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Deep-sea Benthic Fish of the Hawaiian Archipelago, Cross Seamount, and Johnston Atoll[1]

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ABSTRACT: More than 250 benthic fish taxa were photographed and videotaped by Hawaii Undersea Research Laboratory submersibles at depths between 40 and 2000 m in the Hawaiian Archipelago, Johnston Atoll, and Cross Seamount. Most of the 213 identified fish species occurred close to hard substrates with holes, ledges, or caves. Twenty-two species (notably the larger sharks, lutjanids, and carangids) are cosmopolitan. Seventy-six species are restricted to various Indo-Pacific areas, 64 in the Pacific, and 51 in the Hawaiian Archipelago including Cross Seamount and Johnston Atoll. There is a rapid decrease in the number of species from 200 to 400 m depth. One hundred eight species were seen 20 m deeper than previously reported. Eleven of the deeper-dwelling animals were found 20 m shallower than previously recorded. Faunal zones were not recognized at any depth. Species newly recorded in Hawai'i include *Bathypterois grallator* (Goode & Bean), *Bodianus cylindriatus* (Tanaka), *Centrophorus* cf. *granulosus* (Bloch & Schneider), *Chaunax fimbriatus* Hilgendorf, *Caelorinchus spilonotus* Sazonov & Iwamoto, *Notocanthus* sp., *Paratrachichthys prosthemius* Jordan & Fowler, *Prognathodes guezei* (Mauge & Bauchot), and *Sladenia remiger* Smith & Radcliffe. New species collected and reported elsewhere are *Centrodraco rubellus* Fricke et al., *Epigonus glossodontus* Gon, *Owstonia* sp., and *Pseudanthias fucinus* (Randall & Ralston). *Caelorinchus* sp. 2 and *Callanthias* sp. are probably undescribed. It appears that the Hawaiian deep-sea fish fauna has multiple origins and affinities with many regions.

THIS PAPER SUMMARIZES the fish fauna collected, photographed, and videotaped during 500 dives conducted by Hawaii Undersea Research Laboratory (HURL) submersibles *Makali'i* and *Pisces V*. These vehicles operated in the Hawaiian Archipelago from French Frigate Shoals to Lō'ihi Volcano, located off the southeastern end of Hawai'i Island (18° 55′ N, 155° 16′ W); on Cross Seamount, situated southwest of Hawai'i Island (18° 44′ N, 158° 15′ W); and at Johnston Atoll, located southwest of the Hawaiian Archipelago (16° 42′ N, 169° 32′ W). The data were obtained from dives made at depths between 40 and 2000 m from 1982 to 1992.

The deep-sea fish fauna of Hawai'i is now among the best known in the Pacific, when the results of the trawl surveys by Gilbert (1905) and Struhsaker (1973) are combined with results of this submersible study. Trawl studies are limited by factors such as net avoidance and imprecise knowledge of depth of capture (Haedrich et al. 1975, Merrett and Marshall 1981). Submersible studies are biased by attraction or repulsion of organisms and photographic selectivity of the scientists (Ralston et al. 1986, Chave and Jones 1991; HURL records, unpubl. data). Many of the sampling limitations are complementary when precise submersible ob-

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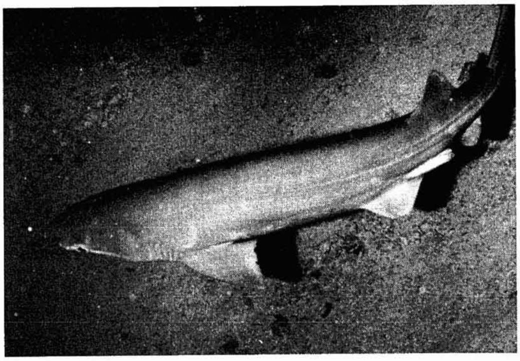


FIGURE 1. *Hexanchus griseus* (HURL photo 43-31, Colin).

Figure 2. *Pseudotriakis microdon* (HURL video 5050, Polovina).

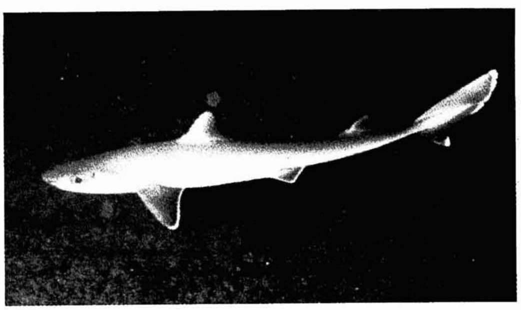


Figure 3. *Squalus mitsukurii* (HURL photo 148-94, Chave).

FIGURE 4. *Echinorhinus cookei* (HURL photo 5039-43, Mullineaux).

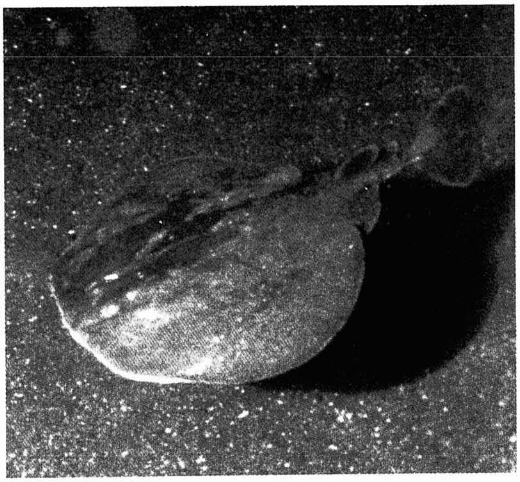


FIGURE 5. *Torpedo* sp. (HURL photo 119-68, Chave).

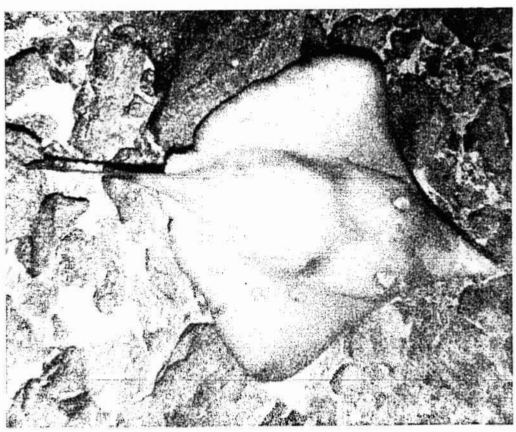


Figure 6. *Hexatrygon longirostra* (HURL photo 5069-06, Moore).

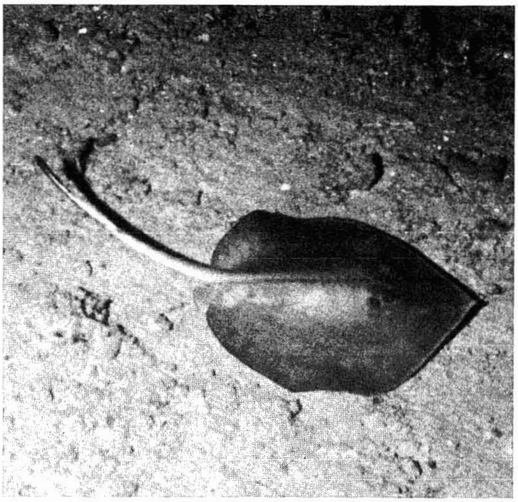


FIGURE 7. *Plesiobatis daviesi* (HURL photo 87-18, Maragos).

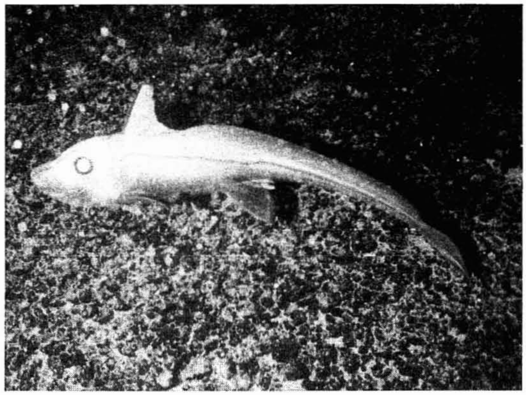


FIGURE 8. *Hydrolagus purpurescens* (HURL photo 238-11, France).

FIGURE 9. An ilyophine eel and the zoanthid *Gerardia* sp. (HURL photo 68-08, Chave).

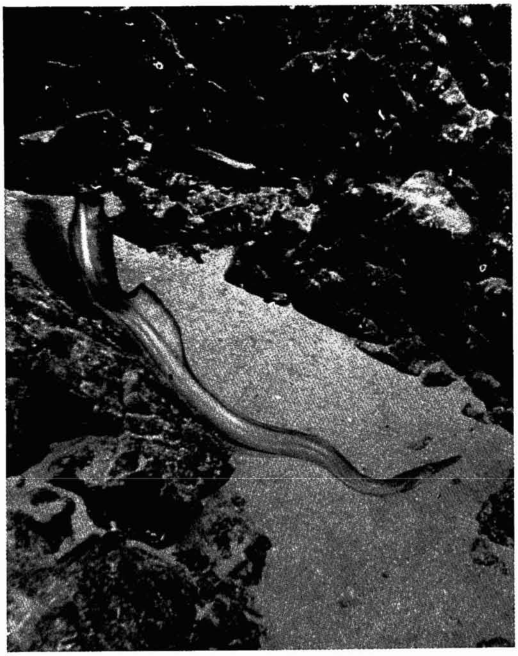


FIGURE 10. *Nettastoma parviceps* (HURL photo 5068-11, Moore).

Figure 12. *Gadomus melanopterus* (HURL photo 5091-76, Malahoff).

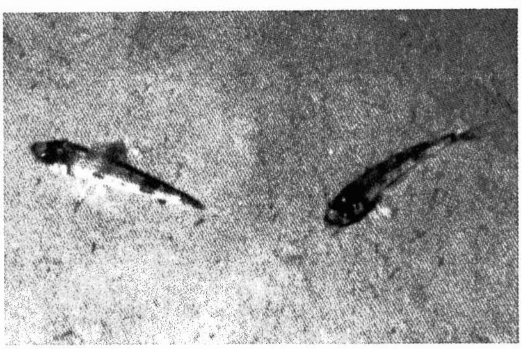


FIGURE 11. *Chlorophthalmus proridens* (HURL photo 123-13, Chave).

Figure 13. *Caelorinchus* sp. 2 (HURL video 5204, Young).

servations of depth and behavior are combined with data on large numbers of specimens and areas sampled by trawls. We can address the biogeography, depth distributions, and ecology of Hawaiian deep-sea fish with greater confidence than previously possible.

MATERIALS AND METHODS

The submersibles' still and video cameras were synchronized to record the same images, enabling subjects seen on the video screen to be photographed. Photos were taken in strobe light. The videocamera ran

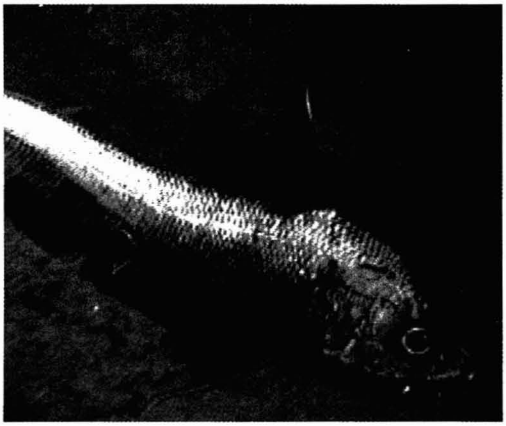


Figure 14. *Coryphaenoides longicirrhus* (HURL video 5180, Malahoff).

FIGURE 15. *Nezumia propinqua* (HURL photo 215-46, Chave).

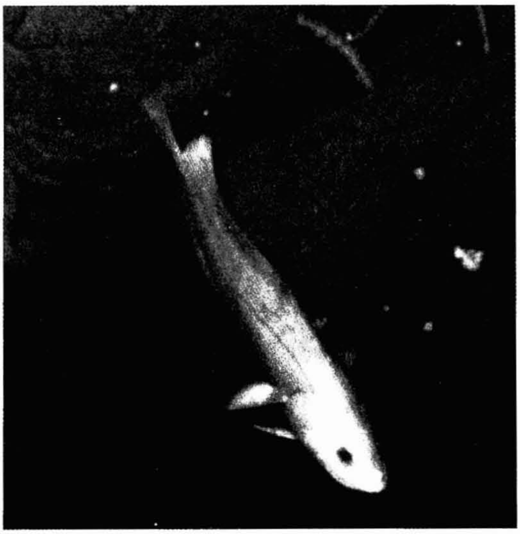


FIGURE 16. *Antimora microlepis* (HURL photo 5145-88, Garcia).

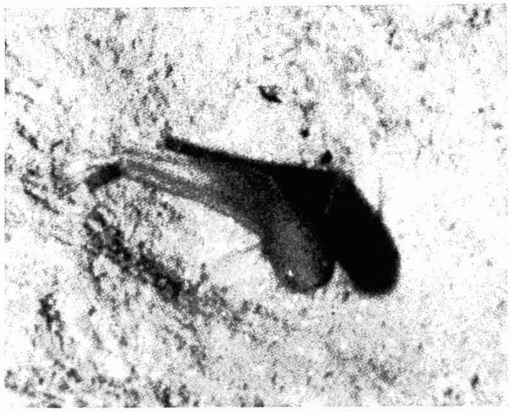


FIGURE 17. *Gadella molokaiensis* (HURL photo 118-25, Chave).

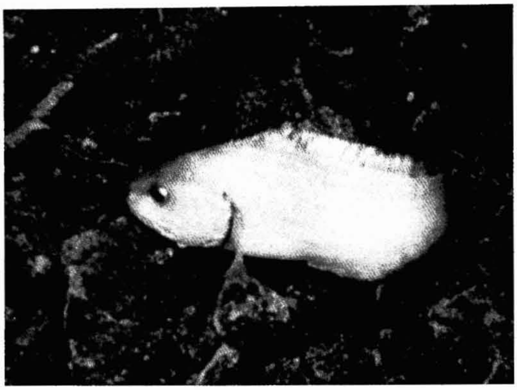


Figure 18. *Pycnocraspedum armatum* (HURL photo 5068-49, Moore).

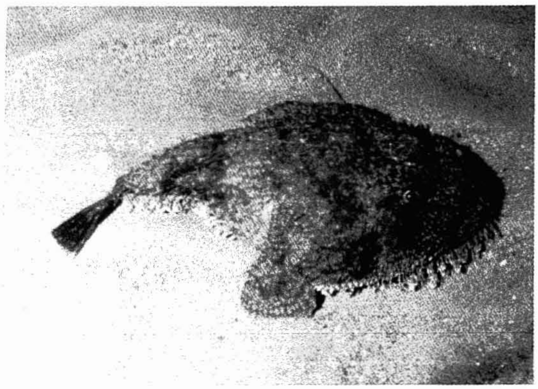


FIGURE 19. *Lophiodes miacanthus* (HURL photo 144-17, Scheuer).

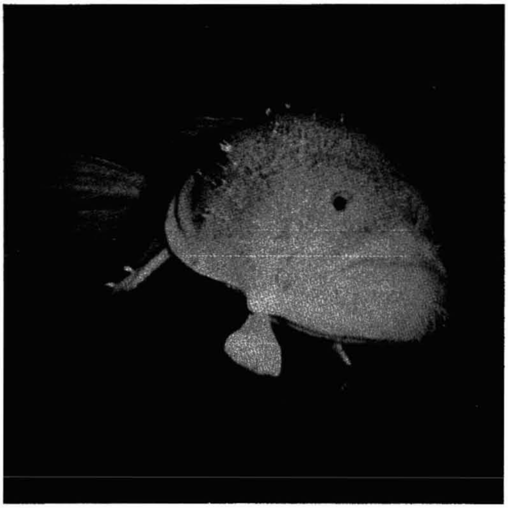


FIGURE 20. *Sladenia remiger* (HURL photo 5186-141, Garcia).

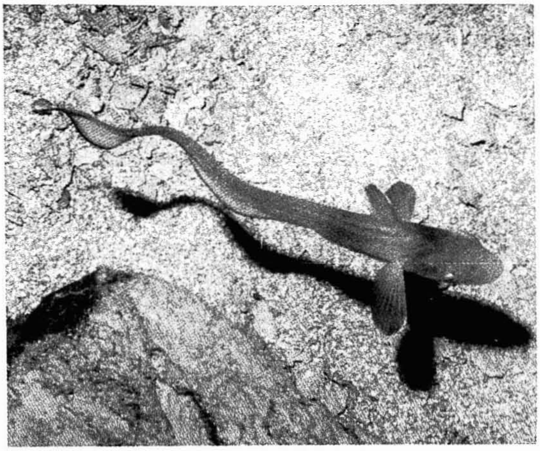


FIGURE 22. *Ijimaia plicatellus* (HURL photo 34-146, Colin).

FIGURE 21. *Malthopsis jordani* (HURL video 2025, Young).

FIGURE 23. *Beryx decadactylus* (HURL photo 215-05, Chave).

throughout the dive, much of the time using the submersible's running lights for illumination. The floodlights were turned to videotape selected subjects. All photographs from depths greater than 40 m were examined. About 2100 of these include identifiable fish and form the data set used in this study. Videotapes, light measurements, water chemistry profiles, depth records, and specimens augment these data.

All specimens and many of the photographs were sent to experts for identification. Some identifications are tentative because specimens were not collected or because the photographs did not show those characteristics used for identification. The photographs and videotapes documenting the fish species in this study are filed in the HURL archives and are available on request. Figures 1–45 and Plates I–IV contain the first published underwater photographs of some

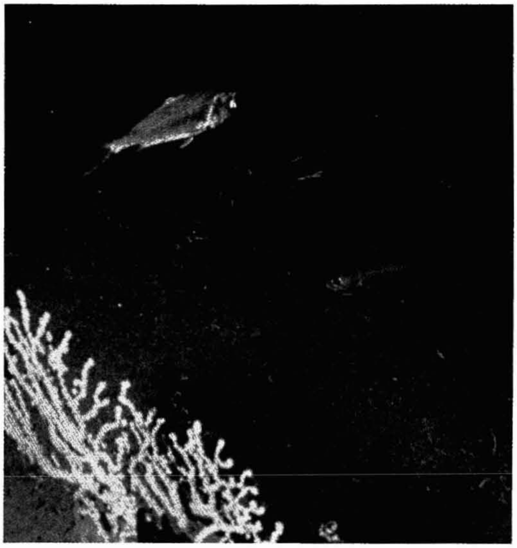


FIGURE 24. *Polymixia berndti* (HURL photo 213-48, Chave).

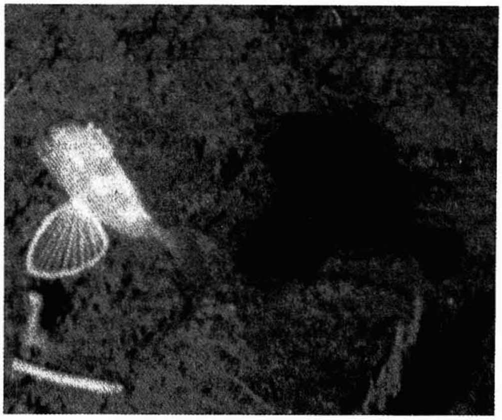


FIGURE 25. *Stethopristis eos* (HURL photo 155-13, Chave).

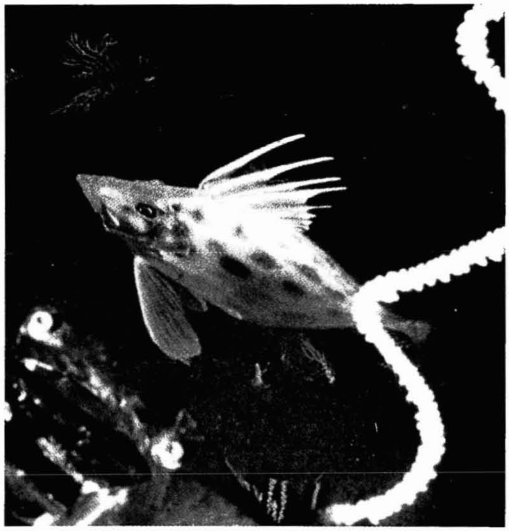


FIGURE 26. *Zenopsis nebulosus* (HURL photo 357-37, Grigg).

FIGURE 27. *Grammicolepis brachiusculus* (HURL video 119, Chave).

of the fishes. Previously published photos taken from HURL submersibles may be found in Randall and Ralston (1984), Randall et al. (1985), Ralston et al. (1986), Jones and Sulak (1990), Chave and Jones (1991), and Pyle and Chave (1994).

Table 1 includes all identified fish taxa, their depth ranges, locations observed, and relative abundances. Table 2 contains new information about some of the fish. The order of species presentation in both tables follows Eschmeyer (1990).

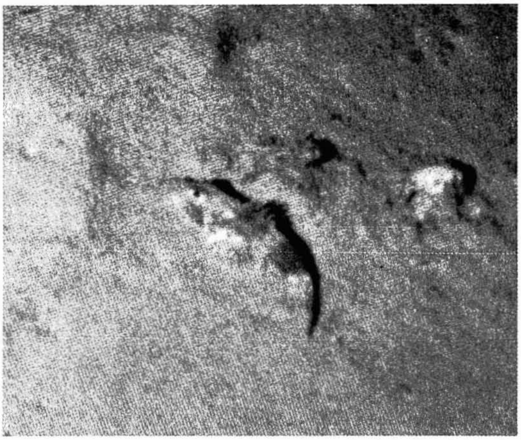


FIGURE 28. *Bembradium roseum* (HURL photo 130-28, Maragos).

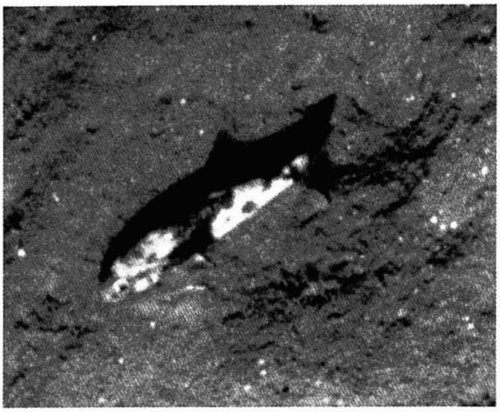


Figure 29. *Synagrops argyrea* (HURL photo 118-18, Chave).

FIGURE 30. *Symphysanodon maunaloae* (HURL video 272, Grigg).

RESULTS AND DISCUSSION

Most fish seen in this study were collected previously in the Pacific (Table 1). Collections made with the HURL submersibles yielded four new species: *Centrodraco rubellus* Fricke et al., *Epigonus glossodontus* Gon, *Owstonia* sp., and *Pseudanthias fucinus* (Randall & Ralston) (Table 2). Two possible new species (*Caelorinchus* sp. 2 and *Callanthias* sp.) and nine other new Hawaiian records (*Bathypterois grallator* [Goode & Bean], *Bodianus cylindriatus* [Tanaka], *Caelorinchus spilonotus* Sazonov & Iwamoto, *Centrophorus* cf. *granulosus* [Bloch & Schneider], *Chaunax fimbriatus* Hilgendorf, *Notocanthus* sp., *Paratrachichthys prosthemius* Jordan & Fowler, *Prognathodes guezei* [Mauge & Bauchot], and *Sladenia remiger* Smith & Radcliffe) are also discussed in Table 2.

Behavior and Morphology

Below 100 m most fish were located on or just above the bottom. This agrees with observations of deep-sea benthic fish seen primarily at 0–5 m from the bottom on the Nazca and Sala-y-Gómez Ridges (Golovan and Pakhorukov 1987). Most species were found on or near hard substrates that contained holes, caves, or other irregularities. On sand, large groups of fish were seen in troughs when the currents were strong. They were only observed above the substrate when currents swept particles through the water at moderate rates (HURL records, unpubl. data).

When the submersibles were operating with their running lights on, most fish did not react to the vehicles. Fishes that did react are

FIGURE 31. An aggregation of *Symphysanodon typus* (HURL photo 337-48, Ralston).

FIGURE 32. *Eumegistus illustris* (HURL photo 5070-16, Moore).

listed in Table 2. When the brighter photo and video lights were turned on, many of the fish that occurred deeper than 100 m reacted by bumping into the bottom, backing away, moving toward or away from the light, or becoming motionless.

Benthic fish deeper than 100 m were commonly eel-like in shape. Many could not be identified from their photos. Ateleopids, macrourids, halosaurids, and congrids were often the most abundant of the eel-like forms. Perhaps this body shape offers less resistance to current flow and allows greater motility for near-bottom animals (Zaferman 1992). Having a long lateral line also may increase sensory capabilities and enable eel-like fish to search for prey without disturbing the bottom (Marshall 1971, Marshall and Merrett 1977).

Biogeography

Of 213 species of fish identified in this study and listed in Table 1, 25 have circumglobal distributions, 73 are found in the Indo-Pacific, and 64 are restricted to Pacific waters. Fifty-one species (24%) are found

FIGURE 33. *Aphareus rutilans* (bottom right) and several *Pristipomoides filamentosus* (HURL photo 336-03, Ralston).

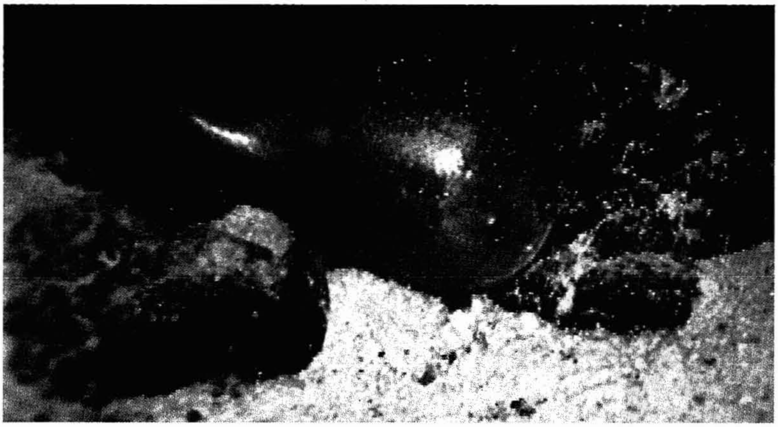
Figure 34. *Etelis carbunculus* (HURL photo 213-74, Chave).

only in the Hawaiian Archipelago, Cross Seamount, and Johnston Atoll. This high number of endemic deep-sea species agrees with calculations that include most of the shallow-water fish in Central Pacific areas (Randall 1985, Randall et al. 1985, Kosaki et al. 1991). All fish seen on Cross Seamount and Lō'ihi were also observed off the Hawaiian Islands (HURL records [unpubl.]; Grigg et al. 1987). This observation was expected because Cross Seamount lies only 190 km to the west and Lō'ihi is 50 km to the south of Hawai'i Island, easily within the range of larval fish dispersal.

Two trends are evident from distribution data in Table 1. Most large, strong swimmers with carnivorous or omnivorous habits (e.g., many of the sharks, lutjanids, and carangids) have ocean-wide distributions. Fish found shallower than 100 m tend to have more specific habitat preferences and wider zoogeographic distributions than deeper-dwelling fish, perhaps because shallower species have been studied more extensively.

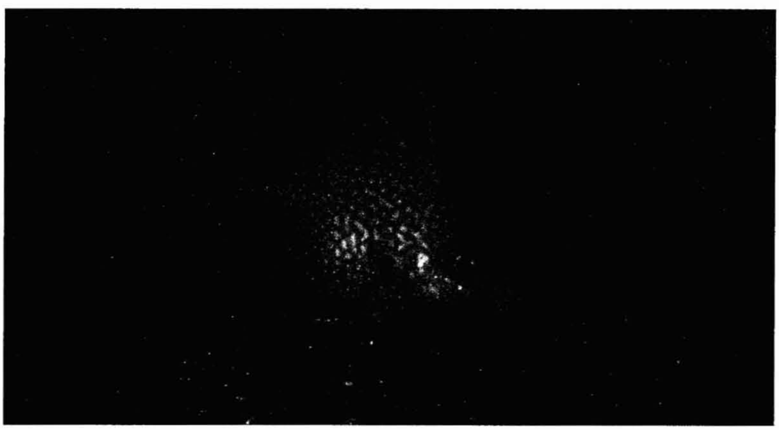
Two hypotheses are currently recognized as explaining the distribution of shallow-water marine organisms in Hawai'i: dispersal and vicariance. Both are discussed at length by Springer (1982) and Newman (1986).

The dispersal hypothesis assumes that the Hawaiian Archipelago was colonized by larval drift of Indo-Pacific fish across "filter bridges" (Gosline 1955, Gosline and Brock 1960) or along "stepping stones" (Wilson and Kaufmann 1987, Kosaki et al. 1991).



a. *Chaunax fimbriatus* (HURL video 5192, Cowan).

b. *Chaunax umbrinus* (HURL photo 232-36, McMurtry).

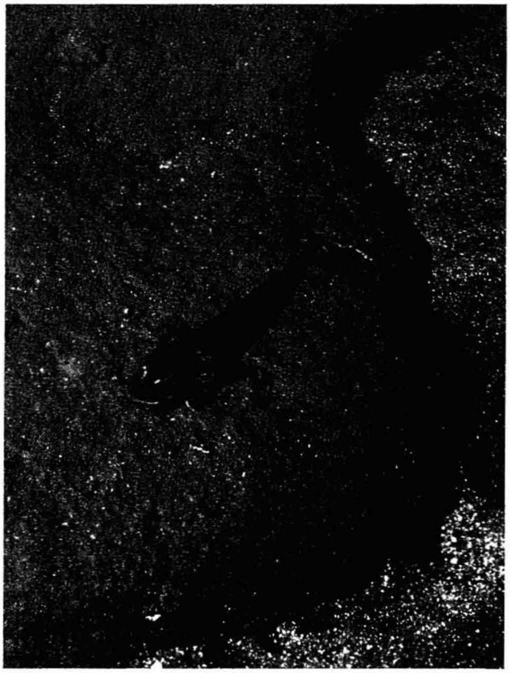


c. *Hollardia goslinei* (HURL photo 118-35, Chave).

a. *Laemonema rhodochir* (top) and *Satyrichthys engyceros* (bottom) (HURL photo 157-27, Maragos).

b. *Antigonia* sp. (HURL photo 174-56, Randall).

c. *Pontinus macrocephalus* (top) and *Plectranthias kelloggi* (bottom) (HURL photo 125-12, Maragos).



d. *Chrionema chryseres* (HURL photo 215-07, Chave).

FIGURE 35. Two *Pristipomoides filamentosus* (middle, bottom right), *Naso maculatus* (top right), and a group of *N. hexacanthus* (HURL photo 374-06, Polovina).

Figure 36. *Synaphobranchus brevidorsalis* (HURL photo 5237-48, France).

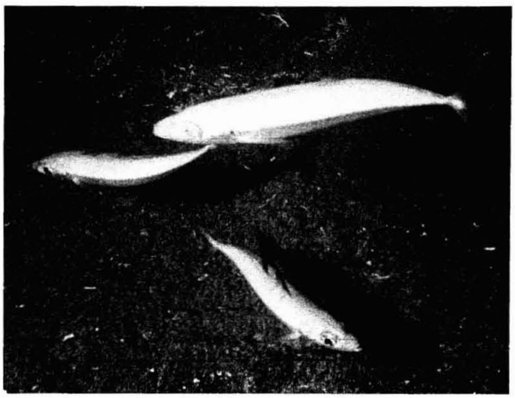


Figure 37. *Decapterus tabl* (HURL photo 148-49, Chave).

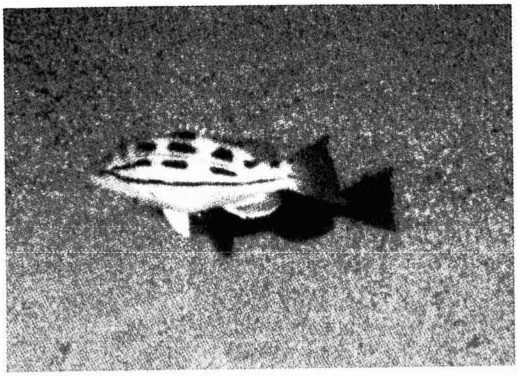


Figure 38. *Bodianus vulpinus* (HURL photo 340-16, Ralston).

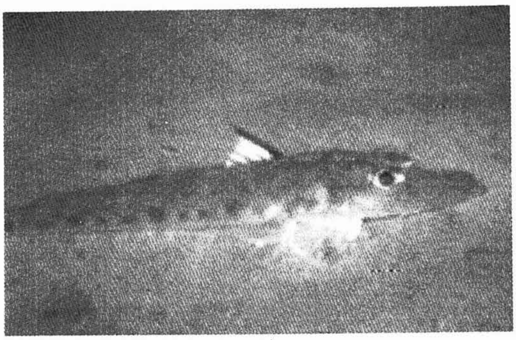


Figure 39. *Bembrops filifera* (HURL video 212, Chave).

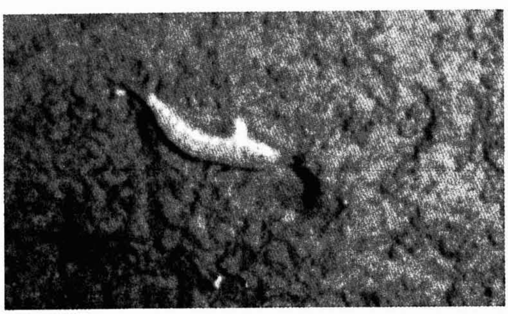


FIGURE 40. *Parapercis roseoviridis* (HURL photo 149-34, Chave).

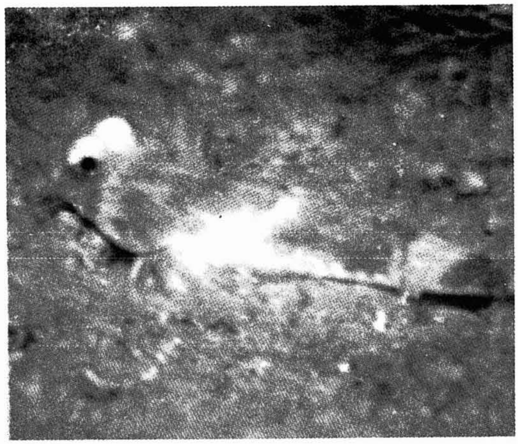


Figure 41. *Draconetta xenica* (HURL video 101, Scheuer).

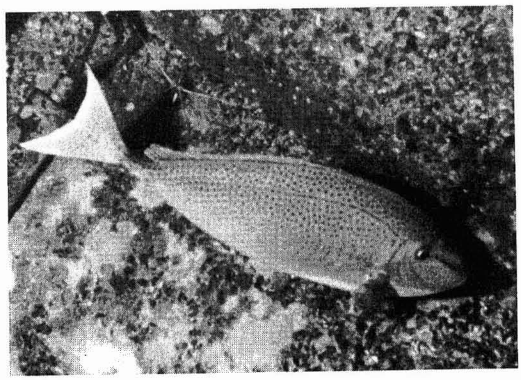


Figure 42. *Naso maculatus* (HURL photo 382-74, Polovina).

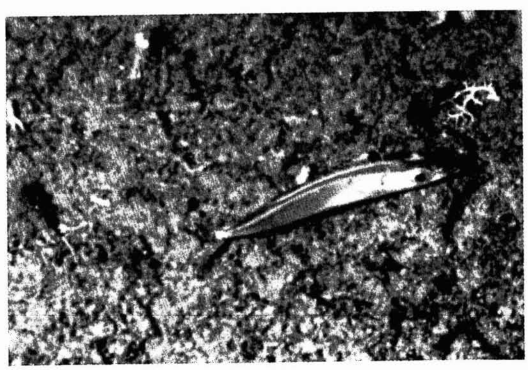


Figure 43. *Rexea nakamuri* (HURL photo 213-61, Chave).

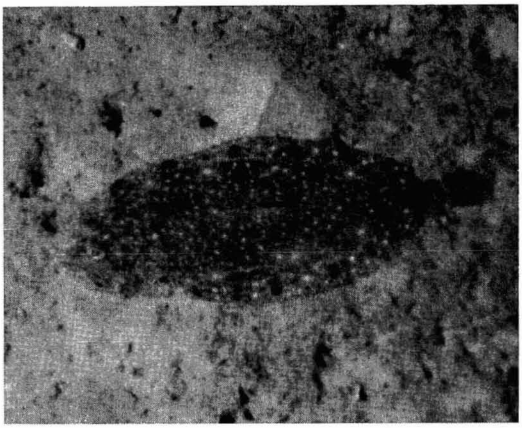


Figure 44. *Chascanopsetta prorigera* (HURL photo 107-25, Chave).

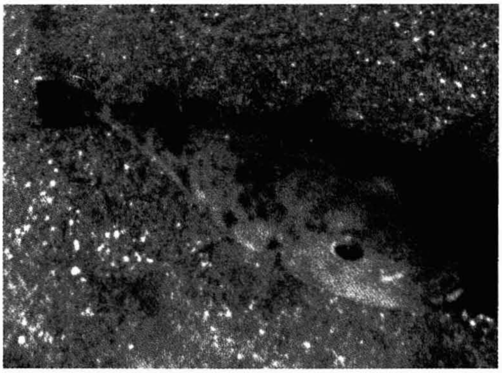


Figure 45. *Sphoeroides pachygaster* (HURL photo 219-31, Polovina).

The primary affinity of the shallow-water Hawaiian fish fauna is thought to be with the Ryukyu Islands and southern Japan, resulting from the dispersal of planktonic larvae via extensions of the Kuroshio Current (Randall et al. 1985, Hourigan and Reese 1987). This suggestion is supported by shallow-water taxa found in Japan and Hawai'i that do not occur elsewhere in the central Pacific. At the generic level, our new Hawaiian records of the deep-water fish *Notocanthus* sp. and *Owstonia* sp. provide examples of affinities with the Japanese deep-water fish fauna. For deep-sea fish this pattern may be the result of lack of sampling in other areas of the Pacific Plate.

The vicariance theory emphasizes the effect of plate tectonics on allopatric shallow-water speciation (Springer 1982, Blum 1989) and the effect of fluctuating sea levels on isolation and integration (Myers 1989, Springer and Williams 1990, Kosaki et al. 1991). Vicariance was suggested by Springer (1982) as an explanation for the near absence of many shorefish taxa from the central Pacific Plate (except Hawai'i). A deep-sea example may be alepocephalid fish. These fish have not been observed with submersibles and have not been captured from the central Pacific Plate except very rarely in the Hawaiian Ridge (Iwamoto 1975, Clarke and Wagner 1976, Iwamoto et al. 1976, Borets 1986). In most of the world's oceans alepocephalids are an abundant component of the deep-sea fish fauna (Okamura and Kitajima 1984, Anderson et al. 1985, Merrett and Domanski 1985, Haedrich and Merrett 1988).

Springer (1982) emphasized that the different hypotheses about origins of Hawaiian fish could be tested by cladistic analyses of Hawaiian species and their nearest relatives. Those cladistic analyses that include shallow-water Hawaiian fish do not support a single origin, and no endemic Hawaiian species have endemic Japanese species as sister taxa (Smith-Vaniz 1976, Caruso 1981, Pietsch and Grobecker 1987, Starnes 1988, Williams 1988, Blum 1989, Markle and Olney 1990, Westneat 1993). The dominant patterns of distribution appear to be either Indo-Pacific or circumglobal. Three cladistic studies involve Hawaiian deep-water fish. Two suggest relationships between Hawaiian populations and those of the eastern Pacific (Markle and Olney 1990) and western Atlantic (Starnes 1988). *Lophiodes miacanthus* (Gilbert) is the only species studied with a distribution that supports a strict southern Japan/Hawaiian affinity (Caruso 1981).

A comparison of Hawaiian deep-sea fish taxa with those of the eastern South Pacific reveals similarities between the taxa of the two areas (Parin 1990, 1991). For example,

TABLE 1

FISHES PHOTOGRAPHED WITH THE HAWAII UNDERSEA RESEARCH LABORATORY SUBMERSIBLES *Makali'i* AND *Pisces V*

TAXON	RANK[a]	DEPTH (m) OBSERVED	SUBSTRATE ON/ABOVE	LOCATION OBSERVED[b]	DEPTH (m) PUBLISHED	LOCATION PUBLISHED	SELECTED REFERENCES (DEPTH, LOCATION, AND/OR PHOTOGRAPH)
Family Hexanchidae							
Hexanchus griseus (Bonnaterre)	R	500–1,400	Midwater	WH, WO	183–1,524	Circumglobal	Compagno 1984, Humphreys et al. 1984, Borets 1986
Family Alopiidae							
Alopias vulpinus (Bonnaterre)	R	320	Midwater	JA	1–366	Circumglobal	Compagno 1984, Randall et al. 1985
Family Pseudotriakidae							
Pseudotriakis microdon Capello	R	500	Sand	LO	200–1,500	Circumglobal	Tinker 1978, Compagno 1984
Family Carcharhinidae							
Carcharhinus amblyrhynchos (Bleeker)	O	10–275	Midwater	JA	10–274	Indo-Pacific	Johnson 1984, Randall et al. 1985, Fielding and Robinson 1987, Myers 1989
Family Squalidae							
Centrophorus cf. *granulosus* (Bloch & Schneider)	R	500	Sand	LO	100–1,200	Circumglobal	Compagno 1984, Masuda et al. 1984
Etmopterus sp.	R	900–970	Sand	LH			
Squalus mitsukurii Jordan & Snyder	R	336–416	Hard	LH, LO, WO	160–545	Pacific	Clarke 1972, Struhsaker 1973, Novikov et al. 1980, Masuda et al. 1984, Parin 1991
Family Echinorhinidae							
Echinorhinus cookei Pietschmann	R	360–420	Sand	CS, LH	11–424	Pacific	Compagno 1984, Humphreys et al. 1984, Golovan and Pakhorukov 1987, Parin 1991
Family Torpedinidae							
Torpedo sp.	R	332	Fine sand	WH	265–476	Hawaiian Is.	Struhsaker 1973
Family Dasyatidae							
Dasyatis latus (Garman)	R	40–75	Sand	LO	40–214	Pacific	Struhsaker 1973, Nishida and Nakaya 1990
Dasyatis brevis (Garman)	R	52–150	Sand	HA	10–148	Pacific	Tinker 1978, Nishida and Nakaya 1990
Family Hexatrygonidae							
Hexatrygon longirostra Chu & Meng	R	750–950	Sand, talus	LH	700–710	Pacific	Okamura and Kitajima 1984
Family Plesiobatididae							
Plesiobatis daviesi (Wallace)	O	287–780	Sand	WH, WO, LO	44–412	Indo-Pacific	Clarke 1972, Struhsaker 1973, Masuda et al. 1984, Nishida 1990

Family Chimaeridae							
Hydrolagus purpurescens (Gilbert)	R	1,150–1,580	Hard	LV, PB	1,750–1,951	Central Pacific	Gilbert 1905, Novikov et al. 1980, Masuda et al. 1984
Family Halosauridae							
Aldrovandia phalacra (Vaillant)	O	955–1,680	Sand	LH, PB	530–1,635	Circumglobal	McDowell 1973, Struhsaker 1973, Kaufmann et al. 1989, Chave and Jones 1991
Family Notocanthidae							
Notocanthus sp.	R	880–940	Sand	LH	768–796	Hawaiian Is.	National Marine Fisheries Service, Southwest Fisheries Science Center (unpubl.)
Family Muraenidae							
Gymnothorax berndti Snyder	O	128–303	Hard, holes	HA, JA	110–225	Indo-Pacific	Struhsaker 1973, Tinker 1978, Myers 1989
Gymnothorax nudivomer (Playfair & Gunther)	O	61–214	Hard, holes	LH, JA, PB	30–165	Indo-Pacific	Clarke 1972, Randall et al. 1985, Myers 1989
Gymnothorax nuttingi Snyder	O	110–291	Hard, holes	HA, JA	165–300	Johnston Atoll, Hawaiian Is.	Clarke 1972, Randall et al. 1985
Family Synaphobranchidae							
ilyophine eel	O	343–396	Hard, *Gerardia*	HI			
Synaphobranchus brevidorsalis Gunther	O	1,175–1,530	Sand, vents	LH, LV, CS	575–1,535	Circumglobal	Robins and Robins 1989
Synaphobranchus cf. *kaupi* Johnson	R	810–1,725	Fine sand	CS, LH	131–2,196	Circumglobal	Robins and Robins 1989
Synaphobranchus sp.	O	1,175–1,400	Sand, hard	HA	550–1,975		
Family Ophichthidae							
Myrichthys maculosus (Cuvier)	R	69–262	Various	JA	1–262	Indo-Pacific	Randall et al. 1985, Myers 1989, Randall et al. 1990
Ophichthus kunaloa McCosker	O	350–382	Fine sand	WO, LO	220–250	Hawaiian Is.	McCosker 1979
Family Congridae							
Ariosoma marginatum (Vaillant & Sauvage)	O	214–490	Fine sand	WH, JA, CS	101–236	Hawaiian Is.	Struhsaker 1973, Humphreys et al. 1984
Bathyuroconger vicinus (Vaillant)	R	750–900	Fine sand	LH	229–1,318	Circumglobal	Smith 1989
Conger oligoporus Kanazawa	O	217–370	Hard, holes	JA, PB	110–365	Johnston Atoll, Hawaiian Is.	Clarke 1972, Struhsaker 1973, Randall et al. 1985
Family Nettastomatidae							
Nettastoma parviceps Gunther	R	775–945	Sand	CS, LH	420–1,140	Indo-Pacific	Tinker 1978, Ohta 1983, Okamura and Kitajima 1984, Smith and Heemstra 1986
Family Aulopodidae							
Hime japonica (Gunther)	R	343–510	Fine sand	CS, LH, WH	201–238	Pacific	Struhsaker 1973, Borets 1986, Parin and Kotlyar 1989

TABLE 1 (continued)

TAXON	RANK[a]	DEPTH (m) OBSERVED	SUBSTRATE ON/ABOVE	LOCATION OBSERVED[b]	DEPTH (m) PUBLISHED	LOCATION PUBLISHED	SELECTED REFERENCES (DEPTH, LOCATION, AND/OR PHOTOGRAPH)
Family Chlorophthalmidae							
Chlorophthalmus proridens Gilbert & Cramer	O	218–510	Fine sand	WH, WM, LL, LO, WO	185–350	Central Pacific	Gilbert & Cramer 1892, Novikov et al. 1980
Family Ipnopidae							
Bathypterois atricolor Alcock	R	1,800–1,920	Fine sand	LH, PB	573–5,150	Indo-Pacific	Sulak 1977, Masuda et al. 1984, Jones and Sulak 1990
Bathypterois grallator (Goode & Bean)	R	1,140–1,460	Fine sand	LH	878–4,720	Circumglobal	Sulak 1977, Jones and Sulak 1990
Family Synodontidae							
Synodus doaki Russell & Cressey	R	52–260	Hard	WH	90–200	Pacific	Waples & Randall 1988
Synodus sp. 3	R	350–352	Sand	WO			
Family Myctophidae							
Benthosema fibulatum (Gilbert & Cramer)	O	330–375	Over sand	WH, LL	75–856	Indo-Pacific	Gilbert and Cramer 1892, Struhsaker 1973, Novikov et al. 1980, Reid et al. 1991
Diaphus chrysorhynchus Gilbert & Cramer	O	340–390	Over sand	WH, LL	75–960	Pacific	Gilbert and Cramer 1892, Struhsaker 1973, Novikov et al. 1980, Reid et al. 1991
Family Bathygadidae							
Gadomus melanopterus Gilbert	R	840–1,350	Sand, talus	CS	799–1,416	Pacific	Gilbert 1905, Howes & Crimmen 1990, Sazonov and Iwamoto 1992
Family Macrouridae							
Caelorinchus spilonotus Sazonov & Iwamoto	R	349–480	Sand	CS, WH, WM	360–600	Pacific	Sazonov and Iwamoto 1992
Caelorinchus sp. 1	R	680–755	Fine sand	LH			
Caelorinchus sp. 2	R	500	Sand, talus	LL			
Coryphaenoides longicirrhus (Gilbert)	R	1,450–1,985	Talus	LV, LL	1,650–2,365	Central Pacific	Tinker 1978, Wilson et al. 1985
Hymenocephalus sp. 1	R	700–840	Fine sand	LH			
Nezumia propinqua (Gilbert & Cramer)	R	350–385	Fine sand	WH	219–870	Indo-Pacific	Okamura et al. 1982, Sazonov and Iwamoto 1992
Ventrifossa sp. 1	R	1,640–1,700	Fine sand	LH			
Family Moridae							
Antimora microlepis Bean	R	1,880–1,885	Hard	LV	1,602–2,403	Pacific	Gilbert 1905, Small 1981
Gadella molokaiensis Paulin	R	339–352	Hard, holes	WH	181–400	Hawaiian Is.	Struhsaker 1973, Paulin 1989
Laemonema rhodochir Gilbert	O	313–404	Hard, holes	LH, LO, WO	280–600	Pacific	Parin 1984, 1991
Physiculus grinnelli Jordan & Jordan	R	150–242	Hard, holes	LH, WH, PB	120–320	Johnston Atoll, Hawaiian Arch.	Struhsaker 1973, Humphreys et al. 1984, Randall et al. 1985, Paulin 1989

Family Ophidiidae							
Brotula multibarbata Temminck & Schlegel	R	95–199	Hard, holes	HA	2–220	Pacific	Gosline 1953, Myers 1989
Pycnocraspedum armatum Gosline	R	750–1,345	Sand	CS, LH	201–335	Hawaiian Is.	Struhsaker 1973
Family Carapidae							
Pyramodon ventralis Smith & Radcliffe	R	367	Hard	LO	100–450	Indo-Pacific	Masuda et al. 1984
Family Lophiidae							
Lophiodes miacanthus (Gilbert)	O	294–700	Various	WH, LO, WO	417–571	Central Pacific	Struhsaker 1973, Novikov et al. 1980, Caruso 1981
Sladenia remiger Smith & Radcliffe	O	780–1,540	Hard	CS, LH, LV	1,200–1,294	Indo-Pacific	Caruso and Bullis 1976, Caruso 1985
Family Chaunacidae							
Chaunax fimbriatus Hilgendorf	R	1,247–1,985	Hard	LV, CS	1300	Pacific	Humphreys et al. 1984, Masuda et al. 1984, Caruso 1989
Chaunax umbrinus Gilbert	O	333–385	Hard	HA	183–400	Hawaiian Is.	Clarke 1972, Struhsaker 1973, Novikov et al. 1980
Family Ogcocephalidae							
Malthopsis jordani Gilbert	R	234–520	Sand	WO, LH	210–430	Central Pacific	Struhsaker 1973, Okamura and Kitajima 1984
Family Ateleopodidae							
Ijimaia plicatellus (Gilbert)	O	336–367	Fine sand	WH, WO, LO	265–500	Hawaiian Is.	Struhsaker 1973, Grigg et al. 1987
Family Trachichthyidae							
Paratrachichthys prosthemius Jordan & Fowler	O	193–195	Hard holes	PB	90–110	Pacific	Struhsaker 1973, Gon 1983, 1987
Paratrachichthys sp.	O	242	Hard holes	NWHI			
Family Berycidae							
Beryx decadactylus Cuvier	O	346–805	Hard	CS, WH, LO, WO	200–760	Circumglobal	Busakhin 1982, Shcherbachev et al. 1985, Borets 1986, Grigg et al. 1987
Family Holocentridae							
Myripristis berndti Jordan & Evermann	O	46–159	Hard, holes	LH, WH, LO, WO	15–50	Indo-Pacific	Strasburg et al. 1968, Greenfield 1974, Randall 1985, Myers 1989
Myripristis chryseres Jordan & Evermann	A	46–211	Hard, holes	HA, JA	12–240	Indo-Pacific	Randall et al. 1985, Ralston et al. 1986, Myers 1989, Randall et al. 1990, Severns & Fiene-Severns 1993
Neoniphon aurolineatus (Lienard)	C	49–188	Hard, holes	LH, WH, JA	30–160	Indo-Pacific	Randall et al. 1985, Ralston et al. 1986, Myers 1989, Randall et al. 1990
Pristilepis oligolepis (Whitley)	O	102–281	Hard, holes	HA	14–345	Pacific	Randall 1981*a*, Randall et al. 1982, Randall et al. 1985

TABLE 1 (continued)

TAXON	RANK[a]	DEPTH (m) OBSERVED	SUBSTRATE ON/ABOVE	LOCATION OBSERVED[b]	DEPTH (m) PUBLISHED	LOCATION PUBLISHED	SELECTED REFERENCES (DEPTH, LOCATION, AND/OR PHOTOGRAPH)
Family Holocentridae (continued)							
Sargocentron microstoma (Gunther)	R	165–183	Hard, holes	JA	1–183	Indo-Pacific	Myers 1989, Randall et al. 1990
Sargocentron spiniferum (Forskål)	R	89–122	Hard, holes	JA, LH	1–122	Indo-Pacific	Strasburg et al. 1968, Myers 1989, Randall et al. 1990
Sargocentron xantherythrum (Jordan & Evermann)	O	61–217	Hard, holes	LH, WH, JA, PB	1–101	Johnston Atoll, Hawaiian Is.	Struhsaker 1973, Randall 1985, Randall et al. 1985
Family Polymixiidae							
Polymixia berndti Gilbert	O	352–585	Sand	CS, LH, LL, WH, LO, WO	99–500	Indo-Pacific	Struhsaker 1973, Uchida and Tagami 1984, Kotlyar 1984, Smith and Heemstra 1986
Family Zeidae							
Stethopristes eos Gilbert	R	343–570	Fine sand	HI	380–622	Pacific	Struhsaker 1973, Humphreys et al. 1984, Parin 1991
Zenopsis nebulosus (Schlegel)	R	349–367	Hard	LO, WO	216–670	Pacific	Struhsaker 1973, Heemstra 1980, Okamura et al. 1982, Golovan and Pakhorukov 1987
Family Grammicolepididae							
Grammicolepis brachiusculus Poey	R	339	Hard, holes	WH	400–800	Circumglobal	Borets 1986, Smith & Heemstra 1986
Family Caproidae							
Antigonia spp. (*A. eos* Gilbert, *A. capros* Lowe)	C	199–367	Various	HA, JA, CS			Parin and Borodulina 1986
Cyttomimus stelgis (Gilbert)	R	336	Fine sand	WH	330–644	Pacific	Gilbert 1905, Parin 1991
Family Aulostomidae							
Aulostomus chinensis (Linnaeus)	O	61–122	Various	LH, JA, PB	1–124	Indo-Pacific	Strasburg et al. 1968, Struhsaker 1973, Myers 1989
Family Syngnathidae							
Dunckerocampus baldwini Herald & Randall	R	125–128	Talus	WH	6–48	Hawaiian Is.	Herald and Randall 1972
Family Macroramphosidae							
Macroramphosid	R	245–366	Hard, sand	WO			
Family Scorpaenidae							
Ectreposebastes imus Garman	R	570–775	Fine sand	LL	150–850	Circumglobal	Struhsaker 1973, Eschmeyer and Randall 1975
Neomerinthe rufescens (Gilbert)	O	153–385	Hard, sand	LH, WH, JA, LO	75–302	Hawaiian Is.	Struhsaker 1973, Eschmeyer and Randall 1975
Pontinus macrocephalus (Sauvage)	C	177–367	Hard	HA, JA	120–366	Johnston Atoll, Hawaiian Is.	Clarke 1972, Struhsaker 1973, Eschmeyer and Randall 1975, Randall et al. 1985

Pterois sphex Jordan & Evermann	R	83–95	Hard	PB	10–124	Hawaiian Is.	Struhsaker 1973, Randall 1985
Scorpaena (*S. colorata*, *S. pele*)	O	122–272	Hard	HA, JA	90–272	Hawaiian Is.	Eschmeyer and Randall 1975, Randall et al. 1985, Ralston et al. 1986
Scorpaenopsis altirostris Gilbert	R	159–190	Hard	LH	79–134	Hawaiian Is., Johnston Atoll	Eschmeyer and Randall 1975
Setarches guentheri Johnson	O	349–780	Hard	CS, HI	185–686	Circumglobal	Struhsaker 1973, Kanayama 1981, Ohta 1983, Parin 1991
Family Triglidae							
Satyrichthys engyceros (Gunther)	O	193–394	Hard, sand	HA, JA	183–503	Central Pacific	Struhsaker 1973, Masuda et al. 1984, Randall et al. 1985, Borets 1986
Satyrichthys hians (Gilbert & Cramer)	R	550	Sand	LO	275–610	Pacific	Tinker 1978, Masuda et al. 1984, Okamura 1985
Family Bembridae							
Bembradium roseum Gilbert	O	309–373	Sand	LH, WM, LO, WO	210–650	Indo-Pacific	Struhsaker 1973, Humphreys et al. 1984, Okamura 1985, Parin 1991
Family Acropomatidae							
Synagrops argyrea (Gilbert & Cramer)	O	346–630	Hard	LH, WH, LL	75–522	Hawaiian Is.	Fraser 1972, Struhsaker 1973
Family Serranidae							
Caprodon schlegeli (Gunther)	R	197–251	Hard, holes	LH, NWHI	260–302	Pacific	Struhsaker 1973, Masuda et al. 1984, Uchida and Tagami 1984, Okamura 1985
Epinephelus quernus Seale	C	89–315	Various	HA, JA	18–350	Johnston Atoll, Hawaiian Is.	Uchida and Tagami 1984, Randall et al. 1985, Ralston et al. 1986, Randall and Heemstra 1991
Holanthias elizabethae (Fowler)	C	107–291	Hard, holes	HI, JA	155–262	Johnston Atoll, Hawaiian Is.	Strasburg et al. 1968, Madden 1973, Randall et al. 1985
Holanthias fuscipinnis (Jenkins)	A	89–260	Hard, holes	HA, JA	55–213	Johnston Atoll, Hawaiian Is.	Strasburg et al. 1968, Randall et al. 1985, Pyle 1991, Severns and Fiene-Severns 1993
Liopropoma aurora (Jordan & Evermann)	R	162–183	Hard, holes	LH, LO, WO	49–183	Hawaiian Is.	Randall and Taylor 1988
Luzonichthys earlei Randall	O	76–205	Hard, holes	LH, WH, PB	40–200	Indo-Pacific	Randall 1981*b*, Randall et al. 1985, Randall and McCosker 1992
Plectranthias helenae Randall	R	122–263	Hard	HI, JA	199–220	Johnston Atoll, Hawaiian Is.	Randall 1980*b*, Randall et al. 1985
Plectranthias kelloggi (Jordan & Evermann)	O	245–370	Hard, holes	HA	221–310	Pacific	Clarke 1972, Struhsaker 1973, Uchida and Tagami 1984
Pseudanthias bicolor (Randall)	R	50–104	Hard, holes	HA	5–68	Pacific	Uchida and Tagami 1984, Myers 1989, Randall et al. 1990

TABLE 1 (continued)

TAXON	RANK[a]	DEPTH (m) OBSERVED	SUBSTRATE ON/ABOVE	LOCATION OBSERVED[b]	DEPTH (m) PUBLISHED	LOCATION PUBLISHED	SELECTED REFERENCES (DEPTH, LOCATION, AND/OR PHOTOGRAPH)
Family Serranidae (continued)							
Pseudanthias fucinus (Randall & Ralston)	C	122–266	Hard, holes	HA, JA	135–280	Johnston Atoll, Hawaiian Is.	Randall and Ralston 1984, Randall et al. 1985, Ralston et al. 1986
Pseudanthias thompsoni (Fowler)	C	49–188	Hard, holes	HA	5–150	Hawaiian Is.	Struhsaker 1973, Randall 1979, Myers 1989
Pseudanthias ventralis (Randall)	A	40–199	Hard, holes	HA	26–120	Pacific	Randall 1979, Hobson and Chave 1990
Family Symphysanodontidae							
Symphysanodon maunaloae Anderson	C	131–398	Various	HA, JA	230–366	Pacific	Struhsaker 1973, Masuda et al. 1984, Uchida and Tagami 1984, Parin 1991
Symphysanodon typus Bleeker	A	80–245	Hard	HA	119–236	Pacific	Anderson 1970
Family Callanthiidae							
Callanthias sp.	O	171–360	Hard, holes	HA, JA	240–330	Johnston Atoll	Ralston et al. 1986
Grammatonotus laysanus Gilbert	O	175–367	Hard, holes	JA	240–354	Pacific	Humphreys et al. 1984, Randall et al. 1985, Ralston et al. 1986, Parin 1991
Family Priacanthidae							
Cookeolus japonicus (Cuvier)	A	131–306	Hard, holes	HA	60–400	Circumglobal	Struhsaker 1973, Humphreys et al. 1984, Okamura 1985, Borets 1986, Starnes 1988
Priacanthus alalaua Jordan & Evermann	O	55–223	Hard, holes	JA, PB	8–250	Pacific	Starnes 1988
Priacanthus meeki Jenkins	C	61–272	Various	HA	3–238	Hawaiian Is.	Struhsaker 1973, Okamoto and Kanenaka 1984, Fielding and Robinson 1987, Starnes 1988
Family Apogonidae							
Apogon kallopterus Bleeker	O	49–158	Sand, hard	PB	1–45	Indo-Pacific	Chave 1978, Hobson 1984, Myers 1989, Randall et al. 1990
Apogon maculiferus Garrett	C	61–153	Sand, hard	LH, PB	3–128	Hawaiian Is.	Struhsaker 1973, Randall 1985
Family Epigonidae							
Epigonus atherinoides (Gilbert)	O	500–540	Sand, hard	LL, LH	500–704	Pacific	Struhsaker 1973, Mochizuki and Shirakihara 1983, Humphreys et al. 1984, Parin 1991
Epigonus fragilis (Jordan & Jordan)	O	312–367	Hard	JA	120–366	Hawaiian Is.	Mayer 1974
Epigonus glossodontus Gon	O	366–520	Hard	LH, WO, LL	366	Hawaiian Is.	Gon 1985

Family Malacanthidae							
Malacanthus brevirostris Guichenot	R	30–61	Sand, hard	PB	14–45	Indo-Pacific	Myers 1989
Family Emmelichthyidae							
Erythrocles scintillans (Jordan & Thompson)	O	221–606	Various	LH, WH, JA, LO, WO	120–320	Pacific	Clarke 1972, Heemstra and Randall 1977, Ralston et al. 1986
Family Bramidae							
Eumegistus illustris Jordan & Jordan	R	306–520	Sand	LH	270–620	Indo-Pacific	Mead 1972, Okamura et al. 1982, Masuda et al. 1984, Ralston et al. 1986
Family Lutjanidae							
Aphareus furca (Lacépède)	R	46–92	Midwater	HA, JA	1–122	Indo-Pacific	Randall et al. 1985, Ralston et al. 1986, Myers 1989
Aphareus rutilans Cuvier	O	61–199	Midwater	HI, JA	100–250	Indo-Pacific	Allen 1985, Randall et al. 1985, Ralston et al. 1986, Smith and Heemstra 1986
Aprion virescens Valenciennes	O	58–120	Various	LH, PB	46–100	Indo-Pacific	Strasburg et al. 1968, Okamoto and Kanenaka 1984, Randall et al. 1990
Etelis carbunculus Cuvier	O	89–398	Various	WH, PB, JA, LO, WO	90–366	Indo-Pacific	Struhsaker 1973, Uchida and Tagami 1984, Okamura 1985, Randall et al. 1985
Etelis coruscans Valenciennes	O	168–396	Midwater	HA, JA	100–357	Indo-Pacific	Anderson 1981, Masuda et al. 1984, Allen 1985, Smith and Heemstra 1986
Lutjanus fulvus (Schneider)	R	46–128	Various	LH, WH	2–75	Indo-Pacific	Allen and Talbot 1985, Myers 1989, Randall et al. 1990
Lutjanus kasmira (Forsskål)	A	28–174	Various	HI	2–265	Indo-Pacific	Allen and Talbot 1985, Randall 1985, Myers 1989, Randall et al. 1990
Pristipomoides auricilla (Jordan, Evermann & Tanaka)	R	160–352	Various	JA, PB	90–360	Indo-Pacific	Randall 1980*a*, Allen 1985, Randall et al. 1985
Pristipomoides filamentosus (Valenciennes)	C	52–343	Various	HA, JA	90–328	Indo-Pacific	Uchida and Tagami 1984, Allen 1985, Randall et al. 1985
Pristipomoides zonatus (Valenciennes)	O	171–352	Various	WH, JA, PB	70–293	Indo-Pacific	Uchida and Tagami 1984, Allen 1985, Randall et al. 1985
Randallichthys filamentosus (Fourmanoir)	R	193–380	Hard	LH, WH	152–293	Pacific	Randall 1981*a*, Masuda et al. 1984
Family Mullidae							
Mulloides vanicolensis (Valenciennes)	O	38–116	Sand	JA, LO, WO	15–113	Indo-Pacific	Randall 1985, Myers 1989, Randall et al. 1990
Parupeneus bifasciatus (Lacépède)	R	68–83	Sand, hard	LH, WH, PB	1–80	Indo-Pacific	Randall 1985, Myers 1989

TABLE 1 (continued)

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Family Mullidae (continued)							
Parupeneus chrysonemus (Jordan & Evermann)	O	46–183	Sand	LH, WH, PB, JA	20–124	Hawaiian Is.	Struhsaker 1973, Tinker 1978
Parupeneus cyclostomus (Lacépède)	R	49–113	Sand	WH, LH, JA, WO, LO, PB	5–125	Indo-Pacific	Randall 1985, Ralston et al. 1986, Myers 1989, Randall et al. 1990
Parupeneus multifasciatus (Quoy & Gaimard)	C	15–161	Various	HI, JA	3–140	Pacific	Strasburg et al. 1968, Struhsaker 1973, Randall et al. 1990
Parupeneus pleurostigma (Bennett)	O	61–120	Various	LH, PB	1–75	Indo-Pacific	Strasburg et al. 1968, Struhsaker 1973, Randall et al. 1990, Severns and Fiene-Severns 1993
Parupeneus porphyreus (Jenkins)	O	40–122	Various	WH, PB, LO	2–140	Hawaiian Is.	Struhsaker 1973, Okamoto and Kanenaka 1984, Randall 1985
Family Chaetodontidae							
Chaetodon auriga Forsskål	R	37–61	Coral heads	JA	3–30	Indo-Pacific	Myers 1989, Randall et al. 1990
Chaetodon fremblii Bennett	R	61–128	Various	LH, WH, PB	4–110	Hawaiian Is.	Struhsaker 1973, Randall 1985
Chaetodon kleinii Bloch	R	41–122	Various	PB	10–61	Indo-Pacific	Strasburg et al. 1968, Myers 1989, Randall et al. 1990
Chaetodon lunula (Lacépède)	R	31–70	Various	LH	1–158	Indo-Pacific	Strasburg et al. 1968, Myers 1989, Randall et al. 1990
Chaetodon miliaris Quoy & Gaimard	A	46–128	Various	LH, WH, JA, PB, LO	1–183	Johnston Atoll, Hawaiian Is.	Strasburg et al. 1968, Okamoto and Kanenaka 1984, Randall et al. 1985
Chaetodon modestus Schlegel	A	89–291	Various	HI, JA	10–255	Indo-Pacific	Allen 1979, Okamura 1985, Randall et al. 1985
Chaetodon multicinctus Garrett	R	43–114	Various	LH, LO, WO	5–62	Johnston Atoll, Hawaiian Is.	Allen 1979, Hobson 1984, Randall 1985, Randall et al. 1985
Chaetodon quadrimaculatus Gray	R	40–43	Various	JA	2–15	Central Pacific	Randall 1985, Randall et al. 1985
Chaetodon tinkeri Schultz	O	76–183	Various	HI, JA	40–160	Central Pacific	Randall 1985, Myers 1989
Forcipiger flavissimus Jordan & McGregor	C	15–128	Various	HI, JA	2–145	Indo-Pacific	Ralston et al. 1986, Myers 1989, Randall et al. 1990
Forcipiger longirostris (Broussonet)	O	43–208	Various	HI	5–60	Indo-Pacific	Strasburg et al. 1968, Myers 1989, Randall et al. 1990
Hemitaurichthys polylepis (Bleeker)	R	40–46	Various	WH	3–40	Pacific	Myers 1989, Randall et al. 1990

Hemitaurichthys thompsoni Fowler	O	46–70	Various	JA	10–114	Central Pacific	Randall et al. 1985, Myers 1989
Heniochus diphreutes Jordan	A	46–177	Various	HI, JA	3–215	Indo-Pacific	Randall 1985, Ralston et al. 1986, Randall et al. 1990
Prognathodes guezei (Mauge & Bauchot)	O	107–214	Hard, sand	HA	60–200	Pacific	Allen 1979
Family Pomacanthidae							
Centropyge potteri Jordan & Metz	O	43–138	Various	LH, WH, PB	10–55	Johnston Atoll, Hawaiian Arch.	Strasburg et al. 1968, Randall 1985, Randall et al. 1985
Genicanthus personatus Randall	O	46–174	Various	LH, WH, PB	24–85	Hawaiian Is.	Randall and Struhsaker 1976, Severns and Fiene-Severns 1993
Holacanthus arcuatus Gray	C	43–208	Various	LH, WH, JA, PB, LO, WO	12–183	Johnston Atoll, Hawaiian Is.	Okamoto and Kanenaka 1984, Randall 1985, Randall et al. 1985
Family Pentacerotidae							
Evistias acutirostris (Schlegel)	O	89–193	Hard, sand	HA	84–183	Pacific	Hardy 1983, Masuda et al. 1984, Okamoto and Kanenaka 1984, Severns and Fiene-Severns 1993
Family Owstoniidae							
Owstonia sp.	O	349–420	Hard, holes	CS, LH, WH			Grigg et al. 1987
Family Carangidae							
Carangoides orthogrammus (Jordan & Gilbert)	R	83–190	Midwater	JA, HA	3–168	Indo-Pacific	Randall et al. 1985, 1990, Myers 1989
Caranx ignobilis (Forsskål)	R	80–188	Various	LH, WH, PB	1–80	Indo-Pacific	Myers 1989, Hobson and Chave 1990, Randall et al. 1990
Caranx lugubris Poey	C	61–291	Hard	JA	12–354	Circumglobal	Randall et al. 1985, 1990, Myers 1989
Caranx melampygus Cuvier	O	31–150	Sand	HA	1–230	Indo-Pacific	Ralston et al. 1986, Myers 1989, Randall et al. 1990
Decapterus macarellus (Cuvier)	R	61–107	Midwater	PB	1–200	Circumglobal	Myers 1989, Randall et al. 1990
Decapterus tabl Berry	O	361–416	Midwater, sand	WO	125–530	Circumglobal	Okamura and Kitajima 1984, Uchida and Tagami 1984, Randall et al. 1990
Elagatis bipinnulata Bennett	R	122–144	Midwater	WH, JA	1–150	Circumglobal	Masuda et al. 1984, Myers 1989, Randall et al. 1990
Pseudocaranx dentex (Bloch & Schneider)	O	104–150	Various	NWHI	80–200	Circumglobal	Randall 1981*a*, Uchida and Tagami 1984, Randall et al. 1990
Seriola dumerili (Risso)	A	50–385	Various	HA, JA	8–335	Circumglobal	Ohta 1983, Randall et al. 1985, 1990, Ralston et al. 1986, Myers 1989
Family Cirrhitidae							
Cirrhitops fasciatus (Bennett)	R	49–52	Hard	PB	Shallow	Indo-Pacific	Randall 1963, Hobson and Chave 1990

TABLE 1 (continued)

TAXON	RANK[a]	DEPTH (m) OBSERVED	SUBSTRATE ON/ABOVE	LOCATION OBSERVED[b]	DEPTH (m) PUBLISHED	LOCATION PUBLISHED	SELECTED REFERENCES (DEPTH, LOCATION, AND/OR PHOTOGRAPH)
Family Cirrhitidae (continued)							
Paracirrhites arcatus (Cuvier)	R	55–57	Coral heads	PB	1–91	Indo-Pacific	Strasburg et al. 1968, Myers 1989, Randall et al. 1990
Family Pomacentridae							
Chromis leucura Gilbert	O	46–122	Various	LH, PB, WO	29–118	Central Pacific	Randall and Swerdloff 1973, Masuda et al. 1984, Randall et al. 1985
Chromis ovalis (Steindachner)	C	46–161	Various	WH, LH, PB	7–45	Hawaiian Is.	Randall and Swerdloff 1973, Struhsaker 1973, Hobson 1984
Chromis struhsakeri Randall & Swerdloff	C	131–250	Various	LH, WO, PB	99–302	Hawaiian Is.	Struhsaker 1973, Uchida and Tagami 1984
Chromis verater Jordan & Metz	A	37–199	Various	HI, JA	10–140	Central Pacific	Randall and Swerdloff 1973, Struhsaker 1973, Randall et al. 1985, Ralston et al. 1986
Dascyllus albisella Gill	C	28–84	Various	LH, JA, PB	1–45	Johnston Atoll, Hawaiian Is.	Randall and Swerdloff 1973, Randall 1985, Randall et al. 1985
Family Labridae							
Anampses chrysocephalus Randall	O	61–139	Various	PB	10–15	Hawaiian Is.	Okamoto and Kanenaka 1984, Severns and Fiene-Severns 1993
Bodianus bilunulatus (Lacépède)	O	52–177	Various	LH, WH, JA	8–200	Indo-Pacific	Okamura 1985, Randall 1985, Ralston et al. 1986
Bodianus cylindriatus (Tanaka)	R	156–183	Hard, holes	PB	240–510	Pacific	Okamura and Kitajima 1984, Randall and Chen 1985
Bodianus sanguineus (Jordan & Evermann)	R	104–168	Various	LH, PB, WO	32–68	Hawaiian Is.	Madden 1973, Gomon and Randall 1978
Bodianus vulpinus (Richardson)	R	185–190	Various	PB	6–183	Pacific	Gomon and Randall 1978, Randall 1981*a*, Humphreys et al. 1984
Coris ballieui Vaillant & Sauvage	R	83	Sand	PB	15–85	Hawaiian Is.	Randall 1985, Severns and Fiene-Severns 1993
Coris flavovittata (Bennett)	R	61–98	Various	PB, LO, WO	1–61	Hawaiian Is.	Strasburg et al. 1968, Randall 1985
Coris gaimard (Quoy & Gaimard)	R	61–78	Hard, holes	PB	1–46	Indo-Pacific	Smith and Heemstra 1986, Myers 1989, Randall et al. 1990
Cymolutes lecluse (Quoy & Gaimard)	R	55–119	Sand	LH, LO, WO	5–30	Hawaiian Is.	Strasburg et al. 1968; Suzumoto, pers. comm., 1991
Labroides phthirophagus Randall	R	46–122	Hard	JA, PB, LO, WO	2–91	Johnston Atoll, Hawaiian Is.	Strasburg et al. 1968, Randall 1985, Randall et al. 1985
Oxycheilinus bimaculatus (Valenciennes)	R	57–92	Talus	PB	2–110	Indo-Pacific	Myers 1989, Randall et al. 1990, Westneat 1993

Oxycheilinus unifasciatus (Streets)	R	61–76	Various	LH	10–160	Pacific	Myers 1989, Randall et al. 1990, Westneat 1993
Polylepion russelli (Gomon & Randall)	R	92–318	Various	LH, JA	240–280	Pacific	Gomon and Randall 1978, Randall et al. 1985
Pseudocheilinus evanidus Jordan & Evermann	R	52–92	Talus	LH, PB	6–42	Indo-Pacific	Masuda et al. 1984, Myers 1989
Pseudojuloides cerasinus (Snyder)	C	49–104	Talus	WH, PB	2–61	Indo-Pacific	Randall 1985, Myers 1989
Suezichthys notatus (Kamohara)	R	122–272	Various	HA	119–204	Pacific	Randall and Kotthaus 1977, Russell 1985
Family Percophidae							
Bembrops filifera Gilbert	R	300–365	Sand	LO, LL	226–440	Central Pacific	Struhsaker 1973, Humphreys et al. 1984, Okamura 1985
Chrionema chryseres Gilbert	O	303–455	Various	LH, WH, LL, LO, WO	234–500	Pacific	Struhsaker 1973, Iwamoto and Staiger 1976, Masuda et al. 1984
Chrionema squamiceps Gilbert	O	306–520	Sand	HA	174–600	Johnston Atoll, Hawaiian Is.	Struhsaker 1973, Iwamoto and Staiger 1976, Randall et al. 1985
Family Pinguipedidae							
Parapercis roseoviridis (Gilbert)	O	150–300	Sand	LH, JA, LO, WO	183–300	Central Pacific	Struhsaker 1973, Masuda et al. 1984, Randall et al. 1985
Parapercis schauinslandi (Steindachner)	C	49–141	Sand	LH, PB, LO, WO	15–170	Indo-Pacific	Struhsaker 1973, Masuda et al. 1984, Randall et al. 1990, Severns and Fiene-Severns 1993
Family Draconettidae							
Centrodraco rubellus Frick, Chave & Suzumoto	R	367	Sand	LO	280–363	Pacific	Fricke 1992
Draconetta xenica Jordan & Fowler	R	284–367	Sand	LO, WO	180–230	Indo-Pacific	Nakabo 1982, Parin 1982
Family Zanclidae							
Zanclus cornutus (Linnaeus)	O	31–147	Various	LH, WH, JA, PB, LO, WO	2–183	Indo-Pacific	Strasburg et al. 1968, Myers 1989, Randall et al. 1990
Family Acanthuridae							
Acanthurus dussumieri Valenciennes	O	31–118	Various	JA, LH, PB	9–131	Indo-Pacific	Randall 1985, Randall et al. 1985, Myers 1989
Acanthurus nigricans (Linnaeus)	R	92–101	Various	FFS, PB	4–67	Indo-Pacific	Randall 1985, Myers 1989
Acanthurus olivaceus Forster	R	44–83	Hard	LH, PB, LO, WO	9–62	Pacific	Struhsaker 1973, Myers 1989, Randall et al. 1990
Acanthurus thompsoni (Fowler)	R	46–119	Sand	JA	4–75	Indo-Pacific	Randall et al. 1985, Myers 1989
Acanthurus xanthopterus Valenciennes	O	31–120	Various	LH, WH, PB	5–90	Indo-Pacific	Myers 1989, Randall et al. 1990

TABLE 1 (continued)

TAXON	RANK[a]	DEPTH (m) OBSERVED	SUBSTRATE ON/ABOVE	LOCATION OBSERVED[b]	DEPTH (m) PUBLISHED	LOCATION PUBLISHED	SELECTED REFERENCES (DEPTH, LOCATION, AND/OR PHOTOGRAPH)
Family Acanthuridae (continued)							
Ctenochaetus strigosus (Bennett)	O	15–113	Various	LH, WH	1–46	Indo-Pacific	Strasburg et al. 1968, Myers 1989, Randall et al. 1990
Naso brevirostris (Valenciennes)	R	54–122	Various	JA, PB	4–46	Indo-Pacific	Strasburg et al. 1968, Myers 1989, Randall et al. 1990
Naso hexacanthus (Bleeker)	C	46–229	Various	HA	6–150	Indo-Pacific	Okamura 1985, Ralston et al. 1986, Myers 1989, Randall et al. 1990
Naso lituratus (Bloch & Schneider)	R	58–76	Various	PB, FFS, LH	4–90	Indo-Pacific	Randall 1985, Myers 1989
Naso maculatus Randall & Struhsaker	O	76–120	Various	PB	43–220	Pacific	Randall and Struhsaker 1981, Okamura 1985
Zebrasoma flavescens (Bennett)	O	15–81	Various	LH, WH, JA	1–50	Pacific	Masuda et al. 1984, Randall 1985, Randall et al. 1990
Family Gempylidae							
Rexea nakamuri Parin	R	378–420	Hard, sand	WO, LL	340–374	Pacific	Struhsaker 1973, Parin 1989
Family Pleuronectidae							
Poecilopsetta hawaiiensis Gilbert	R	245–367	Sand	WM, PB, LL, LO, WO	183–422	Hawaiian Is.	Struhsaker 1973
Family Bothidae							
Chascanopsetta prorigera Gilbert	R	343–367	Sand	LH, WH, LO, WO	260–450	Hawaiian Is.	Struhsaker 1973, Uchida and Tagami 1984
Parabothus coarctatus (Gilbert)	R	180–398	Sand	WH, LO, WO	180–400	Pacific	Uchida and Tagami 1984; Suzumoto, pers. comm., 1990
Taeniopsetta radula Gilbert	R	180–275	Sand	PB, LO, WO	65–116	Hawaiian Is.	Struhsaker 1973
Family Triacanthodidae							
Hollardia goslinei Tyler	O	275–515	Various	CS, LH, LL, WH, LO, WO	335–365	Johnston Atoll, Hawaiian Is.	Clarke 1972, Humphreys et al. 1984, Randall et al. 1985
Family Balistidae							
Aluterus scriptus (Osbeck)	R	55–120	Various	PB, LO, WO	2–116	Circumglobal	Strasburg et al. 1968, Fielding and Robinson 1987, Myers 1989
Balistes polylepis Steindachner	R	47–60	Hard, sand	PB	10–50	Pacific	Gosline and Brock 1960, Randall 1985
Canthidermis maculatus (Bloch)	O	3–20	Midwater	LO	3–40	Circumglobal	Myers 1989
Melichthys niger (Bloch)	R	40–52	Various	PB	4–75	Circumglobal	Randall and Klausewitz 1973, Randall 1985, Myers 1989

Melichthys vidua (Solander)	R	61–80	Sand, hard	PB	4–145	Indo-Pacific	Randall and Klausewitz 1973, Randall 1985, Myers 1989
Pervagor spilosoma (Lay & Bennett)	A	52–138	Sand, talus	LH, PB, LO, WO	6–150	Johnston Atoll, Hawaiian Is.	Hobson 1984, Randall et al. 1985, Hutchins 1986, Fielding and Robinson 1987
Sufflamen fraenatus (Latreille)	O	31–183	Hard, holes	LH, WH, JA, PB	18–170	Indo-Pacific	Randall 1985, Ralston et al. 1986, Myers 1989
Xanthichthys auromarginatus (Bennett)	O	31–161	Hard, holes	HI, JA	12–147	Indo-Pacific	Randall et al. 1978, Randall et al. 1985
Xanthichthys mento (Jordan & Gilbert)	R	61–131	Hard, holes	PB	6–40	Pacific	Randall et al. 1978, Masuda et al. 1984, Severns and Fiene-Severns 1993
Family Tetraodontidae							
Arothron hispidus (Linnaeus)	R	31–73	Sand	LO, WO	1–99	Indo-Pacific	Struhsaker 1973, Randall 1985, Randall et al. 1990
Arothron meleagris (Bloch & Schneider)	R	67–73	Sand	WH, LO	1–14	Indo-Pacific	Randall 1985, Myers 1989
Canthigaster coronata (Vaillant & Sauvage)	O	61–92	Various	PB, LO, WO	11–120	Indo-Pacific	Allen and Randall 1977, Myers 1989, Randall et al. 1990
Canthigaster epilampra (Jenkins)	R	85–119	Sand	PB	9–36	Indo-Pacific	Randall 1985, Myers 1989
Canthigaster inframacula Allen & Randall	R	165–168	Various	JA	124–274	Pacific	Allen and Randall 1977, Matsuura and Yoshino 1984, Randall et al. 1985
Canthigaster jactator (Jenkins)	R	61–89	Various	PB	1–20	Central Pacific	Randall 1985
Canthigaster rivulata (Schlegel)	R	135–278	Various	PB, LO, WO	95–230	Indo-Pacific	Madden 1973, Struhsaker 1973, Allen and Randall 1977, Okamura 1985
Sphoeroides pachygaster (Müller & Troschel)	R	248–367	Sand	WH	80–410	Circumglobal	Struhsaker 1973, Hardy 1981, Smith and Heemstra 1986
Family Diodontidae							
Chilomycterus reticulatus (Linnaeus)	R	61–141	Hard, holes	PB, LO, WO	1–123	Circumglobal	Struhsaker 1973, Masuda et al. 1984, Randall et al. 1990

[a] Number of photographed animals ranked *R*are, 1–9; *O*ccasional, 10–49; *C*ommon, 50 to 99; *A*bundant, greater than 100.

[b] HA, Hawaiian Archipelago; HI, high Hawaiian Islands; WH, windward Hawai'i; LH, leeward Hawai'i; WO, windward O'ahu; LO, leeward O'ahu; PB, Penguin Bank; WM, windward Maui; LL, leeward Lāna'i; LV, Lō'ihi Volcano; CS, Cross Seamount; JA, Johnston Atoll; NWHI, Northwestern Hawaiian Islands; FFS, French Frigate Shoals.

TABLE 2

BEHAVIOR AND TAXONOMIC COMMENTS FOR SELECTED HAWAIIAN FISH SPECIES

FAMILY SPECIES	OBSERVATIONS AND COMMENTS
Alopiidae	
Alopias vulpinus	Followed fishing lures from surface vessel, hit one with its tail, was hooked and collected.
Pseudotriakidae	
Pseudotriakis microdon	Repeatedly poked its nose into and ate heterocarpid prawns in the entrance of a trap. Reported as *P. acrages* by Tinker (1978).
Carcharhinidae	
Carcharhinus amblyrhynchos	Often approached submersible near the surface, circled and accompanied to a maximum depth of 275 m.
Squalidae	
Centrophorus cf. *granulosus**	New record (Compagno, pers. comm., 1991).
Etmopterus sp.	Possibly a new species (Compagno, pers. comm., 1984). Large white patches on body, a pattern not recorded for sharks collected from the Pacific.
Squalus mitsukurii	Usually seen lying on smooth, hard substrate. Swam close to the bottom for short distances. Reported in Hawai'i as *S. blainvillei* by Clarke (1972) and Struhsaker (1973).
Echinorhinidae	
Echinorhinus cookei	Distinctively marked individuals on top of Cross Seamount. Swam slowly around the submersible and moved into the light field when equipment was being deployed or retrieved.
Hexatrygonidae	
Hexatrygon longirostra	Cited as "Family nov." by Struhsaker (1973).
Plesiobatidae	
Plesiobatis daviesi	Dug large pits in the sand and ate unidentified objects in the pits.
Halosauridae	
Aldrovandia phalacra	Often circled the submersible. Usually found in troughs of rippled sediment when currents exceeded 1.5 km/hr. Reported as *A. kauaiensis* by Struhsaker (1973).
Notocanthidae	
Notocanthus sp.*	New record.
Opichthidae	
Ophichthus kunaloa	Backed tail first into crevices in hard substrate. Heads often remained out of cracks but were pulled in when approached.
Congridae	
Ariosoma marginatum	Usually the first animals to arrive when bait was placed on the bottom. Reported in Hawai'i as *A. bowersi* (Struhsaker 1973).
Synaphobranchidae	
ilyophine eel	Had the same depth range as and was usually near or among the branches of colonial zoanthids (*Gerardia* sp.). In currents stronger than 3 km/hr, individuals hugged the lee side of *Gerardia* colonies.
Synaphobranchus brevidorsalis	Seen in the active vent fields of Lō'ihi Volcano.
Nettastomatidae	
Nettastoma parviceps	Swam slightly above or lay on the bottom. Moved into crevices as the submersible approached. Reported in Hawai'i as *Metopomycter denticulatus* (Tinker 1978).
Chlorophthalmidae	
Chlorophthalmus proridens	Eyes reflect red in videolights. Rested on the sediment during the day, sometimes darted upward and snapped at floating objects. Collected in midwater at night (Reid, pers. comm., 1992).
Ipnopidae	
*Bathypterois grallator**	New record (Jones & Sulak 1990). Elongate pelvic and caudal fin rays held body above the sediment. These rays appeared flexible when the fishes swam and stiff when they were perched on the bottom.

Table 2 (continued)

FAMILY / SPECIES	OBSERVATIONS AND COMMENTS
Myctophidae	
Benthosema fibulatum	At night both species occur in midwater from 75 to 190 m depth (Reid, pers. comm., 1993). During the day small groups swam about 1 m over the bottom at depths between 500 and 600 m. Individuals became disoriented in the light field and if headed downward, glanced off the sand and then swam upward, often shedding scales.
Diaphus chrysorhynchus	
Bathygadidae	
Gadomus melanopterus	Swam very slowly. When the long, filamentous fin rays contacted objects, the fish turned toward them and snapped.
Macrouridae	
*Caelorinchus spilonotus**	New record (Iwamoto, pers. comm., 1992).
Caelorinchus sp. 2**	Probably a new species (Iwamoto, pers. comm., 1992).
Nezumia propinqua	Swam a few centimeters above the bottom. Moved backward as well as forward by reversing the undulating motion of its tail.
Moridae	
Gadella molokaiensis	Individuals occupied one or more holes on limestone mounds. Reported in Hawai'i as *Bromisculus* sp. by Struhsaker (1973).
Lophiidae	
Lophiodes miacanthus	Two individuals moved their lures, caught and ate fishes in the light field. They raised their bodies off the bottom by stiffening the pectoral fins.
*Sladenia remiger**	New record (Chave and Jones 1991). Perched on the tops of boulders and did not move until prodded. Swam for short distances. Did not move along the bottom.
Chaunacidae	
*Chaunax fimbriatus**	New record. Caught on seamounts north of Hawaiian Archipelago (Humphreys et al. 1984).
Chaunax umbrinus	Usually perched motionless on hard substrate, sometimes used its lure. Crawled over the bottom on its pelvic and pectoral fins or swam for a short distance when prodded.
Ogcocephalidae	
Malthopsis jordani	Hopped along on its large pectoral and tiny pelvic fins or swam like a frog using its pectoral fins.
Ateleopodidae	
Ijimaia plicatellus	Swam by undulating its tail with dorsal fin raised and pectorals at right angles to the body. Became motionless when the video lights were turned on.
Trachichthyidae	
*Paratrachichthys prosthemius**	New record (Gon 1987). Aggregated under ledges and moved out over sand patches when all lights were turned off.
Berycidae	
Beryx decadactylus	Small or large aggregations hovered off steep cliffs or in areas of irregular, hard terrain near cliffs. Rarely observed in the high Hawaiian Islands, common on Cross Seamount.
Polymixiidae	
Polymixia berndti	Individuals or small aggregations swam rapidly across sand, probing with flexible white barbels. Snapped at objects on the sediment and dug small holes. Often approached the manipulators when objects were being moved or collected.
Zeidae	
Stethopristes eos	Hovered about 1 m above sand. Swam rapidly away when the videolights were turned on. If headed downward, individuals swam to the bottom and repeatedly bumped into it, finally ricocheting off into the water column again.
Zenopsis nebulosus	Swam around the submersible. Raised its dorsal fin and backed away when the video lights were turned on.
Grammicolepididae	
Grammicolepis brachiusculus	Hovered near large zoanthids and backed into them when the video lights were turned on.

Table 2 (continued)

FAMILY SPECIES	OBSERVATIONS AND COMMENTS
Caproidae	
Antigonia spp.	*Antigonia eos* and *Antigonia capros* cannot be differentiated by photographic means. Individuals or small aggregations of both species hovered over hard, irregular terrain. They nudged (cleaned?) larger fishes that approached and hovered in the vicinity.
Macroramphosidae*	New record, not *Macroramphosus scolopax* (Linnaeus), a silvery species caught in Hawai'i (Struhsaker 1973). Deep-bodied and pink, they resembled *Notopogon*, from the South Pacific (see Smith and Heemstra 1986). Individuals hovered near gorgonians.
Scorpaenidae	
Ectreposebastes imus	Lay in small depressions on fine sediment during the day. Caught in midwater trawls at night (Reid, pers. comm., 1992).
Pontinus macrocephalus	Perched on the bottom, occasionally swam short distances. Recognized by long orbital cirri.
Setarches guentheri	Juveniles were brown with yellow caudal fin tips. Adults were red.
Triglidae	
Satyrichthys engyceros	Swam for short distances but most often crawled along bottom on two thickened pectoral fin rays. Seen near traps eating heterocarpid prawns. These fish located prey with their rakelike barbels. The long rostral knobs were used to dig for prey in the sand.
Satyrichthys hians	Had short rostral knobs. Locomotion was the same as that of *S. engyceros.*
Bembridae	
Bembradium roseum	Darted after a small prawn and snapped it up. Became motionless in the video lights.
Acropomatidae	
Synagrops argyrea	Lay motionless on hard substrate during the day. Caught in the water column at night (Reid, pers. comm., 1992).
Serranidae	
Caprodon schlegeli	Swam into caves or across flat areas away from the light field. Solitary.
Epinephelus quernus	Solitary, distinctively marked groupers inhabited territories and chased other large predators away. Young were in shallower water than adults. Adults looked into submersible portholes, swam into collecting baskets, bumped into the manipulators, and ate most of the small animals being collected by the manipulators.
Holanthias elizabethae	Fed in midwater near holes or crevices. Occurred in pairs; sexes similar except that the first rays of the male's pelvic and outer rays of the caudal fins are long and violet in color.
Holanthias fuscipinnis	Fed in midwater near holes or crevices. Seen in small groups of males, females, and juveniles.
Luzonichthys earlei	Formed large feeding aggregations near vertical cliffs. When disturbed, small groups moved into crevices, often sharing crevices with *Gymnothorax nudivomer*.
Plectranthias helenae	Pairs darted about or perched on the bottom.
Plectranthias kelloggi	Individuals darted about picking at objects on rocks or in the sand. They hid in crevices when video lights were turned on.
*Pseudanthias fucinus***	New species (Randall and Ralston 1984). Males had harems of two or three females. Several groups formed feeding aggregations slightly above and within darting distance of the bottom. Both sexes were purple and yellow, females more yellow than males.
Symphysanodontidae	
Symphysanodon maunaloae	Aggregated near the bottom. Darted downward into holes when approached, and two dark bands appeared behind the head.
Symphysanodon typus	Aggregated in midwater near holes in cliffs. Darted into overhangs, holes, or caves when approached.
Callanthiidae	
Callanthias sp.**	Probably a new species. Both sexes yellow and purple in color, small, and had rounded tails. They hovered near holes or among talus near cliffs.
Grammatonotus laysanus	Small groups, usually a male (with a falcate tail) and two or three orange females, swam near small holes in steep slopes.

Table 2 (continued)

FAMILY SPECIES	OBSERVATIONS AND COMMENTS
Priacanthidae	
Cookeolus japonicus	Adults red with dark fins. Color lightened or darkened within seconds. Young mottled silvery red and occurred deeper (262–306 m) than adults (131 to 245 m). Recorded in the Hawaiian Archipelago as *C. boops* (Struhsaker 1973 and Humphreys et al. 1984).
Priacanthus meeki	Juveniles in deeper water (150 to 272 m) than adults (61 to 85 m).
Epigonidae	
Epigonus atherinoides	Aggregations hovered over sand patches near steep, irregular cliffs.
Epigonus fragilis	*E. fragilis* and *E. glossodontus* could not be distinguished from each other in most photographs or videotapes. Small groups of animals were found near steep cliffs. They backed into holes or became quiescent when video lights were turned on. *E. glossodontus* is a new species (Gon 1985).
*Epigonus glossodontus***	
Emmelichthyidae	
Erythrocles scintillans	Individuals swam about 3 m above the bottom. Sometimes found with *Etelis carbunculus*. Reported from Hawai'i as *E. schlegelii* (Clarke 1972).
Bramidae	
Eumegistus illustris	Appeared silvery underwater. Small groups swam around the submersible and veered away when video lights were turned on.
Lutjanidae	
Aphareus rutilans	Individuals or small groups swam around the submersibles in midwater. Often chased schools of small fish.
Etelis carbunculus	Usually solitary. Sometimes hovered above, but usually rested on bottom near small caves or ledges.
Etelis coruscans	Swam from 2 to 10 m above the bottom or next to cliffs.
Pristipomoides filamentosus	Small groups seen 3 to 6 m above the bottom, especially near cliffs. Sometimes swam with schools of deep-water carangids or acanthurids.
Pristipomoides zonatus	Individuals or pairs usually found near cliffs. Sometimes swam rapidly across sand patches from one hard substrate to another.
Randallichthys filamentosus	Large and red. Usually swam 2 m above the bottom. Rarely caught and only if squid used for bait (Randall, pers. comm., 1992).
Chaetodontidae	
Chaetodon modestus	Occurred in pairs or small groups. Often found near large fish such as *Cookeolus japonicus.* Did not pick at the substrate.
*Prognathodes guezei**	New record (Pyle & Chave 1994). Individuals or pairs found in talus or near crevices. Sometimes accompanied *Chaetodon modestus.* Picked at the substrate.
Owstoniidae	
Owstonia sp.**	New species (Smith-Vaniz, pers. comm., 1994). Moved in and out of holes or among talus. Males pink with long, pointed tails and white pelvic fins, females pink with rounded fins.
Carangidae	
Decapterus tabl	Several schools attracted to video lights; some individuals rammed the submersible.
Seriola dumerili	Often circled the submersibles in midwater. Swam near the bottom in the light path feeding on organisms stirred up or being collected. Chased schools of fish in midwater. Occasionally rammed the submersibles and on two occasions broke video lights. Had an oblique dark band between the eye and nape when feeding.
Pomacentridae	
Chromis struhsakeri	Aggregated in midwater near cliffs or ledges containing holes and crevices. Ducked into holes when approached.
Labridae	
*Bodianus cylindriatus**	New Hawaiian record (Randall, pers. comm., 1990).
Bodianus vulpinus	Hawaiian form may be a new species (Randall, pers. comm., 1991).
Suezichthys notatus	Picked at objects on rocks and sand. Moved along the borders of sand patches near irregular, hard surfaces.

Table 2 (continued)

FAMILY SPECIES	OBSERVATIONS AND COMMENTS
Percophidae	
Bembrops filifera	Tan with dark blotches. Moved slowly across sand by flicking its pectoral and pelvic fins.
Chrionema chryseres	Violet with gold spots on its head and body. Perched on or moved slowly across sand or hard, smooth surfaces. Occasionally darted upward in the water or across the substrate and snapped at objects.
Chrionema squamiceps	Brownish pink with dark bands. Perched on or moved about on sand. Either hopped using its pectoral and pelvic fins or darted using its caudal fin.
Pinguipedidae	
Parapercis roseoviridis	Perched near holes dug into sand patches covering limestone. Darted into these holes when approached.
Draconettidae	
*Centrodraco rubellus***	New species (Fricke 1992).
Draconetta xenica	Small with orange and white blotches. When disturbed, they swelled tissues and moved muscles so that the eyes protruded above the level of the head. Traveled over sand in short, darting movements.
Gempylidae	
Rexea nakamuri	Moved rapidly around the periphery of the light field.
Bothidae	
Chascanopsetta prorigera	Commonly collected in Hawaiian Island channels and on Northwestern Hawaiian Island seamounts (Struhsaker 1973, Uchida and Tagami 1984). Rarely seen from submersibles.
Taeniopsetta radula	Lay on sand. Swam above the sand when prodded. Round body shape is a distinguishing feature. Rarely seen from submersibles.
Triacanthodidae	
Hollardia goslinei	Perched on or hovered over hard substrates under or near gorgonian and antipatharian colonies. Able to change color from red to spotted red to pink in a few seconds.
Balistidae	
Pervagor spilosoma	Extremely abundant from 1983 until 1987 because large numbers of juveniles settled out of the plankton. Hundreds of animals aggregated around boulders or pieces of debris. From 1985 to 1989, large numbers of these fish died of unknown causes and washed ashore.
Tetraodontidae	
Sphoeroides pachygaster	Fed on prawns from traps (HURL records [unpubl. data]). Feeds on squid (Smith and Heemstra 1986). Reported in Hawai'i as *S. cutaneus* (Struhsaker 1973).

NOTE: Light field = submersible running lights, videolights = floodlights.
* New Hawaiian record based on submersible videotapes and photographs.
** Undescribed species based on specimens collected or videotaped in this study.

the Hawaiian macrourids are clearly associated with those on the seamounts of the eastern South Pacific Ocean (Sazonov and Iwamoto 1992: table 6). Eleven of the 29 Hawaiian macrourid species (38%) also occur at the Nazca and Sala-y-Gómez Ridges; five of the 11 (45%) are uniquely shared Nazca and Pacific Plate endemics. In contrast, only four species (14%) are found in the tropical West Pacific and these also occur in the eastern South Pacific. Two species in other families (*Stethopristes eos* Gilbert and *Grammatonotus laysanus* Gilbert) are known only from Hawai'i and the Nazca and Sala-y-Gómez Ridges (Parin 1990, 1991; this study). A spreading center rather than a subduction zone separates the Nazca and Pacific Plates and may explain the affinity of the faunas of the two plates (V. G. Springer, pers. comm., 1993). Spreading centers lack deep trenches and well-developed boundary currents generally present around subduction zones.

These currents and trenches may be dispersal barriers to larval fish.

The biogeographic affinities of deep-dwelling Hawaiian fish differ from those suggested for shallow-living species (Randall et al. 1985). If dispersal hypotheses for the origins of Hawaiian fish are valid, these differences may be caused in part by advection of larvae. Larvae of many deep-sea benthic fish, including macrourids, morids, and ophidiiforms, are surprisingly rare in and above the thermocline when compared with larvae of meso- or even bathy-pelagic species (Gordon et al. 1984, Merrett 1989, Boehlert and Mundy 1993). Larvae that occur below the thermocline may be carried in currents of different directions and strength than surface, wind-driven currents. Hydrographic processes that influence the dispersal of larvae of at least some deep-sea benthic species may therefore differ from those that influence larvae of shallow-dwelling species.

Depth Distribution

Depth distributions graphed only from the submersible observations (Figure 46*A*) were less extensive than those combined from this study and from the literature (Figure 46*B*). This is particularly evident at less than 40 m depth because the HURL submersibles rarely operated above this depth. For most shallow and intermediate-depth species in our study, the upper depth limits have been determined by scuba divers. Even so, submersible data recorded 108 species more than 20 m deeper than previously reported and 11 more than 20 m shallower than prior reports (Table 1).

In his trawl-sample analyses, Struhsaker (1973) suggested transitions in the Hawaiian Island deep-sea fish fauna. The species were assembled into faunal groups designated as "outer-shelf" (91–150 m), "upper-slope" (151–250 m), "middle-slope" (251–500 m), and "lower-slope" (501–700 m). Haedrich and Merrett (1990) believe that faunal zones and communities do not exist for deep-sea fish and that the zones reported in the literature are artifacts of sampling limitations. Merrett et al. (1991) suggested that surveys using single sampling devices can result in the identification of zonation when none exists. In our study, changes in faunal composition by depth are gradual (Figure 46*A*), supporting the idea that discrete ichthyofaunal zones do not exist. Figure 46*B*, which combines Struhsaker's data with other surveys, also supports this idea. One reason for Struhsaker's faunal groupings may be that trawls are limited to relatively smooth substrates and therefore he was unable to record the many species associated with irregular terrain observed in our study.

In the submersible survey, species richness was greatest at 100–200 m (107 species) and declined markedly below 400 m (Figure 47*A*). Deeper than 400 m, it was greatest at 700–800 m (12 species) and at 1200–1400 m (8 species). The exponential decline in species richness with depth is similar to that found in many regions (Pearcy et al. 1982, Haedrich and Merrett 1988). Change in species composition in relation to adjacent 100-m depth strata is greatest between 0 and 200 m (225 species or genera added or deleted). It then decreases with depth. There is less fluctuation in species richness with depth when submersible and previously reported depth records are combined, again supporting the idea that zones do not exist for this fauna (Figure 47*B*).

Although faunal groups or zones cannot be distinguished in the Hawaiian deep-sea benthic fish fauna, individual species have distinct depth distributions influenced by environmental characteristics. These characteristics can be separated into resources available to organisms and into physiological gradients. Resources include food availability, space, associated biota, and habitat characteristics such as slope, currents, substrate type, and rugosity (Carney et al. 1983).

Submersible observations confirm the suggestions of Struhsaker (1973) and Pearcy et al. (1989) that substrate type and rugosity are important determinants of deeper-dwelling fish distributions because almost all taxa observed were associated with a limited range of substrates (Table 1). In tropical and subtropical areas, coral reefs are among the most obvious substrates influencing fish distributions. Living coral reefs thrive down to about 50 m and are restricted to depths of about 100 m because of inadequate light (Maragos

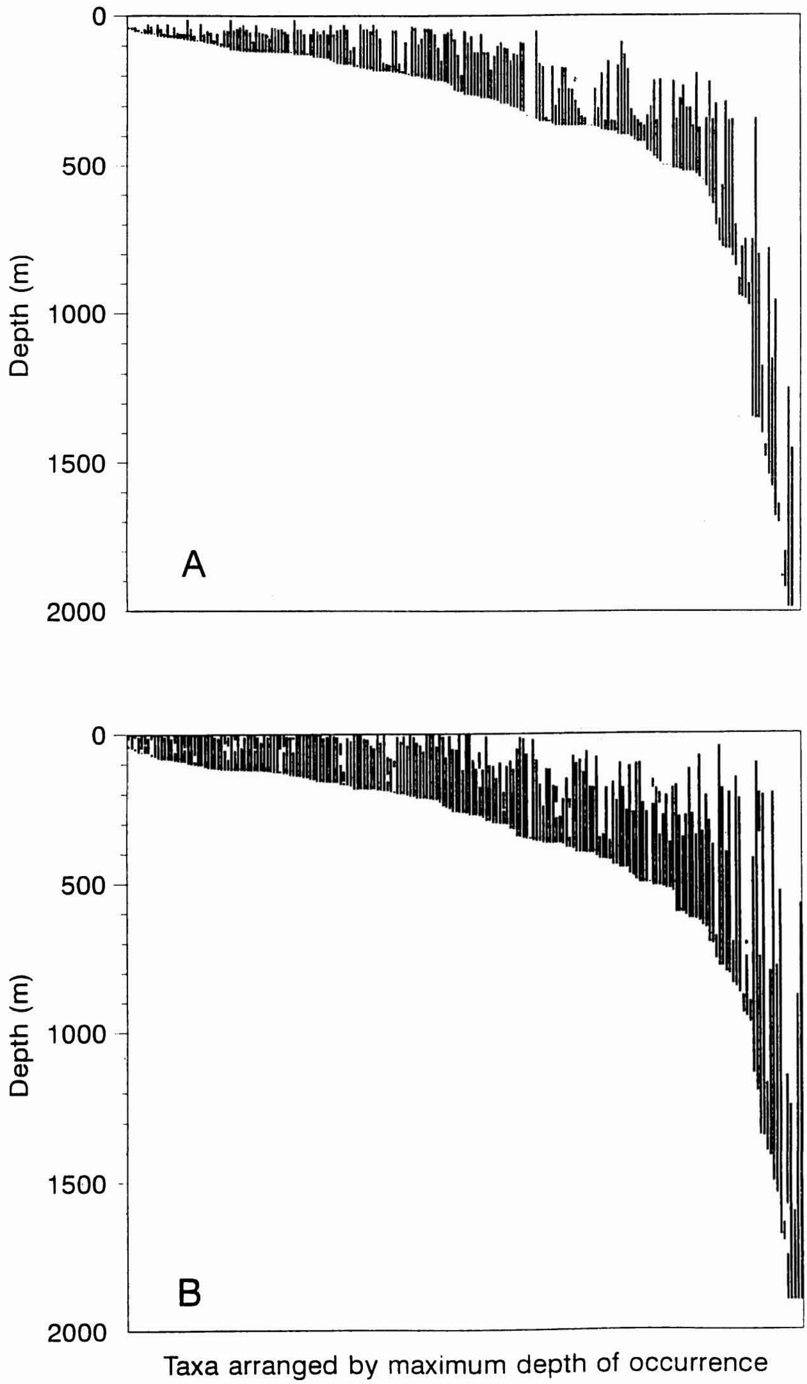

Figure 46. Depth ranges (m) of benthic fish species observed by HURL submersibles. Ranges are the maximum and minimum depths at which species were seen. The taxa are arranged by increasing maximum depth of occurrence and therefore not presented in the same order in 46*A* and 46*B*. (*A*) Data from submersible observations only. (*B*) Data from submersible observations combined with data from the publications listed in Table 1.

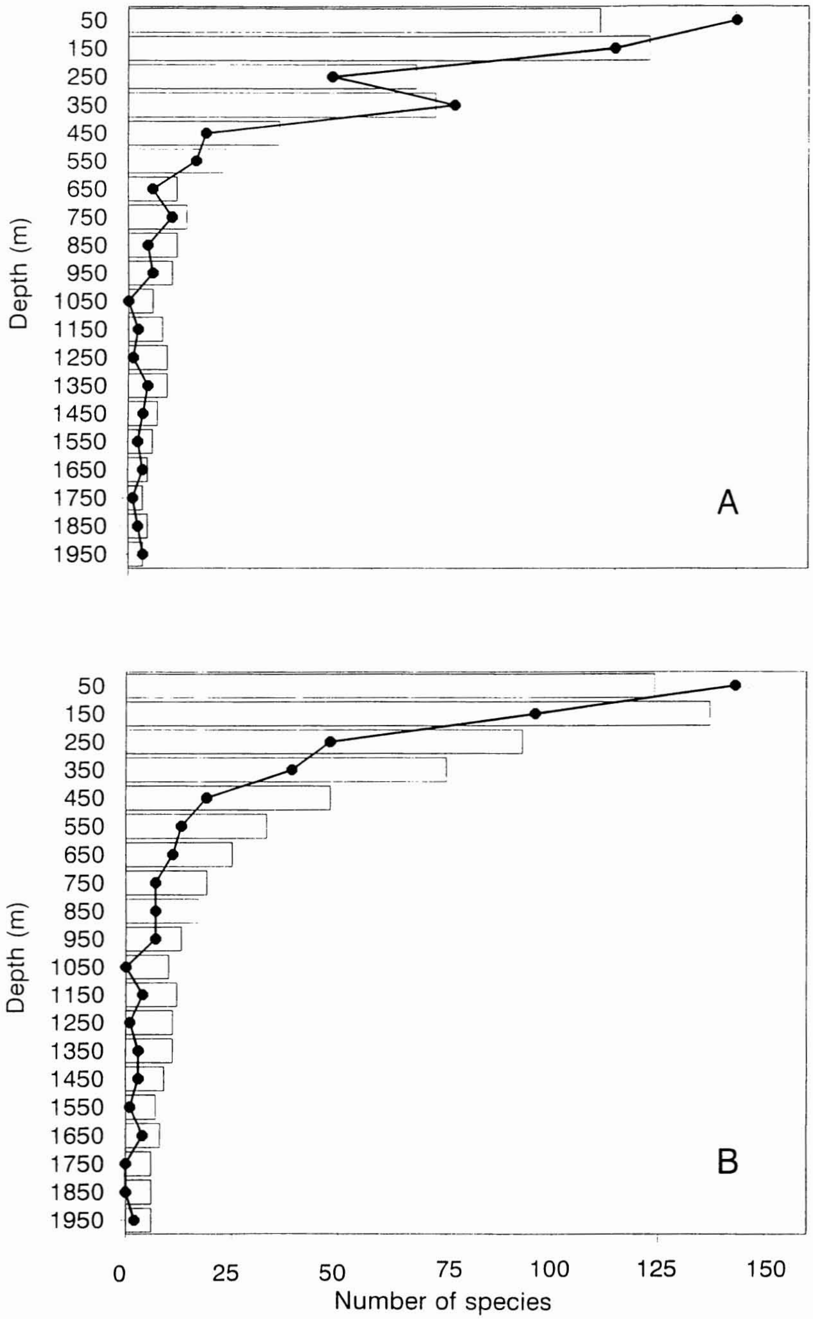

FIGURE 47. Number of species observed (bars) and change in species composition (line) for Hawaiian benthic fish within 100-m depth intervals. Change in species composition is the number of species with their minimum depth of occurrence within the interval, plus the number of species with their maximum depth of occurrence in the interval. The change in species composition may be greater than the number of species because some taxa have both their minimum and maximum depth of occurrence within one interval. (*A*) Data from submersible observations only. (*B*) Data from submersible observations combined with data from the publications listed in Table 1.

and Jokiel 1986). Fish dependent on coral or algae (such as *Zebrasoma flavescens* [Bennett] and *Paracirrhites arcatus* [Cuvier]) are also restricted to these shallow depths. In this and other studies many fish seen on living coral reefs were also seen at depths greater than 100 m (Strasburg et al. 1968, Colin 1974, 1976, Randall et al. 1985, Ralston et al. 1986). The rich fauna observed at 0–200 m was composed largely of reef species, and the steep decline in species richness at about 150 m is largely a result of the maximum depth for these species being reached.

Physiological gradients include salinity, pressure, temperature, oxygen, and light (Carney et al. 1983). In Hawai'i, at any depth less than 1000 m, at least one of these gradients may undergo substantial change (Chiswell et al. 1990; HURL data [unpubl.]). Changes in salinity probably have the least effect on fish. The changes in the other physiological gradients at depths to 1000 m may explain, in part, the lack of distinct zones for deep-sea benthic fish.

In their review of the physiology of deep-sea organisms, Somero et al. (1983) found that those enzyme systems that work efficiently from 500 to 1000 m have impaired function at or below those depths. Enzymes that function efficiently below 500 m do so to at least 4760 m and are impaired at depths of less than 500 m. Deeper-dwelling species tend to have broader depth ranges than shallow-water species (Ralston et al. 1986; Figure 46*A*,*B*). The pressure effects on enzymes might explain this trend.

Water temperature in the Hawaiian Archipelago and Johnston Atoll varies between 23 and 28°C at the surface and drops abruptly from 20–26°C to 9–12°C at the thermocline (located between 100 and 300 m). Temperature then decreases with depth to 2000 m, where it reaches 1 or 2°C (Struhsaker 1973, Chiswell et al. 1990; HURL data [unpubl.]). Temperature may often be a critical factor in fish distribution (Struhsaker 1973, Middleton and Musick 1986). For example, *Genicanthus personatus* Randall and *Epinephelus quernus* Séale occur in shallow water in the Northwestern Hawaiian Islands and are found deeper in the main Hawaiian Islands, where upper water temperatures are warmer (Hobson 1984, Okamoto and Kanenaka 1984). Struhsaker (1973) attributed his proposed faunal change at 250 m to the presence of the thermocline. In our study, many species have upper and lower depth limits between 100 and 400 m that may be associated with the thermocline boundaries (Figures 46, 47).

Oxygen concentrations in Hawaiian waters are high in the surface, mixed layer, and thermocline, with a sharp decline at 300–600 m. An oxygen minimum exists at about 600 m, with a very gradual increase in concentration below 800 m (Struhsaker 1973, Chiswell et al. 1990). The most complete replacement of deep-sea benthic fish species off Hawai'i occurs at about 600–800 m (Figure 46*A*), with only a few percomorph fish found below 600 m and a few eurybathic species found above that depth (Figure 46*B*). Oxygen concentration may be a factor in this transition as well as light and the pressure effects on enzymes.

Light decreases abruptly below the surface, and deeper than 500 m the submersible lights had to be turned on to see anything. Those animals that rely primarily on sight to obtain food are seen at depths above 500 m. Diverse fish (*Hollardia goslinei* Tyler, *Draconetta xenica* Jordan & Fowler, and *Chlorophthalmus proridens* Gilbert & Cramer, for example) rely on their large eyes for spotting prey and must remain in the twilight zone rather than venturing into darkness below 500 m. Fish such as *Bathypterois* spp., the lophiids, and *Gadomus melanopterus* Gilbert are seen below 500 m. These species have small eyes and well-developed fin-ray extensions that may attract or sense food organisms.

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