unknown from Indonesia, but it is recorded from Papua New Guinea and the Philippines (Randall and Hoese 1986).

There are 2 more interesting examples of this distribution. The small puffer *Canthigaster solandri* (Fig. 121) is widespread in the Indian Ocean and the islands of Oceania, but it is replaced in Palau, the Great Barrier Reef, and the islands of the East Indies (except off Padang on the Indian Ocean side of Sumatra where only *solandri* was observed) by the similar *C. papua* (Fig. 122, first considered as a junior synonym of *solandri* by Allen and Randall 1977, but now regarded as a valid species). The labrid *Thalassoma lutescens*, also wide-ranging throughout Oceania, appears to be absent from

New Guinea, Indonesia, and the Philippines except for 1 record of Fowler and Bean (1928) from Babuyan Islands north of Luzon. Randall (1995a) reported it from Oman for the 1st western Indian Ocean record.

The blenny *Cirripectes auritus* would seem to have a disjunct east-west distribution from the records given by Williams (1988: fig. 10), but the author has collected it at the Penyu Islands and Watubela Islands in the Banda Sea and photographed it underwater at Halmahera and Pura, Indonesia.

The preferred explanation of these disjunct distributions by Springer and Williams (1990) is extinction of the species from the East Indian region during glacial sea-level lowering when there was a nearly complete land barrier to east-west dispersal, and the sea in the area was turbid and hyposaline from heavy river runoff, and cool from upwelling. Perhaps some ecological requirement is lacking which is preventing the displaced species from reentering the area. For example, the East Indian region does not have very clear oceanic water that some species may need for their larval development. Or there may be other deterrents to recolonization of the region such as certain predators, competitors, parasites, or diseases that may not have been there before.

An alternative explanation was provided as a note to the Springer-Williams paper by an anonymous reviewer who suggested that the changing environment might have stimulated speciation in the area, and that newly formed species might outcompete and replace their older relatives. Springer and Williams did not accept this concept, stating, "we reject sympatric speciation as an important evolutionary process". I tend to agree, but it is possible for a species to have evolved in the East Indian region in the turbid brackish environment that later prevented its ancestral stock from recolonizing the area. *Canthigaster papua* might have arisen from *solandri*-like stock in the East Indian region and prevailed as a superior competitor to *solandri*. Or it may have evolved initially in some isolated embayment when the sea level was low as hypothesized by Springer and Williams (1990).

Better known than east-west disjunct distributions are north-south displacements, referred to as antitropical. Or when a species is found south of the Tropic of Cancer and north of the Tropic of Capricorn but is still absent from a broad zone of lower latitude, the term antiequatorial is more appropriate. Randall (1982) listed 56 Indo-Pacific

species of fishes with such a distribution that were not mentioned by Hubbs (1952). A correction is in order for the pomacanthid species *Centropyge interruptus*. It was reported by Randall as occurring in Japan, Hawaii, and Réunion. The last-mentioned locality was based on a photograph of a species that has since been described as new, *Centropyge debelius* Pyle. A few of the other antitropical species have been regarded as north-south sister species by some authors, but as will be explained below, the use of subspecies is preferred by the author in at least some of these cases. Additional examples of antitropical and antiequatorial distributions of Indo-Pacific fishes are being prepared by the author and David G. Smith.

Randall (1995b) offered 3 explanations for antitropical distributions. First, subtropical species could range across the tropical zone during an ice age and be isolated to the north and south with the warming of the oceans. Second, fishes could descend into deeper cooler water and thereby transgress the tropical zone during optimal population and sea conditions. Such a mode is more apt to occur among deeper-water or pelagic species (examples provided by Hubbs 1952). The 3rd is the occurrence of shallow-water reefs and islands forming north-south stepping stones across the tropics in the past. Because of subsidence, plate movement, or sea-level rise, these islands and reefs are no longer present or are too deep to support shallow-water organisms, resulting in the north-south discontinuities in some of the distributions today. A 4th basis for antitropicality for those species in the western Pacific is the same as that proposed above for the species displaced east and west, namely extinction within the East Indian region and an inability to recolonize.

Randall (1995b) listed 2 antitropical species that are unique in exhibiting both north-south and east-west discontinuities in their distribution. The cardinalfish *Lachneratus phasmaticus* (Fig. 123) was described from the Hawaiian Islands, Fiji, and the Comoro Islands (Fraser and Struhsaker 1991); and the hawkfish *Cirrhitops fasciatus* (Fig. 124) is known only from the Hawaiian Islands, Mauritius, Réunion, and Madagascar (the listing from Japan by Randall 1964 was an error). It is possible that the cardinalfish will eventually be found at intermediate localities, but the hawkfish seems to be a genuine relic in Hawaii and the 3 islands of the southwestern Indian Ocean. The most spectacular example of east-west disjunct distribution in the Pacific is the moray eel *Enchelycore lichenosa*,

known from Japan and the Galapagos Islands.

ENDEMISM OF SHORE FISHES

The above discussion of distributions of Indo-Pacific fishes has centered on the East Indian region in an effort to explain its extraordinary diversity. Let us turn now to the shore fishes of islands of the Pacific Plate, discussed ably and in detail by Springer (1982). The reader is referred to his treatment of Pacific Plate biota in terms of the geological history of the Plate.

Springer has estimated that there are 1312 species of shore fishes on the Pacific Plate, not including the island groups that lie on the margin of the plate, i.e., the Marianas, Palau, Solomons, Vanuatu, Fiji, and Tonga. He noted that there are no endemic families of fishes on the Pacific Plate and only 10 endemic genera. He divided the Plate endemics into 3 categories: (1) widely distributed endemics occurring in numerous island groups or in widely separated island groups; (2) endemics limited to a few islands or island groups within a limited area on the Plate; and (3) single-island or island-group endemics. Of the 3 kinds of endemic species, he found type 3 to be the most common, particularly those from the Hawaiian Islands, Easter Island, and the Marquesas, all of which are high islands. He estimated that about 20% of the nonmarginal Pacific Plate shore fishes are endemic species, adding that he predicts the total endemism of shore fishes on the Plate to reach 22%-25%. Briggs (1995: 232) took issue to such an estimate of endemism by writing, "Species that are endemic to the Hawaiian Islands are so characterized because they occur at Hawaii and nowhere else. They are the result of evolutionary changes that occurred only around that group of islands. They are not, at the same time, Pacific Plate endemics." Thresher (1991: 417) also did not agree with Springer's conclusion that Hawaii is an integral part of the Pacific Plate biota. Obviously, discussion of endemism must focus separately on the different island groups.

Springer confined his concept of endemism to species. In the analysis below, I have included subspecies as well, providing they have already been given subspecific appellation in the literature. There is too much dissension as to what level of differentiation a geographical variant must exhibit before it can be regarded as a species. What one author emphatically calls a species, another just as emphatically may regard as a subspecies. Gosline

and Brock (1960) stated it well when they wrote, "It should be stressed that the endemics remain endemics whatever interpretation is accepted; it is only the taxonomic level of recognition that is open to differential treatment." Another problem concerns how to treat an endemic species that turns up elsewhere as a stray; or of a waif that arrives from elsewhere to an area, thereby reducing the percentage of endemism. It seems best to follow the opinion of Francis (1993) who wrote, "I have treated extralimited records as a true indication of a species's distribution and excluded them from the list of endemics." Admittedly, this means that the level of endemism is not a constant but will change as our knowledge of fishes and their distributions increases. One problem is how to recognize when a species is just a stray. We long believed that *Balistes polylepis* was a straggler to the Hawaiian region from the eastern Pacific until we recently observed that it had reproduced in Hawaii. Does the sighting of one individual of *Pseudanthias thompsoni* in the Ogasawara Islands (Randall et al. 1997: pl. 6 A) mean that it is a stray from the Hawaiian Islands where it has long been regarded as an endemic, or was the habitat with population abundance of *P. thompsoni* in the Ogasawara Islands simply not found?

The Hawaiian Islands have long been recognized as having the highest percentage of endemic shore fishes of the Indo-Pacific region. Gosline and Brock (1960) wrote that 34% of the reef fishes of the Hawaiian Islands and Johnston Island have not been taken elsewhere. Randall (1976) revised the percentage downward to 29%. Randall (1992) lowered it still further to 25%, explaining that new records of Indo-Pacific fishes in Hawaii and the finding elsewhere of species initially believed to be endemic to Hawaii have simultaneously lowered the percent of endemism. Randall (1995b) again revised the Hawaiian shore-fish endemism to 24.3%. Of the 566 species currently regarded by the author as reef and shore fishes in the Hawaiian Islands (Johnston Island here not included), 131 are not known extralimitally, hence endemism is now 23.1%.

Little Easter Island's percentage of endemism was determined to be 27.3% by Randall (1976). At present, 28 endemics are recognized among the 126 species of shore fishes (Randall and Cea Egaña 1984, DiSalvo et al. 1988), therefore giving a level of endemism of 22.2%. This percentage would be expected to drop more in the future than that of Hawaii, in the expectation that more Indo-Pacific species will be discovered there (given that

far more collecting has taken place in Hawaii), particularly among species toward the deeper end of the 200-m depth limit for shore fishes.

The Marquesas at 10% ranks 3rd in the level of endemism of shore fishes on the Pacific Plate. This is only an approximation, waiting the analysis of existing fish collections and additional collecting.

Randall et al. (1990) reported 256 species of shore fishes from the island of Rapa in French Polynesia (27°36'S, 144°18'W), of which 14 are known only from Rapa, hence 5.5% endemism.

The percentage endemism of shore fishes for Lord Howe Island and Norfolk Island in the southwest Pacific was revised to 7.2% by Randall (1992). Francis (1993) combined the Kermadec Islands fish fauna (145 species) with that of Lord Howe and Norfolk, eliminated any supposed endemics that have been found elsewhere such as Australia, New Zealand, and New Caledonia, and recomputed the endemism as 4.6%.

In the western Pacific, in spite of the richness of the fish fauna, the level of endemism is low if we consider any part of the East Indian region separately because so many of the fishes range from Indonesia to the Ryukyu Islands. Taiwan, for example, has 20 endemic shore fishes (Kwang-Tsao Shao pers. comm.), hence a level of endemism of 0.09% (and some of these may be expected in the future to be found either in the Philippines to the south or the Ryukyus to the north).

All of the islands of high endemism are peripheral in Oceania, and all are subtropical except the Marquesas which lie at latitude 8-10.5°S; however, the latter archipelago has a cool sea temperature for that latitude as a distant effect of the Humboldt Current that is deflected westward from South America. In his study of the blennioid fish genus *Entomacrodus*, Springer (1967) noted that 9 of 15 central and western Pacific species of the genus have their distributions on or near the boundary of the tropical and subtropical zones, and 7 of the 9 are endemics. He added, "A perusal of several recent revisions of Indo-Pacific fishes indicates to me that many species will be found whose distributions in the central and western Pacific are restricted to the periphery of the area". He cited the work of Matthew (1915) based mainly on mammals, who postulated the displacement of primitive forms from a central area by the development of more progressive forms there.

More important, these 5 insular regions with the highest endemism in Oceania are the most isolated geographically and hydrographically of all the islands of the central and western Pacific. More

than 800 nautical miles (about 1500 km) separate the Hawaiian Islands (including Johnston Island) and Easter Island (including Sala y Gomez) from the closest island or reef. The nearest reef to the Hawaiian Islands is Kingman Reef in the Line Islands, and the nearest island to Easter is Ducie Atoll of the Pitcairn Group. Fatu Hiva, the southernmost island of the Marquesas is 275 nautical miles (510 km) from Temoe, the nearest Tuamotu Atoll. Lord Howe Island lies 300 nautical miles (556 km) east of Australia, and Rapa is 290 nautical miles (537 km) from Raivavae in the Austral Islands. In all of these cases the present-day current patterns are not directed toward these islands from these nearest shoal localities.

A successful spawning of a shore fish, coupled with the appearance of an unusual current pattern at just the right time could result in a pulse of larvae to a distant new shoal area. If this event is followed by a long period of little or no gene flow, speciation may take place in the new locality, particularly if ecological conditions there are different. No vicariant event is needed unless one wants to regard the vagaries of ocean currents and eddies as a form of vicariance.

HAWAIIAN ENDEMIC FISHES

Analysis of the endemic fishes at these islands of high endemism reveals 2 types, those which seem to be relatively recent derivatives of species that can be identified today from another area, and those that appear to be relics, i.e., having no known close relatives. Examples among Hawaiian endemic fishes that can be paired with what are believed to be allopatric sister species are as follows (Hawaiian species given last): *Priacanthus hamrur* - *P. meeki* (Figs. 125, 126), *Chaetodon guentheri* - *C. miliaris* (Figs. 127, 128), *Abudefduf vaigiensis* - *A. abdominalis* (Figs. 129, 130), *Dascyllus trimaculatus* - *D. albisella*, *Anampses caeruleopunctatus* - *A. cuvier* (Figs. 131-134), *Calotomus japonicus* - *C. zonarchus*, *Cantherines pardalis* - *C. sandwichiensis* (Figs. 135, 136), and *Canthigaster janthinoptera* - *C. jactator*. The pair of species of the genus *Abudefduf* is of particular interest because *A. vaigiensis* is a successful new immigrant to Hawaii (Randall 1996).

Randall (1995b) discussed in some detail the routes whereby shore fishes have colonized the Hawaiian Islands. The prevailing ocean current now reaching the Hawaiian Islands is the westward-moving North Equatorial Current. Any fish

larvae transported to Hawaii in this current would most likely come from California or northern Mexico. Not only is there a distance of well over 4000 km for larvae to survive, but the subtropical sea of Hawaii is too warm for most such fishes. Only 7 species of shore fishes are known which are common to Hawaii and the eastern Pacific that are believed to be of eastern Pacific origin: *Dasyatis brevis*, *Encheliophis dubius*, *Priacanthus alalaua*, *Sectator ocyurus*, *Euthynnus lineatus*, *Balistes polylepis*, and *Xanthichthys mento*; however, the last-mentioned triggerfish is a wide-ranging antitropical species, so its 1st route to Hawaii is uncertain.

Gosline (1955) proposed the Line Islands as the major source of fishes that have immigrated to Hawaii, with Johnston Island serving as a way station. Myers (1989: fig. 7) showed the same mode of transport. With our expanding knowledge of the fish faunas of the central and western Pacific and noting the current patterns of today, the more likely route for shallow-water fishes to reach Hawaii as larvae would be from the islands of southern Japan, commencing with the Kuroshio Current and arriving via eddies to shallow seamounts and reefs at the northwestern end of the Hawaiian chain. Examples of species of shore fishes unique to Japan and Hawaii include *Synodus ulae*, *Sargocentron spinosissimum*, *Oplegnathus fasciatus*, *O. punctatus*, and *Centropyge interruptus*. That there would also seem to have been an influx of some fishes from the south is evident from a few species that are known from the Line Islands and not the western Pacific, such as *Sebastapistes coniora*, *Centropyge loriculus*, *Cirripectes quagga*, *Eviota epiphanes*, and *Acanthurus achilles*. More difficult to explain are antitropical species, such as *Synodus capricornis*, *Kelloggella oligolepis*, and *Engyprosopon arenicola* involving Hawaii in the north and such islands as Rapa, Pitcairn, and Easter Island to the south. A few other fishes are known only from Hawaii and islands of French Polynesia, such as *Hemiramphus depauperatus* and *Ostracion whitleyi*. Rehder (1980) noted that 10 of 67 nonendemic species of mollusks of Easter Island are otherwise known only from the Hawaiian Islands. For such present disjunct distributions we must postulate that there were more shallow-water areas in intermediate locations in the central Pacific than there are today. Rehder wrote, "This could well have been when many of the submarine mountain ranges, seamounts, and guyots present now in the central Pacific were at or near the surface and some 23° to the southeast of their present

location (Ladd, 1960, 148; Ladd, Newman, and Sohl 1974, 518)."

Relics could result from the hypothesis of Matthew (1915) mentioned previously. The Hawaiian Islands have been forming over a fixed hot spot in the mantle of the Pacific Plate for at least 68-70 million years (Grigg 1988). We know this from the age of the oldest Emperor seamount that was once a high island where the island of Hawaii and the newly forming volcano Loihi (900 m below the sea surface) are located today. Of course, this is not to say that any relic fish in Hawaii is 68-70 million years old, but only to point out that there is ample time for relic species to evolve and survive in the islands, whereas their ancestral stock elsewhere in the Indo-Pacific region may have long become extinct from such a cause as efficient predatory or competitor species that have not reached Hawaii. Some examples of Hawaiian relic fishes are *Dendrochirus barberi* (Fig. 137), *Pterois sphex* (Fig. 138), *Epinephelus quernus* (Fig. 139), *Chaetodon fremblii* (Fig. 140), *Genicanthus personatus* (proposed by Randall 1975, as the most primitive species of the genus) (Figs. 141, 142), *Centropyge potteri* (Fig. 143), *Desmoholacanthus arcuatus* (the only species of the genus) (Fig. 144), *Coris flavovittata* (Figs. 145, 146), and *Chlorurus perspicillatus* (Figs. 147, 148).

EASTER ISLAND ENDEMIC FISHES

Easter Island and nearby Sala y Gomez lie on the Nazca Plate, but they are considered faunistically as part of the Pacific Plate by Springer (1982) and others. Easter Island is unique not only in its high percentage of endemic fishes but in its very impoverished fish fauna: 165 species, of which, as mentioned, 126 are shore fishes. One manifestation of the small number of species is less interspecific competition. Some of the Easter Island shore fishes occur over a broad range of depth and habitat. Fishes such as certain of the Gobiidae and Pomacentridae that generally sort out by habitat and depth zones at other islands may be found from exposed tide pools to depths of 30-40 m at Easter Island. An example is *Chrysiptera rapanui* (Fig. 149).

There are 4 reasons for the paucity of fish species at Easter Island. First, the island is the most isolated in the Pacific. Second, it is relatively young, geologically speaking, having emerged by volcanism from the 3000-m sea floor 2.5 million years ago (DiSalvo et al. 1988). Next is its location

at 27°10'S. Summer sea surface temperatures at the island are usually 22-24 °C, and winter lows generally 17.5 °C, with one record to 15.7 °C (DiSalvo et al. 1988). In spite of the subtropical position, 45% of the shore-fish fauna consists of wide-ranging tropical Indo-Pacific species. This far south, the island would surely lose a large percentage of its warm-water fishes during a period of substantially reduced sea temperature. On the other hand, 23% of its shore fishes are antitropical or southern subtropical, hence the fauna would be subject to extinctions during unusual warm periods. The 4th reason is the small size of Easter Island, only 160 km², and hence a small target for drifting larval fishes. Furthermore, its small populations of fishes are more vulnerable to factors that could cause extinctions. When the author first visited the island in 1969, there were meadows of *Sargassum* and very little coral. Two herbivorous fishes were common in the *Sargassum*, *Girellops nebulosus*, and *Leptoscarus vaigiensis*. On a return trip in 1985 there was surprisingly little *Sargassum* and much more coral. The 2 herbivorous fishes were not observed then nor on a 3rd trip in 1986.

Some of the southern subtropical species at Easter Island, such as *Enchelycore ramosa* (Fig. 150), *Trachypoma macracanthus* (Fig. 151), *Cirripectes alboapicalis* (Fig. 152), and *Anampses femininus* (Figs. 153, 154) range all the way to Australia. One of the 2 Easter Island species that occur in Chile is *Gymnothorax porphyreus* (Fig. 155); it also ranges west to Lord Howe Island (Randall and McCosker 1975). The other is *Amphichaetodon melbae*, otherwise known only from Isla San Felix off the coast of Chile (Fig. 156; photograph taken at Easter Island in 61 m, below the thermocline).

Easter Island endemic fishes that can be paired with close relatives from elsewhere in the Indo-Pacific are as follows (Easter Island species listed last): *Scorpaena cookii* - *S. orgila* (see Eschmeyer and Allen 1971) (Figs. 157, 158), *Kuhlia sandvicensis* - *K. nutabunda* (see Regan 1913) (Figs. 159, 160); *Priacanthus alalaua* - *P. nasca* (see Starnes 1988), *Apogon chalcicus* - *A. apogonides* (see Fraser and Randall 1986), *Centropyge jocularis* - *C. hotumatua* (see Allen 1979), *Chromis pamae* - *C. randalli* (see Randall and McCosker 1992), *Pseudolabrus torotai* - *P. semifasciatus* (see Russell and Randall 1981) (Figs. 161, 162), and *Cantherhines verecundus* - *C. rapanui* (see Randall 1964) (Figs. 163, 164). Relatively few Easter Island endemic shore fishes appear to lack close relatives: *Cheilodactylus plessisi*

(Fig. 165), *Parupeneus orientalis* (Fig. 166), *Chaetodon litus* (Fig. 167), and *Canthigaster cyanetron* (Fig. 168). Two Easter Island endemics with close relatives from Pitcairn Island to the Austral Islands or Rarotonga are *Sargocentron wilhelmi* (Fig. 169) and *Chromis randalli* (Fig. 170).

Gosline and Brock (1960) observed that many of the endemic fishes of the Hawaiian Islands are the most abundant species of their genera. This was also noticed by the author at Easter Island. Of the 13 most abundant shore fishes at the island, 6 are endemics and 2 others are restricted to Easter Island, Rapa, and Pitcairn (Randall 1976). It was suggested that the endemics have evolved in these areas for a long period of time and therefore have had ample opportunity to become fully adapted to the environment. This might confer some ecological or behavioral advantages over competitor species that arrived later to the islands.

RED SEA ENDEMIC FISHES

Goren and Dor (1994) gave the rate of endemism for the entire Red Sea fish fauna as 13.7%. Many of the endemic fishes extend into the Gulf of Aden, and a few straggle over as waifs to the southern coast of Oman, but these are still regarded as Red Sea endemics. This is probably the highest level of endemism for the Indian Ocean region. As would be expected, the percentage of endemism varies greatly from family to family. Of 33 morays (Muraenidae) recorded from the Red Sea, only 2 are confined to the Sea (Randall and Golani 1995, McCosker and Smith 1997). Of 13 squirrelfishes and soldierfishes (Holocentridae), 3 are endemic. Of 38 serranid fishes, 6 are endemic. Of 11 pseudochromid fishes, all but *Haliophis guttatus* are endemic. Of 17 butterflyfishes (Chaetodontidae), 7 are endemic. The level of endemism of the Gobiidae is high (actual percentage deferred, pending a review of the Red Sea species by Menachem Goren). As has long been noted, endemism is higher in smaller fishes (the pseudochromids and gobiids mentioned above being obvious examples). This may be due in part to the more rapid generation time of small fishes. Also, as mentioned, many of the small fishes such as these two families, the Blenniidae, Apogonidae, and Syngnathidae, lay demersal ova, or the males incubate the ova, hence there is, in general, a shorter larval life.

The Red Sea was isolated from the Indian Ocean several times during the Pliocene-Pleis-



Fig. 3. *Amphiprion akallopisos*, Sumatra, Indonesia.



Fig. 4. *Amphiprion sandarminos*, Papua New Guinea.

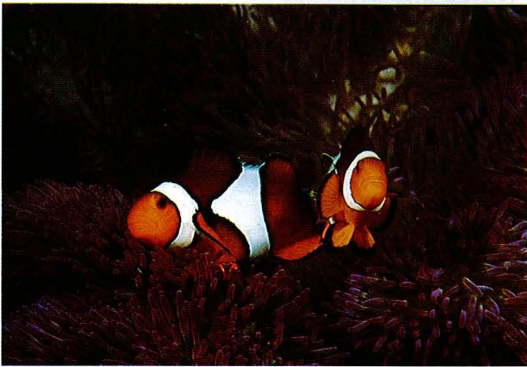


Fig. 5. *Amphiprion ocellaris*, Sulawesi, Indonesia.

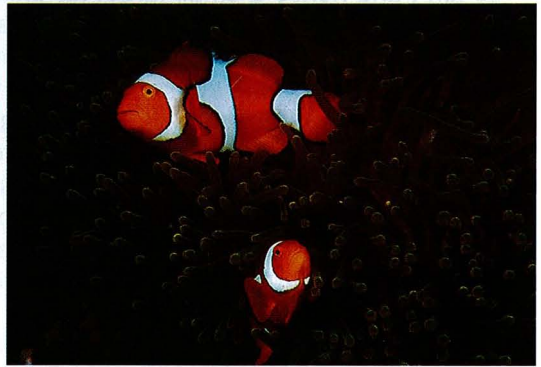


Fig. 6. *Amphiprion percula*, Papua New Guinea



Fig. 7. *Siganus guttatus*, Bali, Indonesia.



Fig. 8. *Siganus lineatus*, Sri Lanka.



Fig. 9. *Siganus doliatus*, Heron Island, Great Barrier Reef.



Fig. 10. *Siganus virgatus*, Sri Lanka.



Fig. 11. *Pseudochromis moorei*, male, Negros, Philippines.



Fig. 12. *Pseudochromis steenei*, male, Bali, Indonesia.



Fig. 13. *Apogon abrogramma*, Maldive Islands.



Fig. 14. *Apogon exostigma*, night, Papua New Guinea.



Fig. 15. *Apogon aureus*, Papua New Guinea.



Fig. 16. *Apogon fleurieu*, Mombasa, Kenya.



Fig. 17. *Apogon chrysopomus*, Komodo, Indonesia.



Fig. 18. *Apogon sealei*, Sulawesi, Indonesia.



Fig. 19. *Apogon cyanosoma*, Alor, Indonesia.



Fig. 20. *Apogon rubrimacula*, Papua New Guinea.



Fig. 21. *Apogon dispar*, Wetar, Indonesia.



Fig. 22. *Apogon melanoproctus*, Sipadan Island, Sabah.



Fig. 23. *Apogon neotes*, Balicasag Island, Philippines.



Fig. 24. *Apogon parvulus*, night, Adonara, Indonesia.



Fig. 25. *Cheilodipterus alleni*, Papua New Guinea.



Fig. 26. *Cheilodipterus macrodon*, Lombok, Indonesia.



Fig. 27. *Caesio teres*, Bali, Indonesia.

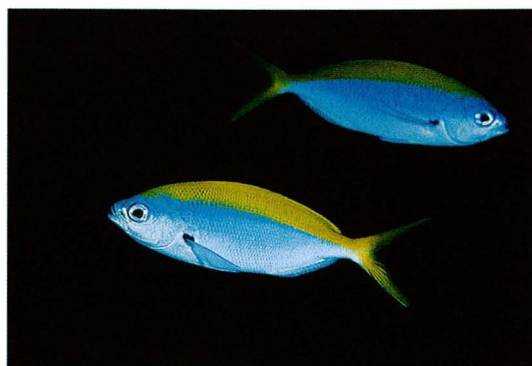


Fig. 28. *Caesio xanthonota*, Mentawai Islands, Indonesia.



Fig. 29. *Chaetodon baronessa*, Palau.

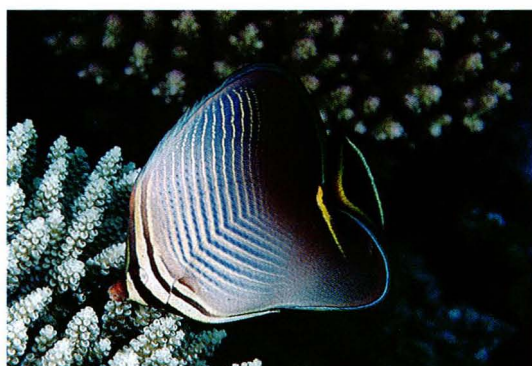


Fig. 30. *Chaetodon triangulum*, Maldives Islands.



Fig. 31. *Chaetodon decussatus*, Bali, Indonesia.



Fig. 32. *Chaetodon vagabundus*, Oman.



Fig. 33. *Chaetodon falcula*, night, Maldives Islands.



Fig. 34. *Chaetodon ulietensis*, Oahu, Hawaiian Islands.



Fig. 35. *Chaetodon lineolatus*, Line Islands.



Fig. 36. *Chaetodon oxycephalus*, Palau.



Fig. 37. *Chaetodon lunulatus*, Marshall Islands.



Fig. 38. *Chaetodon trifasciatus*, Maldives Islands.

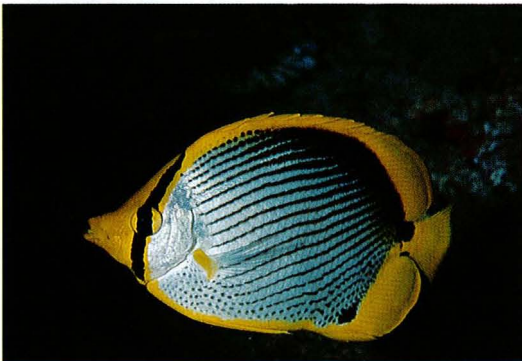


Fig. 39. *Chaetodon melannotus*, Maldives Islands.

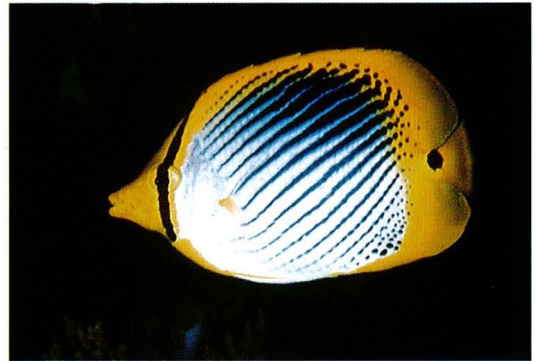


Fig. 40. *Chaetodon ocellicaudus*, Halmahera, Indonesia.



Fig. 41. *Chaetodontoplus mesoleucos*, Sulawesi, Indonesia.

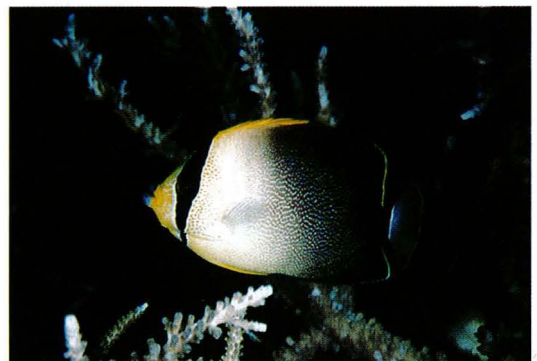


Fig. 42. *Chaetodontoplus* sp., Halmahera, Indonesia.



Fig. 43. *Chrysiptera sinclairi*, Solomon Islands.



Fig. 44. *Chrysiptera springeri*, Flores, Indonesia.



Fig. 45. *Dascyllus carneus*, Seychelles.



Fig. 46. *Dascyllus reticulatus*, Bali, Indonesia.



Fig. 47. *Anampses lineatus*, female, Seychelles.



Fig. 48. *Anampses melanurus*, female, Ogasawara Islands.



Fig. 49. *Halichoeres chrysus*, male, Negros, Philippines.



Fig. 50. *Halichoeres leucoxanthus*, male, Maldives Islands.



Fig. 51. *Halichoeres margaritaceus*, female, Marshall Islands.



Fig. 52. *Halichoeres nebulosus*, female, Moyo Island, Indonesia.



Fig. 53. *Halichoeres margaritaceus*, male, Ogasawara Islands.



Fig. 54. *Halichoeres nebulosus*, male, Bali, Indonesia.



Fig. 55. *Halichoeres melanurus*, male, Papua New Guinea.



Fig. 56. *Halichoeres vrolikii*, male, Java, Indonesia.



Fig. 57. *Pseudojuloides cerasinus*, male, Cebu, Philippines.



Fig. 58. *Pseudojuloides kaleidos*, male, Gunung Api, Indonesia.



Fig. 59. *Chlorurus bleekeri*, male, Bali, Indonesia.

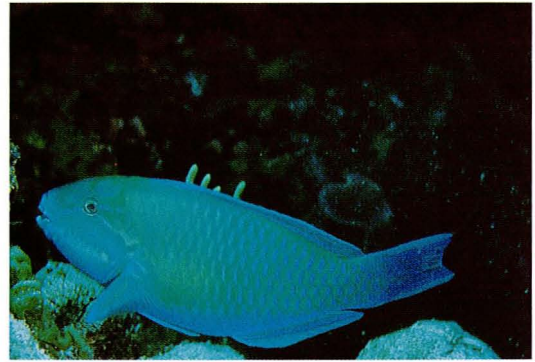


Fig. 60. *Chlorurus troschelii*, male, Bali, Indonesia.



Fig. 61. *Scarus spinus*, male, Osprey Reef, Coral Sea.



Fig. 62. *Scarus viridifucatus*, male, Maldives Islands.



Fig. 63. *Ecsenius axelrodi*, Halmahera, Indonesia.



Fig. 64. *Ecsenius bathi*, Komodo, Indonesia.



Fig. 65. *Salarias ceramensis*, Waigeo, Indonesia.



Fig. 66. *Salarias fasciatus*, Tonga.



Fig. 67. *Discotrema crinophila*, Alor, Indonesia.



Fig. 68. *Discotrema* sp., Balicasag Island, Philippines.

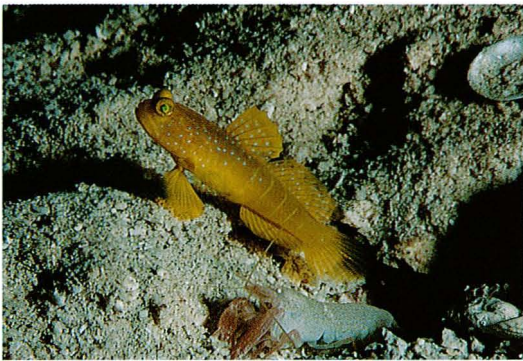


Fig. 69. *Cryptocentrus cinctus*, Palau.



Fig. 70. *Cryptocentrus fasciatus*, Bintan, Indonesia.



Fig. 71. *Ctenogobiops feroculus*, Maldives Islands.

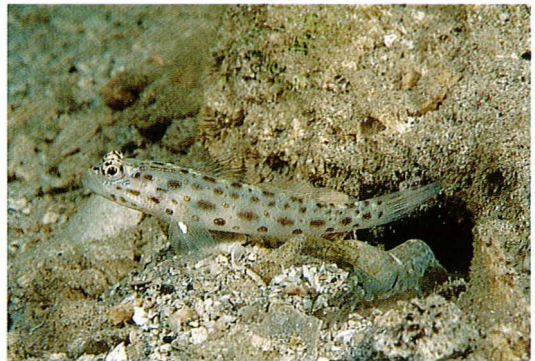


Fig. 72. *Ctenogobiops pomastictus*, Palau.

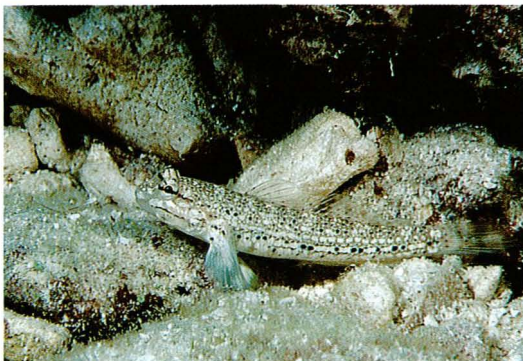


Fig. 73. *Istigobius goldmanni*, Heron Island, Great Barrier Reef.



Fig. 74. *Istigobius nigroocellatus*, Flores, Indonesia.



Fig. 75. *Trimma naudei*, Maldives Islands.



Fig. 76. *Trimma* sp., Solomon Islands.

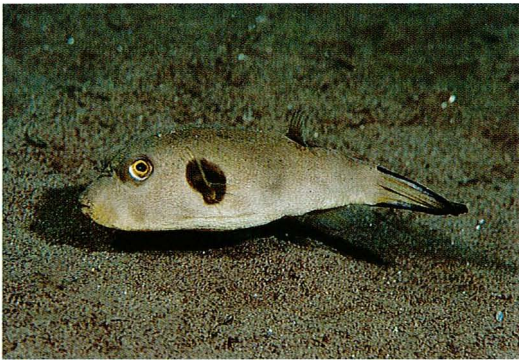


Fig. 77. *Arothron immaculatus*, Flores, Indonesia.



Fig. 78. *Arothron manilensis*, Flores, Indonesia.



Fig. 79. *Cephalopholis microprion*, Flores, Indonesia.



Fig. 80. *Cephalopholis* sp., Sumatra, Indonesia.



Fig. 81. *Archamia zosterophora*, Halmahera, Indonesia.



Fig. 82. *Archamia* sp., Mentawai Islands, Indonesia.



Fig. 83. *Halichoeres kallochroma*, female, Mentawai Islands, Indonesia.



Fig. 84. *Halichoeres leucurus*, female, Palau.



Fig. 85. *Scarus flavipectoralis*, male, Lizard Island, Great Barrier Reef.



Fig. 86. *Scarus* sp., male, Mentawai Islands, Indonesia.



Fig. 87. *Pseudanthias dispar*, male, Pulau Islands, Indonesia.



Fig. 88. *Pseudanthias ignitus*, male, Similan Islands, Andaman Sea.



Fig. 89. *Pseudanthias pulcherrimus*, male, Maldives Islands.



Fig. 90. *Pseudanthias randalli*, male, Palau.



Fig. 91. *Chaetodon madagaskariensis*, Maldives Islands.



Fig. 92. *Chaetodon mertensii*, Guam, Mariana Islands.



Fig. 93. *Chromis alpha*, Tuamotu Archipelago.



Fig. 94. *Chromis nigroanalis*, Malindi, Kenya.



Fig. 95. *Chromis atripes*, Palau.



Fig. 96. *Chromis xutha*, Maldives Islands.



Fig. 97. *Chromis dimidiata*, Seychelles.



Fig. 98. *Chromis iomelas*, Tuamotu Archipelago.



Fig. 99. *Coris cuvieri*, male, Seychelles.



Fig. 100. *Coris gaimard*, female, Marshall Islands.

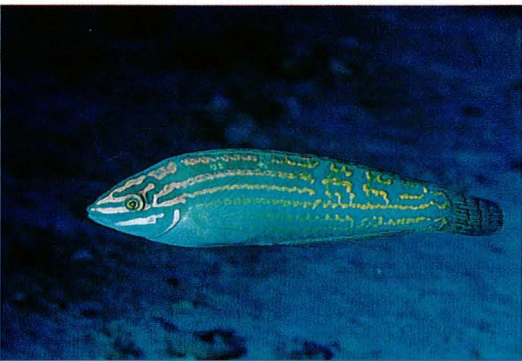


Fig. 101. *Halichoeres cosmetus*, male, Maldives Islands.



Fig. 102. *Halichoeres ornatissimus*, male, Gunung Api, Indonesia.



Fig. 103. *Halichoeres pallidus*, female, Gunung Api, Indonesia.



Fig. 104. *Halichoeres trispilus*, female, Maldives Islands.



Fig. 105. *Chlorurus microrhinos*, male, Marshall Islands.



Fig. 106. *Chlorurus strongylocephalus*, male, Maldives Islands.



Fig. 107. *Zebrasoma desjardini*, Maldives Islands.



Fig. 108. *Zebrasoma veliferum*, Bali, Indonesia.



Fig. 109. *Pogonoperca punctata*, Banda Islands, Indonesia.



Fig. 110. *Pogonoperca punctata*, Seychelles.



Fig. 111. *Chaetodon unimaculatus*, Tonga.



Fig. 112. *Chaetodon unimaculatus*, Maldives Islands.



Fig. 113. *Pygoplites diacanthus*, Tahiti, Society Islands.



Fig. 114. *Pygoplites diacanthus*, Seychelles.



Fig. 115. *Labroides dimidiatus*, Bougainville Reef, Coral Sea.



Fig. 116. *Labroides dimidiatus*, Natal, South Africa.



Fig. 117. *Naso lituratus*, night, Osprey Reef, Coral Sea.



Fig. 118. *Naso lituratus*, Gulf of Aqaba, Red Sea.



Fig. 119. *Balistapus undulatus*, Bali, Indonesia.

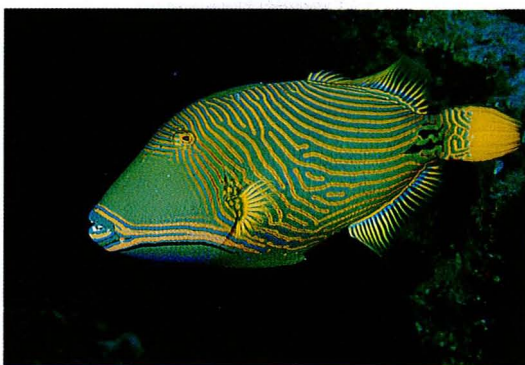


Fig. 120. *Balistapus undulatus*, Maldives Islands.



Fig. 121. *Canthigaster solandri*, Sumatra.



Fig. 122. *Canthigaster papua*, Bali, Indonesia.



Fig. 123. *Lachneratus phasmaticus*, Kona, Hawaii.



Fig. 124. *Cirrhitops fasciatus*, Oahu, Hawaiian Islands.



Fig. 125. *Priacanthus hamrur*, Marshall Islands.



Fig. 126. *Priacanthus meeki*, Oahu, Hawaiian Islands.

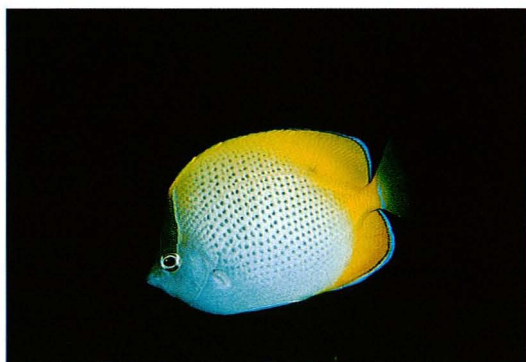


Fig. 127. *Chaetodon guentheri*, Komodo, Indonesia.

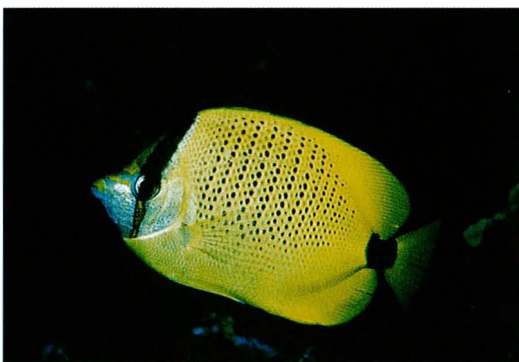


Fig. 128. *Chaetodon miliaris*, Midway, Hawaiian Islands.



Fig. 129. *Abudefduf vaigiensis*, Maui, Hawaiian Islands.



Fig. 130. *Abudefduf abdominalis*, Kona, Hawaii.

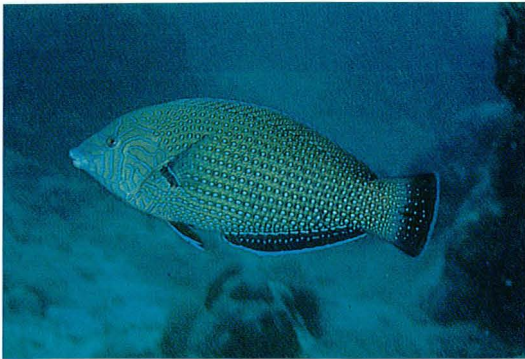


Fig. 131. *Anampses caeruleopunctatus*, female, Seychelles.

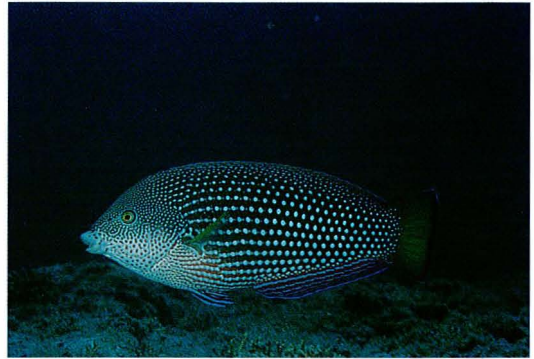


Fig. 132. *Anampses cuvier*, female, Oahu, Hawaiian Islands.



Fig. 133. *Anampses caeruleopunctatus*, male, Phuket, Thailand.



Fig. 134. *Anampses cuvier*, male, Maui, Hawaiian Islands.



Fig. 135. *Cantherhines pardalis*, Sangihe Islands, Indonesia.



Fig. 136. *Cantherhines sandwichiensis*, Maui, Hawaiian Islands.



Fig. 137. *Dendrochirus barberi*, Johnson Island.



Fig. 138. *Pterois sphex*, Kona, Hawaii.



Fig. 139. *Epinephelus quernus*, Midway, Hawaiian Islands.



Fig. 140. *Chaetodon fremblii*, Oahu, Hawaiian Islands.



Fig. 141. *Genicanthus personatus*, female, Midway, Hawaiian Islands.



Fig. 142. *Genicanthus personatus*, male, Midway, Hawaiian Islands.



Fig. 143. *Centropyge potteri*, Oahu, Hawaiian Islands.



Fig. 144. *Desmoholacanthus arcuatus*, Midway, Hawaiian Islands.



Fig. 145. *Coris flavovittata*, female, Midway, Hawaiian Islands.

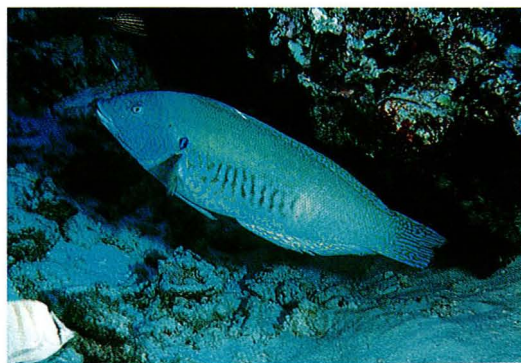


Fig. 146. *Coris flavovittata*, male, Midway, Hawaiian Islands.



Fig. 147. *Chlorurus perspicillatus*, initial phase, Midway, Hawaiian Islands.

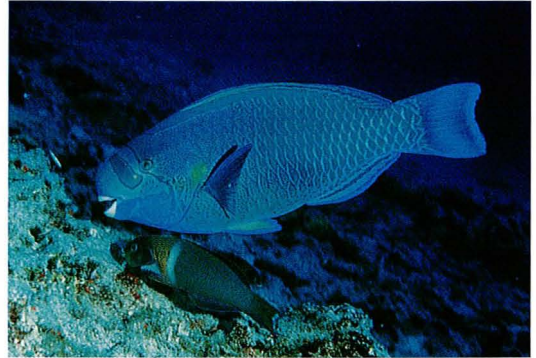


Fig. 148. *Chlorurus perspicillatus*, male, Midway, Hawaiian Islands.



Fig. 149. *Chrysiptera rapanui*, Easter Island.



Fig. 150. *Enchelycore ramosa*, Easter Island.



Fig. 151. *Trachypoma macracanthus*, Easter Island.



Fig. 152. *Cirripectes alboapicalis*, Easter Island.



Fig. 153. *Anampses femininus*, female, Easter Island.

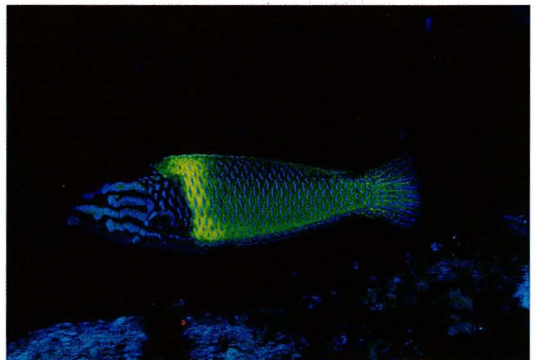


Fig. 154. *Anampses femininus*, male, Easter Island.



Fig. 155. *Gymnothorax porphyreus*, Easter Island.



Fig. 156. *Amphichaetodon melbae*, Easter Island.



Fig. 157. *Scorpaena cookii*, Lord Howe Island.



Fig. 158. *Scorpaena orgila*, Easter Island.



Fig. 159. *Kuhlia sandvicensis*, Maui, Hawaiian Islands.



Fig. 160. *Kuhlia nutabunda*, Easter Island.



Fig. 161. *Pseudolabrus torotai*, Rapa.



Fig. 162. *Pseudolabrus semifasciatus*, Easter Island.



Fig. 163. *Cantherhines verecundus*, Oahu, Hawaiian Islands.



Fig. 164. *Cantherhines rapanui*, Easter Island.



Fig. 165. *Cheilodactylus plessisi*, Easter Island.

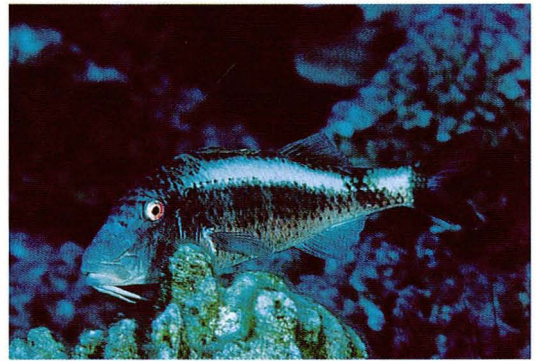


Fig. 166. *Parupeneus orientalis*, Easter Island.

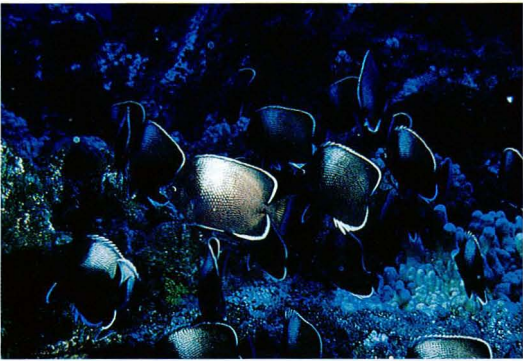


Fig. 167. *Chaetodon litus*, Easter Island.



Fig. 168. *Canthigaster cyanetron*, Easter Island.



Fig. 169. *Sargocentron wilhelmi*, Easter Island.



Fig. 170. *Chromis randalli*, Easter Island.

ocene when sea levels dropped, and a barrier formed at the narrow shallow entrance. One might expect allopatric speciation to have resulted in the Red Sea at such times; however, the Sea may have become too saline for fishes to survive if isolated for long periods. It has also been suggested that seasonal upwelling in the Gulf of Aden could provide a barrier to dispersal between the Red Sea and the Indian Ocean (Sheppard et al. 1992). Many of the endemic shore fishes of the Red Sea are confined to the northern part (Roberts et al. 1992). This part of the Sea remains cooler than one would expect from the higher latitude alone because it is deep and the circulation pattern results in the cool deeper water coming to the surface. Therefore, the very warm sea temperature of the middle and southern parts of the Red Sea would be a barrier to fishes adapted to the cooler northern waters.

SPECIES VS. SUBSPECIES

There is a major taxonomic problem, alluded to above, as to how to classify fishes from 2 widely separated insular areas that differ very slightly. Some ichthyologists prefer to treat 2 such populations as species when samples from both can be differentiated 100% of the time, regardless of how slight the difference might be — even a single spot of color. There are no intermediates, so they say there should be 2 species. Other ichthyologists, the author included, try to decide from the level of differentiation if fishes from each population are likely to interbreed naturally, should they be given the opportunity to do so. If the differences are slight and clearly less than the characters that separate other related species of the genus, a subspecies name seems advised. Generally speaking, it does not require much of a genetic change to produce a small difference in color in a population, or a shift in the modal count of fin rays or scales. Surely when that 1st slight difference becomes apparent, there has not been enough change to form a barrier to reproduction with the progenitor stock. On the other hand, there are species that have evolved into 2 allopatric populations that show very little color, meristic, or morphological differentiation, but they may differ ecologically or behaviorally to such an extent that they would never interbreed. I maintain that the use of subspecies is preferred when the differences of the 2 populations is slight and the systematist is faced with difficulty in deciding whether to regard them as

2 species or not. If he calls them 1 species without the trinomial, we have lost information on their distribution. If he calls them 2 species, we have also lost information on the close relationship of the 2 populations. Consider the convict surgeonfish *Acanthurus triostegus* which occurs in continuous distribution from East Africa to Mexico. In Hawaii it looks the same except for a longer dark marking at the pectoral-fin base. If it is called by the available name *Acanthurus sandvicensis*, the reader may wonder how such a wide-ranging species as *A. triostegus* failed to reach the Hawaiian Islands. Conversely, naming the Hawaiian population *A. triostegus* ignores the consistent difference in color. *Acanthurus triostegus sandvicensis* is the author's preferred taxonomic treatment.

Much systematic research is being done today using molecular techniques such as electrophoresis and DNA sequencing. These are very valuable adjuncts to our traditional morphological approach of determining species. They are of particular value in the differentiation of 2 closely related sympatric species, as when Shaklee and Tamaru (1981) showed with electrophoresis that there are 2 look-alike species of *Albula* in the Hawaiian Islands. In the same study they determined that there are 2 species of the genus in the western Atlantic, neither of which is the same as the 2 in Hawaii. What was once called *Albula vulpes* is now 4 species (and possibly 5 if an eastern Atlantic population proves to be a species).

In the opinion of the author, too much emphasis is now being placed on biochemical characters (just as the examination of otoliths was once the vogue). Given enough effort, DNA analysis of 2 allopatric populations of a fish may eventually yield a difference, and the systematist may decide that this is worthy of nomenclatural recognition. Or the reverse may happen. Robert Chapman (pers. comm.) has informed me that his DNA analysis showed that the western Atlantic groupers *Epinephelus striatus* and *Mycteroperca bonaci* belong in the same genus. Given the strong morphological and other differences, he knows this seems unlikely, but he finds his DNA study difficult to ignore. Let us treat these new taxonomic methods as providing additional characters for our studies but not allow them to dominate our basic tool of morphology. When molecular studies are in agreement with the morphological, our conclusions are strengthened, but when they differ, it is not wise to disregard solid morphological evidence. We as systematists must strive for stability in our classification. If we find evidence that a name of a taxon

might be changed, then let us make the change only when the evidence is trenchant.

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印度太平洋沿岸魚類之動物地理分布

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東印度群島地理區（印尼、新幾內亞和菲律賓）為世界上海水魚相最豐富的地區，約有 2800 種沿岸魚類。種數會由東印度群島向東遞減至夏威夷之 566 種，伊斯特 (Easter) 島之 126 種。東印度群島海洋生物多樣性高的主要原因是在於此地冰河期之海水相對溫度穩定、棲所面積大及複雜度高；且近大陸及大島的棚區，有豐富之陸源營養物質流入，比大洋性小島更適合孕育許多浮游期短無法長期漂流，且又需要豐富餌料生物的魚種；同時這裡又可以接受周邊地區所進化出許多新種的幼生。這是因為在冰河期時（過去 70 萬年內至少發生過 3-6 次）海平面下降阻隔了這裡海水魚的東西向擴散，加上此地大量河川淡水及湧昇冷流造成低鹽低溫的綜合效應。另外於低水位期，這裡的港灣及局部海域，亦有種化作用。這類隔離所造成的成對種 (geminant species)，在外形及體色上極為相似，本文列舉出其中的 65 例，當然也可能其中還有很多實在因為太相近而尚未被發掘出來的例子。另有 15 例是真正屬於西印度洋及西太平洋的成對種，因他們在東印度群島並未重疊；有 8 例其體色在兩大洋間雖有差異，但目前還未被視為不同的種；另有 5 例過去曾被引用為安達曼海及西印尼種，可能是因為安達曼海在晚第三紀 (Neogene) 時期幾近隔絕所造成的效應。文中亦利用海平面下降造成物種滅絕來解釋魚種在東印度群島東西兩邊不同的分布，同時亦討論魚類呈反熱帶分布的原因。

太平洋島嶼魚類特有種的比例隨著當地陸續發現許多印度太平洋新記錄魚種數的增加而降低，只有夏威夷仍特別高，當地特有種佔了 23.1%，伊斯特島次之佔 22.2%。亞種仍應鼓勵使用，特別是那些受地理阻隔的族群，在形態上已有不同，但其差別仍低於同域內的同屬不同種時。為了維護魚類分類的持續穩定性，希望大家不要把由生化或分生方法所得的形質資料視為比系統學中最基礎的形態形質來得重要。

關鍵詞：東印度，種化，本地特有性，亞種，成對種。

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