

## Fishes of the Remote Southwest Palau Islands: A Zoogeographic Perspective<sup>1</sup>

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**ABSTRACT:** Fishes of the Southwest Palau Islands (SWPI) recorded from the SWPI Expedition of 1992 were analyzed for patterns of distribution, species richness, diversity, evenness, and similarity between island localities. Fifty-three timed visual transects and supplemental observations were made at Helen Reef (Hotsarihie Atoll) and the islands of Tobi, Merir, Pulo Anna, Sonsorol, and Fanna. A total of 602 species was observed, including 596 species and morphs on transects. Fifty-four new records were identified, including nine species new to Micronesia. The species reported compose 64.1% of the known Palauan fish fauna. A latitudinal gradient in species richness, decreasing from north to south, is apparent. Species diversity is less pronounced latitudinally, is significantly different between island localities in most pairwise comparisons, and is seemingly dependent upon the degree of habitat complexity. This complexity may be a function of locality relative size. Patterns of similarity in faunal composition also appear to be related to relative size of locality. Helen Reef had the most distinct fauna, followed by Tobi. Merir and Sonsorol, and Pulo Anna and Fanna, respectively, were more similar to each other.

THE PALAU ISLANDS have a remarkably rich fish fauna, certainly with the highest level of diversity in all of Micronesia (Myers 1989). This is likely a result of the archipelago's position marginally at the Philippine and Pacific Plates, its relative proximity to the Indo-Malayan area, and the high degree of habitat complexity relative to most other Micronesian localities.

The Southwest Palau Islands (SWPI), a remote group of islands located ca. 270–600 km southwest of the main Palauan archipelago (MPA), ca. 240 km north of Kepulauan Asia atoll and east of the high volcanic island of Morotai in Indonesia, have a fish fauna that is largely unknown. The islands consist of one atoll, Helen Reef (Hotsarihie Atoll), and five raised coral islands: Tobi, Merir,

Pulo Anna, Sonsorol, and Fanna (Figure 1). All are situated atop ancient volcanic seamounts of the Palauan Ridge (Maragos 1993). Helen Reef has considerable marine habitat complexity compared with the other islands, which are characterized by fringing reefs with relatively narrow reef flats and steep drop-offs. The exception is Merir, which has greater reef flat development and a deep terrace on the northern reef (Maragos 1993). The proximity to Indonesia of these islands, particularly Tobi and Helen Reef, increases the likelihood that fish faunal affinities are convergent upon the "Indo-Malayan Center of Diversity" (Briggs 1974, but see Woodland 1983, Donaldson 1986), rather than the "Palau-Carolines Corridor" (Springer 1982) or "conduit" (Myers 1989). Seasonally influenced current patterns, however, dictate some Pacific Plate and Australo-Papuan influences in faunal composition, especially at Helen Reef and Tobi (Johannes 1981, Maragos 1993). The islands also experience diel and seasonal fluctuations in local current patterns, with formation of wake eddies or gyres (Johannes 1981, Maragos 1993) that may

<sup>1</sup>This is Contribution No. 91 of the Tatsuo Tanaka Memorial Biological Station and Contribution No. 362 of the University of Guam Marine Laboratory. Manuscript accepted 15 June 1995.

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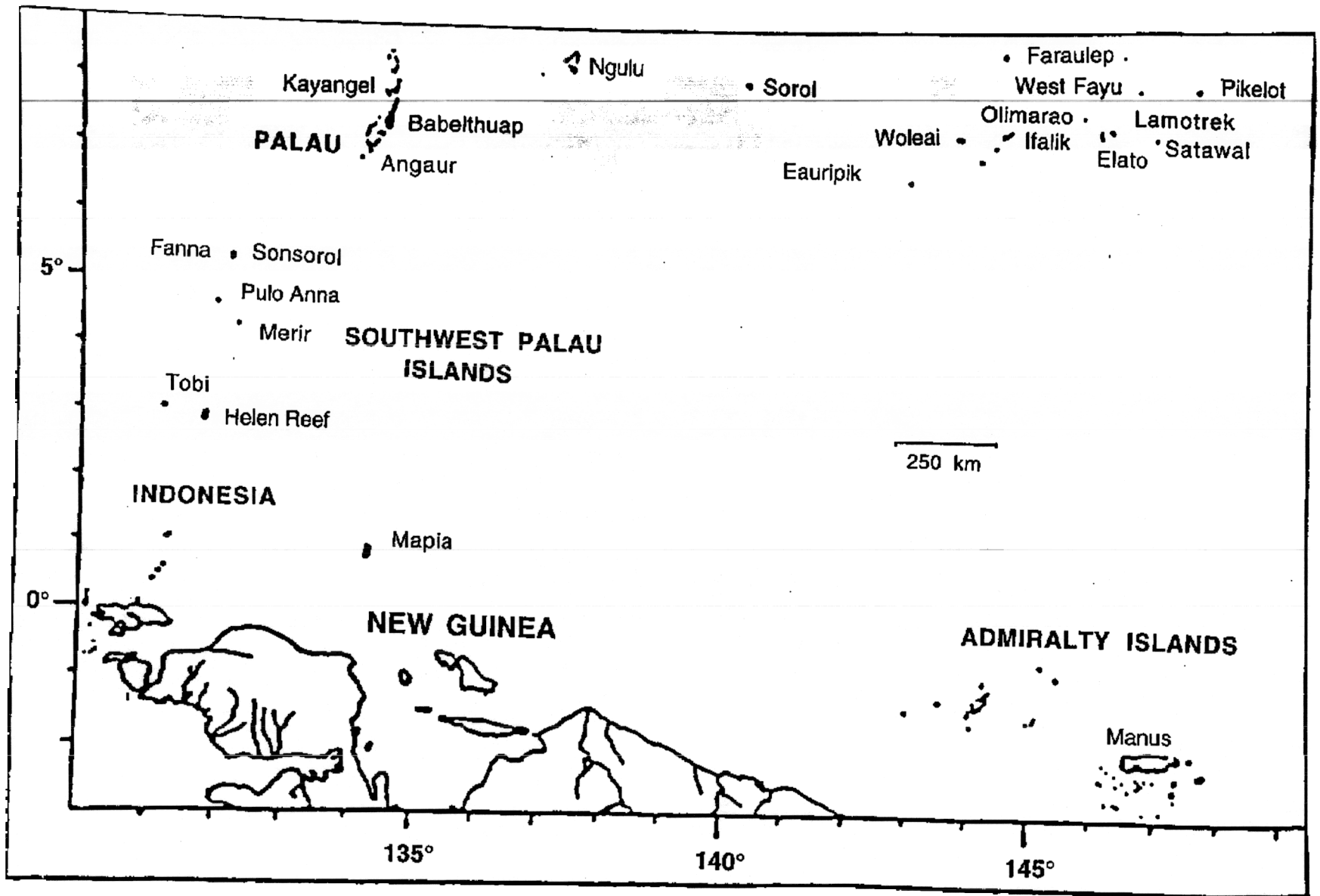


FIGURE 1. The Southwest Palau Islands in relation to the main Palau Archipelago and northern Indonesia.

trap locally produced larvae, promoting self-recruitment of reef fishes (e.g., Lobel and Robinson 1983, Lobel 1989).

The Southwest Palau Islands Expedition, conducted by The Nature Conservancy, the U.S. Fish and Wildlife Service, and Greenpeace on behalf of the Government of Palau, provided an opportunity to assess shallow-water habitats (generally less than 25–30 m in depth) to determine the species composition of resident fish assemblages. Here, I provide a comparative analysis of patterns of species distribution, richness, diversity, evenness, endemism, and similarity between the fish faunas of each island. Because of the islands' geographical location, they provide an opportunity for biogeographical comparisons with the fish fauna of Palau.

A prediction of ecological theory is that species diversity increases with increased habitat complexity and with greater numbers of habitat types (Williams 1964, Ricklefs 1973, Roughgarden 1979). This increased complexity may be a function of time. Alternatively, complexity may also be a function of relative size. The two are not mutually exclusive with respect to fluctuations in sea level. The SWPI has fewer numbers of habitat types and lower habitat complexity compared with the MPA (unpubl. data). Species richness and diversity is predicted to be greater in the MPA compared with the SWPI. Within the SWPI, Helen Reef is predicted to have greater species richness and diversity compared with the remaining islands.

Faunal similarities are predicted to be influenced by latitudinal differences between islands relative to Indonesia to the south and the MPA to the north. Tobi and Helen Reef faunas are predicted to be more similar to one another and to the faunas of northern and eastern Indonesia. Similarity will decrease with increasing latitude, so that the faunas of Pulo Anna and Merir, and Sonsorol and Fanna will be more similar to each other, respectively.

## MATERIALS AND METHODS

### *Stations and Surveys*

Stations were designated a priori from charts and aerial photographs of each island (Maragos 1993). The number of stations varied between localities (Table 1) and ranged from 22 at Helen Reef to five at Fanna. Differences in sampling effort were attributed to locality size. Stations were delineated by distinct habitat types.

Fishes were visually surveyed during timed swims with scuba (transects) along a depth gradient at each station. Generally, transect surveys were 30 min long, commencing at a depth of ca. 20 m and ascending at a steady pace until the shallowest possible depth was reached. Usually, the first 15 min were spent between 10 and 20 m and the second 15 min at 0–10 m. Reef topography, current, and surface conditions determined actual depths

TABLE 1  
PHYSIOGRAPHY AND SAMPLING EFFORT OF LOCALITIES IN THE SOUTHWEST PALAU ISLANDS  
(PHYSIOGRAPHIC DATA CITED IN MARAGOS [1993])

LOCALITY	LATITUDE	LONGITUDE	VARIABLE	
			REEF PERIMETER (OCEAN SLOPE)	NO. STATIONS
Helen Reef	131° 49' E	2° 59' N	61.7 km <sup>2</sup>	22
Tobi	131° 11' E	3° 1' N	7.0 km <sup>2</sup>	8
Merir	132° 19' E	4° 19' N	9.5 km <sup>2</sup>	10
Pulo Anna	131° 58' E	4° 40' N	4.7 km <sup>2</sup>	5
Sonsorol	132° 13' E	5° 9' N	7.0 km <sup>2</sup>	6
Fanna	132° 13' E	5° 21' N	4.3 km <sup>2</sup>	5

at the onset and completion of the transect. Reef margins could not be surveyed at some stations because of heavy surf. Occasionally, some transects began as deep as 30 m, and six stations were confined to depths of less than 2 m from onset to completion. Two of the latter stations, both at Merir, had to be sampled by walking at low tide. Additional time, in 15-min increments, was allowed at a few stations. Nearly all transects were affected by current patterns, ranging from swift to slack, and distances covered were quite variable.

Species observed were recorded on plastic paper and with underwater photography. Specimens were identified to the lowest taxon possible. Identifications were confirmed from several sources, including Masuda et al. (1984), Smith and Heemstra (1986), Myers (1989), Randall et al. (1990), Allen (1991), Randall and Heemstra (1991), and Kuitert (1992).

Physical limitations prevented making accurate counts for each species because large numbers of species and individuals were encountered on many transects (i.e., >50–150 species per transect and for some, such as pomacentrids, hundreds of individuals of each species). Therefore, fishes were identified to species and enumerated on the basis of presence-absence only. Some taxa (e.g., Cirrhitidae, Serranidae, Pinguipedidae, Pomacanthidae, Scorpaenidae) were quantified and those results presented elsewhere (unpubl. data). The number of stations per locality in which a species was observed was determined by inspection of the data sheets after the conclusion of the expedition. Estimates of species diversity at each locality were based upon determinations of the number of occurrences.

### Analyses

Presence-absence data limit hypothesis testing, and analyses were relatively simple. Species richness, species diversity, evenness, and similarity in species composition between localities were calculated and compared.

Species richness consists of the number of species at each station and the total number of species at each locality. Values within and between localities were analyzed with chi-

square tests. The null hypothesis was that patterns of richness between stations or localities were equivalent. The relationship between species richness at localities and locality size was examined in two ways. First, species richness and the size of the locality (i.e., total reef area) were examined with the nonparametric Spearman's correlation analysis (Sokal and Rohlf 1981). Then, a species-area curve was plotted and a regression analysis made of log-transformed values. Second, species richness was related to the number of stations and was analyzed with the same test. The null hypothesis in both tests was that the correlation between each pairing was not different from zero.

Species diversity was calculated with the Shannon Index of Diversity (Magurran 1988), modified to reflect the proportional representation of a species at each locality based upon the number of stations where it occurs. The index is calculated as:

$$H' = - \sum p - i \ln p - 1$$

where  $p - i$  is the proportional distribution of the  $i$ -th species from all stations at each locality. A modified  $t$ -test (Magurran 1988) was used to test for significant differences in  $H'$  between localities. The null hypothesis was that  $H'$  was equivalent between localities in pairwise comparisons.  $H'$  values were related to locality size and were tested for significance with Spearman's correlation analysis.

Shannon Evenness,

$$E' = H' / \ln S$$

where  $S$  is the number of species, was calculated to estimate the ratio of observed diversity to maximum diversity (Pielou 1969), inferred from the proportion of stations at a locality in which species were present.

Similarity of species composition between localities was measured by pairwise calculation of the Sorenson Qualitative Similarity Index (Magurran 1988), given as:

$$C_S = 2j / (a + b)$$

where  $J$  is the number of species occurring at both localities,  $a$  is the number of species at locality A, and  $b$  is the number of species at locality B. Values ranged from 0.0 (no sim-

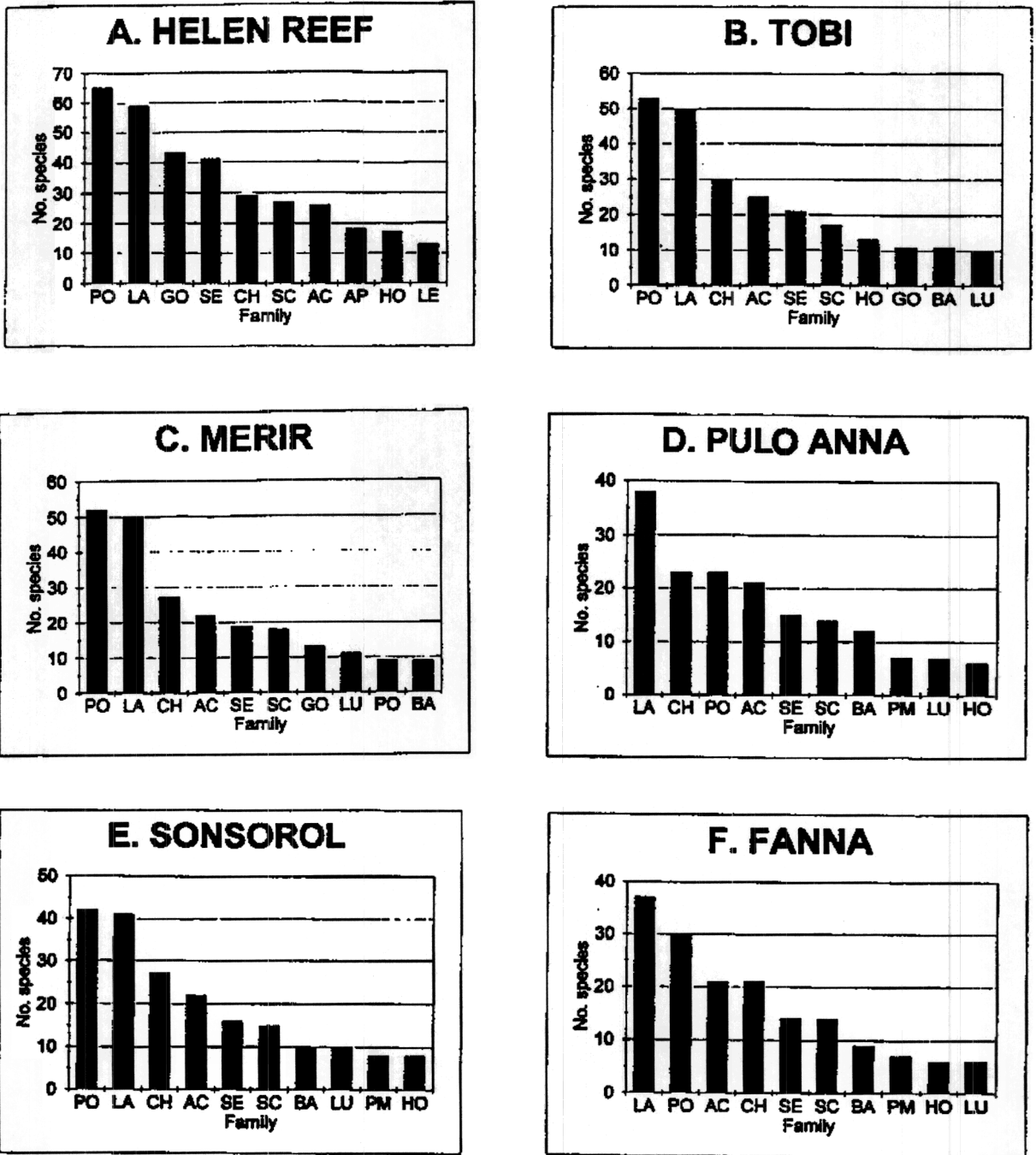


FIGURE 2. The 10 most speciose families at each locality. Family name abbreviations are as follows: AC, Acanthuridae; AP, Apogonidae; BA, Balistidae; CH, Chaetodontidae; GO, Gobiidae; HO, Holocentridae; LE, Lethrinidae; LU, Lutjanidae; PM, Pomacanthidae; PO, Pomacentridae; SC, Scaridae; SE, Serranidae.

ilarity) to 1.0 (complete similarity). This index is considered the most robust for presence-absence data (Magurran 1988). Similarity values were arranged in a matrix and sub-

jected to cluster analysis (CLUSTER procedure, UPMGA method [Norusis and SPSS 1990] to examine faunal relationships between localities.

## RESULTS

*Species Richness and Endemism*

At least 602 species of fishes were identified from the SWPI (Appendix). Of these, 596, including distinct morphs of two species that may differ on a molecular basis, were observed on one or more of 53 transects. The remainder were collected from pelagic waters between localities (Appendix). Fifty-four species are new records for Palau, including nine species new to Micronesia. These will be discussed elsewhere (T.J.D. and R. F. Myers, unpubl. data). The observed fish compose about 64.3% of the known Palauan fish fauna (Myers 1989; T.J.D. and R. F. Myers, unpubl. data; R. F. Myers, T.J.D., and J. E. Randall, unpubl. data). Sampling error was almost certainly a variable because surveys were conducted during daylight or just before sunset and at relatively shallow depths. Thus, the surveys probably failed to account for a number of nocturnal, near-shore pelagic, cryptic, and deeper-dwelling reef species.

Sixty-three of the 96 families reported by Myers (1989) were observed. The 10 most speciose were damselfishes (Pomacentridae: 81 spp.); wrasses (Labridae: 70 spp.); gobies (Gobiidae: 49 spp.); groupers, fairy basslets, and soapfishes (Serranidae: 47 spp.); butterflyfishes (Chaetodontidae: 32 spp.); surgeonfishes (Acanthuridae: 31 spp.); parrotfishes (Scaridae: 30 spp.); squirrelfishes and soldierfishes (Holocentridae: 20 spp.); cardinalfishes (Apogonidae: 19 spp.); jacks (Carangidae: 15 spp.); emperors (Lethrinidae: 15 spp.); and snappers (Lutjanidae: 15 spp.). The 10 most speciose families by locality are shown in Figure 2.

Species richness ranged from 488 species at Helen Reef to 195 species at Fanna (Table 2). Tobi had the second highest value of species richness, followed by Merir, Sponsorol, and Pulo Anna. Differences between each locality in pairwise comparisons were significant in all pairings except three, Tobi-Merir, Merir-Sponsorol, and Pulo Anna-Fanna (Table 3).

There was a significant rank correlation between species richness and locality size (Spearman's  $r_s = 0.90$ ,  $df = 5$ ,  $P < 0.05$ ). The

TABLE 2

SPECIES RICHNESS (S), SHANNON DIVERSITY ( $H'$ ), AND SHANNON EVENNESS ( $E'$ ) OF SOUTHWEST PALAU ISLAND FISH ASSEMBLAGES

LOCALITY	CODE	N	S	%	$H'$	$E'$
Helen Reef	H	22	488	52.1	1.9958	0.7198
Tobi	T	8	317	33.9	1.5467	0.7948
Merir	M	10	294	31.4	1.6805	0.8081
Pulo Anna	P	5	198	21.2	1.2710	0.9168
Sponsorol	S	6	250	26.7	1.6607	0.9269
Fanna	F	5	195	21.8	1.2878	0.9290

N, Number of stations at each locality. Percent is the proportion of known Palau and Southwest Palau Islands fauna (936 species)  $\times 100$ .

TABLE 3

MATRIX OF PAIRWISE COMPARISONS OF BETWEEN-LOCALITY SPECIES RICHNESS, S

	LOCALITY					
	T	H	M	P	S	F
T	—					
H	35.39***	—				
M	0.8658	47.57***	—			
P	27.50***	122.60***	18.73***	—		
S	7.92**	76.75***	3.56	6.04*	—	
F	29.07***	125.69***	20.04***	0.02	6.77**	—

NOTE: Values are chi square. See Table 2 for locality codes. \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ,  $df = 1$ .

plot of species richness on the species-area curve (Figure 3) has the regression equation:  $\text{Log species richness} = 2.128 + 0.33 \cdot \text{log area}$ ,  $r^2 = 0.86$ ,  $P < 0.007$ .

A significant rank correlation between species richness and the number of stations sampled at each locality was also found (Spearman's  $r_s = 0.9167$ ,  $df = 5$ ,  $P < 0.05$ ). Size of the locality sampled, and hence the number of habitat types, both were positively correlated with species richness.

Fish species varied proportionally in their distribution among islands (Table 4), and families having species with wide ranges also had species with extremely narrow ranges within the SWPI. About 17.5% of all species were recorded at all six localities, and 35.6%

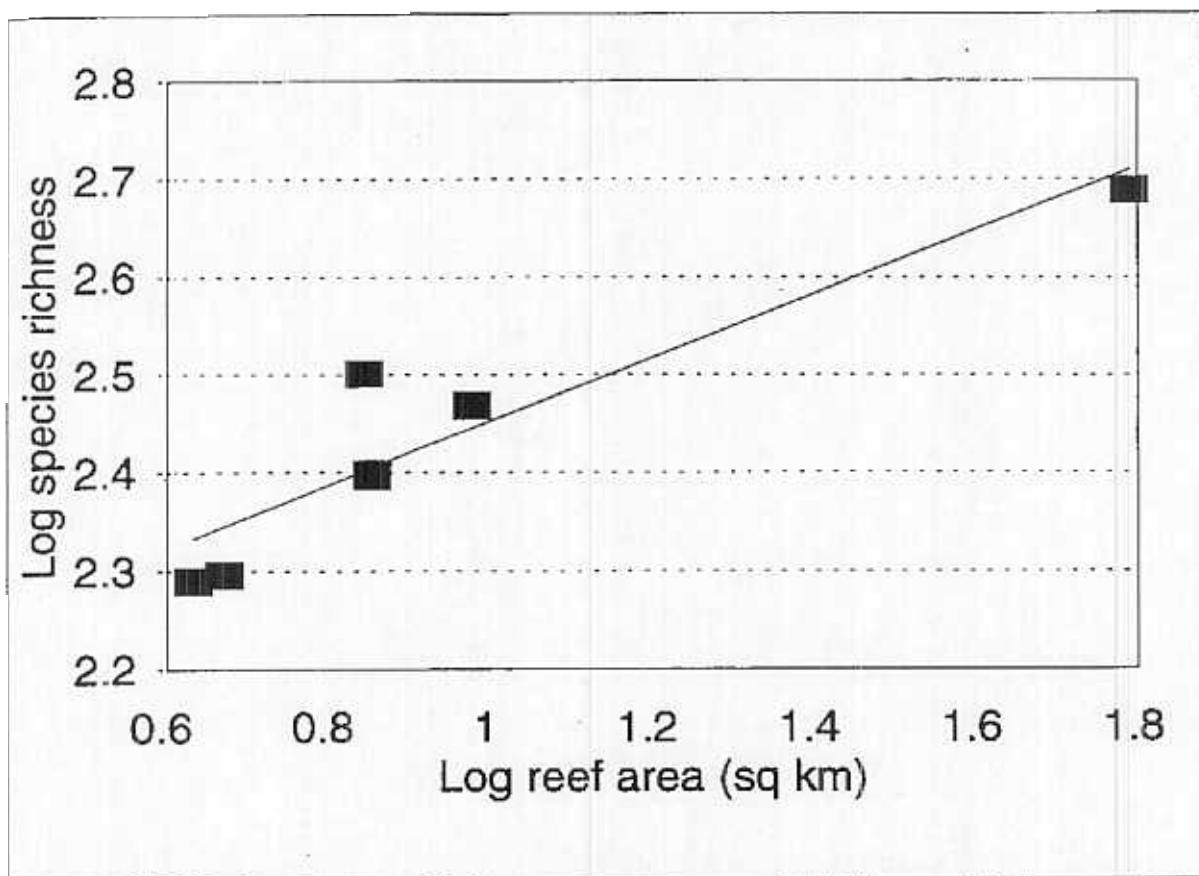


FIGURE 3. Log-log plot of species richness of fishes. The line represents the best fit power function of the regression.

occurred only at one locality. The Appendix provides an indication of taxa with narrow versus wide ranges in the SWPI. Generally, wide-ranging species included members of the families Acanthuridae, Balistidae, Carangidae, Carcharhinidae, Caesionidae, Chaetodontidae, Cirrhitidae, Holocentridae, Labridae, Lethrinidae, Lutjanidae, Microdesmidae, Mullidae, Pomacanthidae, Pomacentridae, Scaridae, Serranidae, and Sphyraenidae. Of these, the Chaetodontidae were especially well distributed, with 28 of 32 species occurring at four or more localities. Those families with narrow ranges included members of the Apogonidae, Blenniidae, Carangidae, Gobiidae, Haemulidae, Labridae, Muraenidae, Pomacanthidae, Pomacentridae, Serranidae, Siganidae, and Syngnathidae. Several of these families have species that are cryptic, noctur-

nal, deep-dwelling, or highly mobile, which may have escaped notice.

Species endemic to Palau account for only 0.17% of the fauna. A single endemic species, *Epibulus* sp. 2 (Labridae), was observed at Sonsorol. This species has also been reported from the MPA, which has only four additional endemic species, two of which occur in freshwater (Myers 1989).

#### *Species Diversity and Similarity*

Helen Reef, the largest locality in terms of reef area, had the most diverse fish fauna (Table 2), over three times that of Pulo Anna and Fanna, the two smallest localities, and 1.5 times as diverse as Merir, Tobi, and Sonsorol. The latter three are somewhat similar in area, compared with Pulo Anna and

TABLE 4

PROPORTIONAL DISTRIBUTION OF FISH SPECIES IN THE SOUTHWEST PALAU ISLANDS ( $n = 6$  localities; 596 species were observed on transects)

NO. OF LOCALITIES	NO. OF SPECIES	%
	212	35.6
2	102	17.1
3	79	13.3
4	54	9.1
5	50	8.4
6	104	17.5

TABLE 5

MATRIX OF PAIRWISE COMPARISONS OF  $t$ -TESTS OF SHANNON DIVERSITY ( $H'$ ) VALUES FOR SOUTHWEST PALAU ISLAND FISHES

	LOCALITY					
	T	M	P	S	F	
T	—	803	610	506	546	489
H	6.29*	—	781	681	721	664
M	2.12*	4.50*	—	536	525	468
P	4.95*	11.46*	7.60*	—	445	388
S	2.02*	5.23*	0.36	8.50*	—	444
F	4.81*	11.49*	7.56*	0.40	8.56*	—

NOTE: Lower numbers are calculated  $t$  values. Upper numbers are degrees of freedom. See Table 2 for locality codes. \*,  $P < 0.05$ .

Fanna, or Helen Reef. Differences in species diversity ( $H'$ ) were significant in all pairwise comparisons between localities except Merir-Sonsorol, and Pulo Anna-Fanna (Table 5). Shannon Evenness ( $E'$ ) ranged from 0.7198 at Helen Reef to 0.9290 at Fanna.

There was a significant rank correlation between locality size and species diversity ( $r_s = 0.99$ ,  $df = 5$ ,  $P < 0.05$ ). There was no significant rank correlation between  $H'$  and the number of stations sampled, however ( $r_s = 0.7429$ ,  $df = 5$ ,  $P < 0.05$ ).

Fish assemblages at all localities appear to be moderately similar to one another (Table 6), with  $C_s$  values ranging from 0.4927 (Helen Reef-Pulo Anna) to 0.7353 (Merir-Sonsorol). The term "moderate" is subjective and should be viewed with caution because

TABLE 6

MATRIX OF SORENSON'S QUALITATIVE SIMILARITY INDEX ( $C_s$ ) VALUES FROM PAIRWISE COMPARISONS OF SPECIES COMPOSITION BETWEEN ISLAND LOCALITIES

	LOCALITY					
	T	H	M	P	S	F
T	—					
H	0.6196	—				
M	0.6939	0.5985	—			
P	0.6019	0.4927	0.6341	—		
S	0.6349	0.5664	0.7353	0.6920	—	
F	0.5820	0.4978	0.6053	0.7277	0.7056	—

NOTE: See Table 2 for locality codes.

strict criteria for evaluating similarities were absent (Sale 1991). Values were useful in showing patterns of association in a dendrogram generated from cluster analysis (Figure 4). Merir and Sonsorol were very similar in species composition and, in turn, were more similar to Tobi than the other localities. The fish faunas of Pulo Anna and Fanna were very similar to one another and formed a second group. Helen Reef, the largest and most species rich, formed a third group.

## DISCUSSION

### *Faunal Composition and Geography*

The fish fauna of Palau is the most diverse in Micronesia but has the least number of endemic species. Over 96% of the Micronesian fish fauna and 35% of all Indo-Pacific inshore species occur there. East of Palau, the number of species decreases from west to east along a "corridor" (Springer 1982) or "conduit" (Myers 1989) extending from Palau through the Caroline Islands to the Marshall Islands. Active dispersal of Indo-Pacific species on to the Pacific Plate likely occurred via this route (Springer 1982, Myers 1989). Conversely, the number and proportion of endemic species increases from west to east along this line and well into Oceania (Randall 1992), and the low rate of endemism in Palau is a reflection of this pattern.



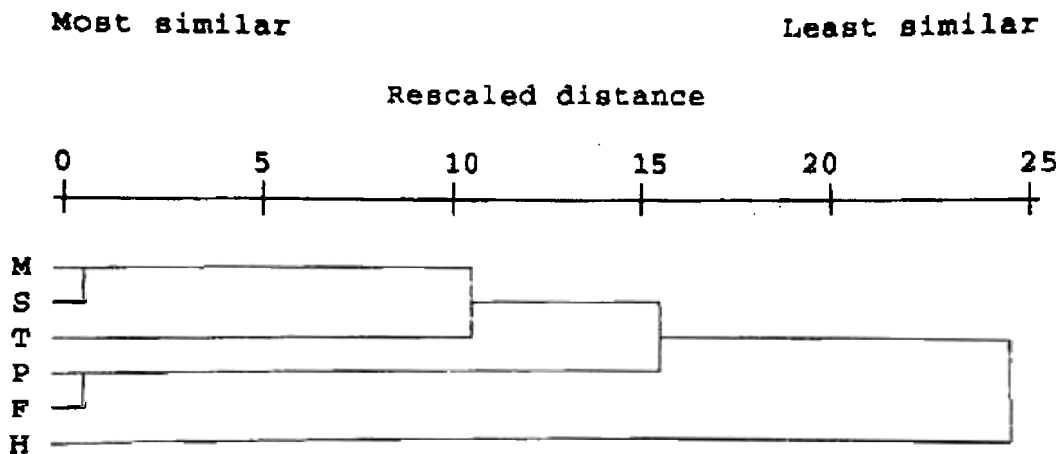


FIGURE 4. Dendrogram depicting relationships between fish assemblages recorded from island localities. Relationships were determined from cluster analysis of Sorenson's Qualitative Similarity Index ( $C_S$ ) values in a matrix of pairwise comparisons. Distance is given as a relative measure of similarity. Localities are Merir (M), Sonsorol (S), Tobi (T), Pulo Anna (P), Fanna (F), and Helen Reef (H).

The SWPI fish fauna closely resembles those of Palau and, to a lesser extent, the Pacific Plate. The SWPI, however, are located south of the corridor or conduit and are proximate to the most northerly and easterly islands of Indonesia. Although data that would allow for comparisons of similarity between SWPI and northern Indonesia fish faunas are lacking, close affinities appear to exist. Fishes representative of the highly diverse Indonesian fauna (e.g., Kuitert 1992) but absent from Micronesia occur in the SWPI, especially at Helen Reef and Tobi. Some examples include *Diploprion bifasciatum* (Serranidae: Grammistinae), *Cirrhichthys aprinus* (Cirrhitidae), *Amphiprion ocellatus* and *A. frenatus* (Pomacentridae), and *Choerodon fasciatus* (Labridae).

Seasonal current patterns (e.g., Johannes 1981, Santelices 1992, Maragos 1993) indicate that the SWPI may also receive dispersing larval fishes from the Australo-Papuan area, the southern Philippines, and the Pacific Plate. Both Indonesia and the southern Philippines are part of the "center of diversity" within the Indo-Malayan triangle, hypothesized by Briggs (1974) as having the greatest diversity of marine organisms. This center, however, may be nothing more than an area of overlap between Pacific and Indian Ocean faunas in a region historically subject to alternating

changes in sea level during the Quaternary (Woodland 1983, Donaldson 1986). This view is strengthened by the dispersal westward of Pacific Plate species to marginal areas, including Palau, via seasonal current flows (e.g., Myers 1989). The completion of species lists from these adjacent areas will facilitate comparative analyses of similarity with the fauna of the SWPI.

#### *Habitat Complexity, Species Richness, Diversity, and Similarity*

Another hypothesis central to this study is that islands with greater size, and hence greater habitat complexity by virtue of increased numbers of habitat types, will have greater species richness and diversity compared with small islands. Habitat heterogeneity has been shown to be a reliable predictor of species richness (Boecklen 1986). Thus, Helen Reef, the largest locality, with at least 13 separate major habitats, should have greater richness and diversity than Fanna, the smallest locality. This is indeed the case, and a similar comparison of the faunas of Helen Reef and the MPA yields an outcome that is much the same (unpubl. data). The latter locality had greater habitat development, including mangrove, sea grass, mudflat, estuaries, and secondary freshwater

habitats, and species richness and diversity exceeding those of Helen Reef.

The remaining SPWI appear to have levels of species richness and diversity relative to their size and, in turn, level of habitat complexity, with the exception of Tobi, which had greater species richness and diversity than Merir, despite having fewer habitat types. This single difference may be related to geographic proximity to Indonesia. Islands similar in size and complexity will be similar in faunal composition given reasonable geographic proximity to one another. This pattern is borne out in the similarities between Merir and Sonsorol, Tobi, and the smallest localities, Pulo Anna and Fanna.

Tests of these hypotheses are complicated by the effects of locality age (e.g., Smith 1992), dietary and feeding requirements of fishes, the mode of spawning among fishes at a locality (Thresher 1991), the influence of local gyres (Lobel and Robinson 1983, Lobel 1989), the effects of a dynamic equilibrium (MacArthur and Wilson 1967) and interaction between the effects of area and habitat complexity (Williams 1964), and sampling error and the effects of passive sampling (e.g., Connor and McCoy 1979). With the exception of sampling error, elaboration of these factors is beyond the scope of this paper.

Sampling error, particularly the failure to account for species actually present in a given area, influences comparisons of richness and diversity. Thus, the measure of species richness is a result of sampling intensity in a given area (Connor and McCoy 1979). In this study, 35.9% of the species known to occur in the MPA (Myers 1989; T.J.D. and R. F. Myers, unpubl. data; R. F. Myers, T.J.D., and J. E. Randall, unpubl. data) were not recorded. Sources of error vary. The use of visual counts exclusively without augmentation from collecting likely resulted in lower counts of cryptic species (e.g., Muraenidae, Bythitidae, Ophichthidae, Antennariidae, Scorpaenidae, certain Apogonidae, Pseudochromidae, Callionymidae, Gobiidae, Bothidae). Restriction of sampling to daylight hours or just before sunset ignored many nocturnal species (e.g., Apogonidae, Holocentridae, Priacanthidae), although several

species were observed in holes and caves exposed to view during surveys. Restriction of sampling because of dive safety limitations, to depths of less than 25 m in most instances, ignored deeper-dwelling species (some Serranidae, Pomacanthidae, Chaetodontidae, Pomacentridae). Inadequate sampling of near-shore pelagic species (e.g., Carcharhinidae, Clupeidae, Belonidae, Hemirhamphidae, Exocoetidae, Scombridae) likely resulted in lower counts, as well. Doubtless, further sampling will result in observations of or range extensions within the SWPI for a number of species, many of which are common elsewhere (Myers 1989, Kuitert 1992). Ironically, some deep-dwelling species (e.g., *Aphareus rutilans* [Lutjanidae]) were observed in deep channels at Helen Reef, subject to upwelling and strong tidal influences.

#### CONCLUSIONS

The fish fauna of the SWPI described here composes ca. 64% of the known Palauan fauna. Species richness varies latitudinally, decreasing from south to north. Species diversity appears dependent upon the degree of habitat complexity between localities, and increased diversity may also be a function of locality size. Affinities with the Australo-Papuan fauna known from Indonesia exist but remain to be elucidated pending further determinations of both faunas. Numerous gaps in the knowledge of SWPI reef fish distribution patterns relative to habitat types, depth, and diel pattern can be filled with additional effort. Tracing the evolution of the islands' fish fauna will be possible with additional sampling and comparison with neighboring areas, particularly Indonesia, and by the application of historical methods (e.g., Brooks and McLennan 1991) after phylogenetic relationships and patterns of distribution among species are made clearer.

#### ACKNOWLEDGMENTS

I am grateful to J. Maragos for extending an invitation to join the Southwest Palau Is-

lands Expedition, and to C. Cook, S. Geermans, N. Idechong, R. Hunter-Anderson, K. Kepler, K. McDermid, J. Maragos, S. Patris, B. Smith, and R. Smith for their help in the field. Captain E. Gosse and S. McNab of the *M/V Pegasus II*, and J. Noble and V. Getz of Greenpeace provided additional assistance. M. Wilkins, S. Wilkins, and G. Donaldson are thanked for their last-minute logistical support. J. M. Fitzsimons critically read the manuscript and offered improvements. The constructive criticism of two anonymous reviewers is greatly appreciated. This paper is based upon a report submitted to the Government of Palau for research undertaken by The Nature Conservancy, with the support of the U.S. Fish and Wildlife Service, the John D. and Catherine T. MacArthur Foundation, the South Pacific Regional Environment Programme, Greenpeace, Micronesian Archaeological Services, and the Division of Marine Resources and Conservation Office of the Government of Palau. The manuscript was written while I was a Japan Society for the Promotion of Science Foreign Research Fellow at Kyushu University.

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## APPENDIX

## CHECKLIST AND DISTRIBUTION OF FISHES OBSERVED DURING THE SOUTHWEST PALAU ISLANDS EXPEDITION

FAMILY/SPECIES	LOCALITY <sup>a</sup>						TOTAL	%
	T	H	M	P	S	F		
Orectolobidae								
<i>Nebrius concolor</i> (Rüppell)		1					1	16.7
Hemigaleidae								
<i>Triaenodon obesus</i> (Rüppell)		3					3	50.0
Carcharhinidae								
<i>Carcharhinus albimarginatus</i> (Rüppell)	1	2	1				3	50.0
<i>C. amblyrhynchos</i> (Bleeker)	3	4		1		1	4	66.7
<i>C. melanopterus</i> (Quoy & Gaimard)	2		1				3	50.0
Dasyatididae								
<i>Taeniura melanospilos</i> Bleeker							1	16.7
Myliobatidae								
<i>Aetobatis narinari</i> (Euphrasen)	1						1	
Mobulidae								
<i>Manta alfredi</i> (Kreffft)		1				2	2	33.3
Muraenidae								
<i>Gymnothorax javanicus</i> (Bleeker)	1	1					3	50.0
<i>G. meleagris</i> (Shaw & Nodder)					1		1	16.7
<i>Sideria picta</i> (Ahl)			2				1	16.7
<i>Uropterygius goslinei</i> McCosker & Randall								
<i>U. micropterus</i> * (Bleeker)			1				1	16.7

## APPENDIX (continued)

FAMILY/SPECIES	LOCALITY <sup>a</sup>						TOTAL	%
	T	H	M	P	S	F		
Congridae								
<i>Conger cinereus</i> Rüppell	1							16.7
<i>Gorgasia</i> sp.		1						16.7
Clupeidae								
<i>Spratelloides delicatulus</i> (Bennett)		5						
Synodontidae								
<i>Saurida gracilis</i> (Quoy & Gaimard)		1						16.7
<i>Synodus binotatus</i> Schultz		5						16.7
<i>S. dermatogenys</i> Fowler		1					2	33.3
<i>S. jaculum</i> Russell & Cressey		1					1	16.7
Atherinidae								
<i>Hypoatherina ovalaua</i> (Herre)							1	16.7
Belonidae								
<i>Strongylura incisa</i> (Valenciennes)			1				1	16.7
<i>S. leiura leiura</i> (Bleeker)	1						1	16.7
Exocoelidae								
<i>Exocoetus volitans</i> L.							#?	
<i>Paraexocoetus mento mento</i> Valenciennes							#?	
Holocentridae								
<i>Myrpristis adusta</i> Bleeker	3	6					2	33.3
<i>M. amaenus</i> (Castlenau)	1	1				2	3	50.0
<i>M. berndti</i> Jordan & Evermann				1		2	2	33.3
<i>M. hexagona</i> (Lacépède)	2						1	16.7
<i>M. kumtee</i> Cuvier	1	2	2		2		4	66.7
<i>M. murdjan</i> (Forsskål)	3	6	6	2	3	3	6	100.0
<i>M. pralina</i> Cuvier		9			6		2	33.3
<i>M. violacea</i> Bleeker	1	1			1		3	50.0
<i>M. vittata</i> Cuvier		1						33.3
<i>Neoniphon argenteus</i> (Valenciennes)		1					1	16.7
<i>N. opercularis</i> (Valenciennes)	1	6	2				3	50.0
<i>N. sammara</i> (Forsskål)		3			1		2	33.3
<i>Sargocentron caudimaculatum</i> (Rüppell)	3	6	6	3		2	5	83.3
<i>S. diadema</i> (Lacépède)		2			4		2	33.3
<i>S. ittodai</i> (Jordan & Fowler)		1	1	2		3	4	66.7
<i>S. melanospilos</i> (Bleeker)		1						33.3
<i>S. microstoma</i> (Günther)								16.7
<i>S. prasinum</i> (Lacépède)	1			1			2	33.3
<i>S. spiniferum</i> (Forsskål)	3	7		1	2	1	5	83.3
<i>S. tiere</i> (Cuvier)	1	1			4		3	50.0
<i>S. violaceum</i> (Bleeker)		1					2	33.3
Aulostomidae								
<i>Aulostomus chinensis</i> (L.)	1	8		1			3	
Fistularidae								
<i>Fistularis commersoni</i> Rüppell	2	2					2	33.3
Syngnathidae								
<i>Corythoichthys intestinalis</i> (Ramsay)		2					1	16.7
<i>Corythoichthys</i> sp.		1					1	16.7
Caracanthidae								
<i>Caracanthus maculatus</i> * (Gray)		1	3		2	3	4	66.7
Scorpaenidae								
<i>Sebastapistes cyanostigma</i> (Bleeker)					2		2	33.3
<i>Pterois radiata</i> Cuvier	1						2	33.3
<i>P. volitans</i> (L.)	1							16.7
Serranidae								
<i>Luzonichthys watei</i> (Fowler)	1			2			3	50.0
<i>Pseudoanthias cooperi</i> (Regan)		2					1	16.7

## APPENDIX (continued)

FAMILY/SPECIES	LOCALITY <sup>a</sup>						TOTAL	%
	T	H	M	P	S	F		
<i>P. huchti</i> (Bleeker)	4	6	4	1	3	1	6	100.0
<i>P. squamipinnis</i> (Peters)	3	7	5	3	1	4	6	100.0
<i>P. bartlettorum</i> (Randall & Lubbock)	5	8	4	3	3	1	6	100.0
<i>P. dispar</i> (Herre)		5	3		1	3	4	66.7
<i>P. pascalus</i> (Jordan & Tanaka)	3	7	5	3	5	3	6	100.0
<i>P. randalli</i> (Lubbock & Allen)	2	3					2	33.3
<i>P. smithvanizi</i> (Randall & Lubbock)	1						1	16.7
<i>P. tuka</i> Herre & Montalban	2	5			2		3	50.0
<i>Serranocirrhites latus</i> Watanabe		2	1				2	33.3
<i>Aethuloperca rogaa</i> Forsskål	1	6	2	1	1	3	6	100.0
<i>Anyperodon leucogrammicus</i> Valenciennes		4			1		2	33.3
<i>Cephalopholis argus</i> Schneider	6	12	5	4	5	3	6	100.0
<i>C. boenack</i> Bloch		2					1	16.7
<i>C. cyanostigma</i> * Valenciennes		2					1	16.7
<i>C. leopardus</i> Lacépède	4	2	3	1	5	2	6	100.0
<i>C. microprion</i> ** Bleeker		1					1	16.7
<i>C. miniata</i> Forsskål	2	6	3	1	1	1	6	100.0
<i>C. sexmaculata</i> Rüppell	4		1				2	33.3
<i>C. sonnerati</i> (Valenciennes)		3					1	16.7
<i>C. spiloparaea</i> (Valenciennes)	4	3	1		4		4	66.7
<i>C. urodeta</i> (Bloch & Schneider)	5	8	8	4	6	4	6	100.0
<i>Gracila albomarginatus</i> (Fowler & Bean)	3	6	6	4	5	1	6	100.0
<i>Epinephelus caeruleopunctatus</i> (Bloch)		4	1				3	50.0
<i>E. fuscoguttatus</i> (Forsskål)	1	2					2	33.3
<i>E. hexagonatus</i> (Schneider)	4	2			1		3	50.0
<i>E. howlandi</i> Günther				1	3		3	50.0
<i>E. lanceolatus</i> (Bloch)		1					1	16.7
<i>E. malabricus</i> Schneider		4						16.7
<i>E. melanostigma</i> Schultz		2		2		1	3	50.0
<i>E. merra</i> Bloch	1	6					2	33.3
<i>E. spilotoceps</i> * Schultz	3		3	1			3	50.0
<i>E. tauvina</i> Forsskål		1					1	16.7
<i>Plectropomus areolatus</i> (Rüppell)		9						16.7
<i>P. laevis</i> (Lacépède)		6	1				2	33.3
<i>P. leopardus</i> (Lacépède)		1					1	16.7
<i>P. oligocanthus</i> Bleeker		2					1	16.7
<i>Variola louti</i> (Forsskål)		3	3	1		1	4	66.7
<i>Belonoperca chaubanaudi</i> Fowler & Bean		1					1	16.7
<i>Grammistes sexlineatus</i> Thünberg		1					1	16.7
<i>Diploprion bifasciatum</i> ** Cuvier		1					1	16.7
<i>Pogonoperca punctata</i> * (Valenciennes)			1				1	16.7
<b>Pseudochromidae</b>								
<i>Pseudochromis cyanotaenia</i> Bleeker					1		1	16.7
<i>P. fuscus</i> Müller & Troschel		2					1	16.7
<i>P. porphyreus</i> Lubbock & Goldman		7	3				2	33.3
<b>Cirrhitidae</b>								
<i>Cirrhitichthys aprinus</i> ** Cuvier	1	1	1				3	50.0
<i>C. falco</i> Randall		1	8		1		3	50.0
<i>C. oxycephalus</i> (Bleeker)	4	6		4	3	2	5	83.3
<i>Cirrhitus pinnulatus</i> (Bloch & Schneider)	3	2					2	33.3
<i>Oxycirrhites typus</i> * Bleeker	1	2	8				3	50.0
<i>Paracirrhites arcatus</i> (Cuvier)	7	8	8	4	6	4	6	100.0
<i>P. forsteri</i> Schneider	6	8		2	5	4	5	83.3
<i>P. hemistictus</i> * (Günther)	1							16.7
<i>Paracirrhites</i> sp.*	2						1	16.7

## APPENDIX (continued)

FAMILY/SPECIES	LOCALITY <sup>a</sup>						TOTAL	%	
	T	H	M	P	S	F			
<b>Apogonidae</b>									
<i>Apogon coccineus</i> (Rüppell)							1	16.7	
<i>Apogon</i> sp. ( <i>amboinensis</i> ?)							1	16.7	
<i>A. angustatus</i> (Smith & Radcliffe)	1						1	16.7	
<i>A. compressus</i> (McCulluch)		3						16.7	
<i>A. "cyanosoma"</i> ** Bleeker							1	16.7	
<i>A. exostigma</i> (Jordan & Starks)		1					1	16.7	
<i>A. fuscus</i> (Quoy & Gaimard)		2						16.7	
<i>A. gilberti</i> (Jordan & Seale)		2					1	33.3	
<i>A. kallopterus</i> Bleeker		1						16.7	
<i>A. lateralis</i> Valenciennes								16.7	
<i>A. nigrofasciatus</i> Lachner		1					2	33.3	
<i>A. novemfasciatus</i> Cuvier				1			2	33.3	
<i>A. semilineatus</i> ** Schlegel		1						16.7	
<i>Archamia fucata</i> (Cantor)		2					1	16.7	
<i>A. zosterophora</i> (Bleeker)		2						16.7	
<i>Cheilodipterus lineatus</i> L.		4					1	16.7	
<i>C. macrodon</i> (Lacépède)		1			1		2	33.3	
<i>C. quinquelineata</i> (Cuvier)		3					1	16.7	
<i>Siphamia orbicularis</i> (Cuvier)		2					1	16.7	
<b>Priacanthidae</b>									
<i>Priacanthus hamrur</i> Forsskål	1						1	16.7	
<b>Malacanthidae</b>									
<i>Malacanthus brevisrostris</i> (Guichenot)							2	33.3	
<i>M. latovittatus</i> (Lacépède)									
<b>Echeneidae</b>									
<i>Remora remora</i> (L.)	1						1	16.7	
<b>Carangidae</b>									
<i>Carangoides dinema</i> Bleeker		1			1		3	33.3	
<i>C. ferdau</i> (Forsskål)		2					1	16.7	
<i>C. fulvoguttatus</i> (Forsskål)		1					1	16.7	
<i>C. orthogrammus</i> Jordan & Gilbert		1					1	16.7	
<i>C. plagiotaenia</i> (Bleeker)	1	6	1				3	50.0	
<i>Caranx ignobilis</i> (Forsskål)	1		3		1		3	50.0	
<i>C. lugubris</i> Poey	1	5	1			1	4	66.7	
<i>C. melampygus</i> (Cuvier)		6	5				2	33.3	
<i>C. papuensis</i> Alleyne & MacLeay						1	2	33.3	
<i>C. sexfasciatus</i> Quoy & Gaimard		1					1	16.7	
<i>Gnathodon speciosus</i> (Forsskål)	1						1	16.7	
<i>Elagatis bipinnulatus</i> (Quoy & Gaimard)	4		2			3	2	4	66.7
<i>Seriola rivoliana</i> Valenciennes							1	16.7	
<i>Trachinotus bailloni</i> (Lacépède)		2					1	16.7	
<i>T. blochii</i> (Lacépède)		1					1	16.7	
<b>Coryphaenidae</b>									
<i>Coryphaena hippurus</i> L.								#	
<b>Gerreidae</b>									
<i>Gerres acinaces</i> ** Bleeker		1					1	16.7	
<i>G. filamentosus</i> Cuvier		1					1	16.7	
<b>Lutjanidae</b>									
<i>Aphareus furca</i> (Lacépède)		9	4		2	5	2	6	100.0
<i>A. rutilans</i> Cuvier			1						16.7
<i>Aprion virescens</i> Valenciennes	4	8	3		1	4	3	6	100.0
<i>Macolor macularis</i> Fowler	3	3	3			2		5	83.3
<i>M. niger</i> (Forsskål)	3	2	3		1	3		5	83.3
<i>Lutjanus argentimaculatus</i> ? (Forsskål)		1	1			1		3	50.0

## APPENDIX (continued)

FAMILY/SPECIES	LOCALITY <sup>d</sup>						TOTAL	%
	T	H	M	P	S	F		
<i>L. biguttatus</i> (Valenciennes)		4					1	16.7
<i>L. bohar</i> (Forsskål)	4	12	7	3	6	3	6	100.0
<i>L. decussatus</i> (Cuvier)	4	7	3				4	66.7
<i>L. ehrenbergi</i> (Peters)						1		16.7
<i>L. fulvus</i> (Schneider)	3		3		3	1	4	66.7
<i>L. gibbus</i> (Forsskål)		10	1				3	50.0
<i>L. kasmira</i> (Forsskål)		6						16.7
<i>L. monostigmus</i> Cuvier	6	5	6	2	4	3	6	100.0
<i>L. semicinctus</i> Quoy & Gaimard	2		6	3		1	4	66.7
Caesionidae								
<i>Caesio caeruleaurea</i> (Lacépède)		1					1	16.7
<i>C. cuning</i> (Bloch)	3	2	2		2		4	66.7
<i>C. lunaris</i> Cuvier	1	6	3		3	1	5	83.3
<i>C. teres</i> Seale	3	2		1	1	2	5	83.3
<i>Pterocaesio lativittata</i> Carpenter		4	3				2	33.3
<i>P. tile</i> (Cuvier)	3	3					2	33.3
<i>P. pisang</i> (Bleeker)	1	5	1				3	50.0
<i>P. trilineata</i> Carpenter	1		3		5		3	50.0
Haemulidae								
<i>Diagramma pictum</i> (Thünberg)		1					1	16.7
<i>Plectorhinchus chaetodonoides</i> (Lacépède)		2	1				2	33.3
<i>P. gibbosus</i> * (Lacépède)		1					1	16.7
<i>P. orientalis</i> (Bloch)	3		5			2	3	50.0
<i>P. picus</i> * (Cuvier)	2	3		1			4	66.7
<i>Plectorhinchus</i> sp.**		2						16.7
<i>Pomadasyus kaakan</i> (Cuvier)		1					1	16.7
Nemipteridae								
<i>Scolopsis bilineatus</i> (Bloch)	1	5	1				3	50.0
<i>S. ciliatus</i> (Lacépède)		1					1	16.7
<i>S. lineatus</i> Quoy & Gaimard	1	2	1	1	2		5	83.3
<i>S. trilineatus</i> Kner	1	3					2	33.3
<i>Pentapodus caninus</i> (Cuvier)		1						16.7
Lethrinidae								
<i>Ginathodentex aurolineatus</i> (Lacépède)					2	2	2	33.3
<i>Gymnocranius euanus</i> * (Günther)		1				1	2	33.3
<i>G. grandoculus</i> * Valenciennes		1						16.7
<i>G. griseus</i> * (Schlegel)		2						16.7
<i>G. microdon</i> * (Bleeker)		1					1	16.7
<i>Lethrimus erythracanthus</i> Cuvier		1	1				2	33.3
<i>L. erythropterus</i> Valenciennes			1				1	16.7
<i>L. harak</i> (Forsskål)	2	1			1		3	50.0
<i>L. lentjan</i> Lacépède		1						16.7
<i>L. microdon</i> Valenciennes	2	2	4				3	50.0
<i>L. olivaceus</i> Valenciennes		1						16.7
<i>L. semicinctus</i> * Valenciennes	1	1					2	33.3
<i>L. xanthocheilus</i> (Klunzinger)	6	1	3				3	50.0
<i>Monotaxis grandoculus</i> (Forsskål)	5	15	3	3	5	2	6	100.0
<i>Monotaxis</i> sp. B?		9	1		4	3	4	66.7
Mullidae								
<i>Mulloides flavolineatus</i> (Lacépède)		4					1	16.7
<i>M. vanicolensis</i> (Valenciennes)		1			1		2	33.3
<i>Parupeneus barberinoides</i> (Bleeker)			1				1	16.7
<i>P. barbinus</i> (Lacépède)		7					2	33.3
<i>P. bifasciatus</i> (Lacépède)	4	11	5	3	5	3	6	100.0
<i>P. cyclostomus</i> (Lacépède)	1	5		1	2	2	5	83.3



## APPENDIX (continued)

FAMILY/SPECIES	LOCALITY <sup>a</sup>						TOTAL	%
	T	H	M	P	S	F		
<i>P. indicus</i> (Shaw)		1					1	16.7
<i>P. multifasciatus</i> (Quoy & Gaimard)	2	12	3	2	2	2	6	100.0
Pempheridae								
<i>Parapriacanthus ransonneti</i> (Steindachner)		1					1	16.7
<i>Pempheris ovalensis</i> Cuvier	1		2	1	3		4	66.7
Kyphosidae								
<i>Kyphosus cinerascens</i> (Forskål)	4	3	2	1	3	4	6	100.0
<i>K. vaigiensis</i> (Quoy & Gaimard)	1	2	1		1		4	66.7
Chaetodontidae								
<i>Chaetodon auriga</i> Forsskål	4	7	3	3	3	3	6	100.0
<i>C. baronessa</i> Cuvier	1	5	2		1		4	66.7
<i>C. bennetti</i> Cuvier	1	6	2	1	3		5	83.3
<i>C. citrinellus</i> Cuvier		5	1	2	1	1	5	83.3
<i>C. ephippium</i> Cuvier	6	11	4	2	6	3	6	100.0
<i>C. kleini</i> Bloch	3	14	6	4	2	4	6	100.0
<i>C. lineolatus</i> Cuvier	2	4	1	1			4	66.7
<i>C. lunulu</i> (Lacépède)	3	1	4	4	3	3	6	100.0
<i>C. melannotus</i> Bloch	3	7	3	3	3	2	6	100.0
<i>C. meyeri</i> Schneider	1	4	4	1	3	2	6	100.0
<i>C. octofasciatus</i> Bloch	2	4					2	33.3
<i>C. ornatisimus</i> Solander	1	1				2	3	50.0
<i>C. oxycephalus</i> Bleeker	3	2	2	3	6		5	83.3
<i>C. punctatofasciatus</i> Cuvier	1	1	1	1	6	1	6	100.0
<i>C. raffelii</i> Bennett	2	9	2				3	50.0
<i>C. reticulatus</i> Cuvier	1		4	3	6	3	5	83.3
<i>C. semelon</i> Bleeker	1	9	2		3	1	5	83.3
<i>C. speculum</i> (Kuhl & Van Hasselt)	6	3	1	2	4	3	6	100.0
<i>C. trifasciatus</i> (Quoy & Gaimard)	3	6	4	3	2	1	6	100.0
<i>C. trifasciatus</i> Park	3	12	2		1		4	66.7
<i>C. ulietensis</i> Cuvier	2	7	1	2	5	3	6	100.0
<i>C. unimaculatus</i> Bloch		2		3	2	1	4	66.7
<i>C. vagabundus</i> L.	2	8	6	4	3		5	83.3
<i>Chaetodon</i> sp.**	1						1	16.7
<i>Forcipiger flavissimus</i> Jordan & McGregor	3	4	3	2	5	3	6	100.0
<i>F. longirostris</i> (Broussonet)	4	3	1	1	1	3	6	100.0
<i>Hemitaurichthys polylepis</i> (Bleeker)	2	6	3	3	3	3	6	100.0
<i>Hemiochus acuminatus</i> (L.)	1	3	2	1	1		5	83.3
<i>H. chrysostomus</i> Cuvier	3	7	1	2	3	2	6	100.0
<i>H. monoceros</i> Cuvier	3	5			1	3	4	66.7
<i>H. singularis</i> Smith & Radcliffe	1		2	2	2		4	66.7
<i>H. varhus</i> Cuvier	2	5	2		2	1	4	66.7
Pomacanthidae								
<i>Apolemichthys trimaculatus</i> (Lacépède)	2		6	4	4	4	5	83.3
<i>Centropyge bicolor</i> (Bloch)		9	6	3	1	1	5	83.3
<i>C. bispinosus</i> (Günther)	1	6	1	1	3		5	83.3
<i>C. flavicauda</i> Fraser-Brunner			1			1	2	33.3
<i>C. loriculus</i> (Günther)	1				1		2	33.3
<i>C. multifasciatus</i> (Smith & Radcliffe)	2	2	1				3	50.0
<i>C. shepardi</i> * Randall & Yasuda	4						1	16.7
<i>C. tibicen</i> (Cuvier)		3	2	1	1	1	5	83.3
<i>C. vrolicki</i> (Bleeker)	5	10	7	3	5	4	6	100.0
<i>Fygoplites diacanthus</i> (Boddaert)	6	13	6	4	6	4	6	100.0
<i>Chaetodontophus mesoleucus</i> (Bloch)		5					1	16.7
<i>Pomacanthus imperator</i> (Bloch)	3	5	3	4	3	2	6	100.0
<i>P. navarchus</i> (Cuvier)		3					1	16.7

## APPENDIX (continued)

FAMILY/SPECIES	LOCALITY <sup>a</sup>						TOTAL	%
	T	H	M	P	S	F		
<b>Pomacentridae</b>								
<i>Amphiprion chrysopterus</i> Cuvier	3	5					3	50.0
<i>A. clarki</i> (Bennett)		1	3		2	2	4	66.7
<i>A. frenatus</i> ** Brevoort		1					1	16.7
<i>A. melanopus</i> Bleeker		3					1	16.7
<i>A. peridaeraion</i> Bleeker	1	1	3	1			4	66.7
<i>A. ocellaris</i> ** Cuvier	1	3					2	33.3
<i>Amphiprion</i> sp.**		1					1	16.7
<i>Chromis acares</i> Randall & Swardloff	2	3	3	3	4	2	6	100.0
<i>C. agilis</i> Smith	1	2	2			1	4	66.7
<i>C. alpha</i> Randall	1						1	16.7
<i>C. amboinensis</i> (Bleeker)		2	1		1		3	33.3
<i>C. analis</i> (Cuvier)	2	5	2	1	4	2	6	100.0
<i>C. atripectoralis</i> Welander & Schultz		4			1		3	50.0
<i>C. atripes</i> Fowler & Bean	1	5	1			1	5	83.3
<i>C. caudalis</i> Randall	1	4	1		1	1	5	83.3
<i>C. delta</i> Randall	3	4	1		3	1	5	83.3
<i>C. elerae</i> Fowler & Bean		1			1		2	33.3
<i>C. lepidolepis</i> Bleeker	3	6	2	3	5	2	6	100.0
<i>C. margaritifer</i> Fowler	1	1	3	4	3	4	6	100.0
<i>C. retrofasciata</i> Weber	1	7	1		3		4	66.7
<i>C. ternatensis</i> Bleeker	1	10	3	2	3	1	6	100.0
<i>C. viridis</i> Cuvier		5					1	16.7
<i>C. weberi</i> Fowler & Bean	4	4	4	1	1	1	6	100.0
<i>C. xanthochir</i> (Bleeker)	4	11	6	2	6	2	6	100.0
<i>C. xanthura</i> (Bleeker)	7	14	6			2	5	83.3
<i>Dascyllus aruanus</i> (L.)	2	7					2	33.3
<i>D. melanurus</i> Bleeker		3	1				3	33.3
<i>D. reticulatus</i> (Richardson)		4	4	3	4	2	5	83.3
<i>D. trimaculatus</i> (Rüppell)	5	7	8	4	6	3	6	100.0
<i>Lepidozygus tapeinosoma</i> (Bleeker)	1	4	2		2		4	66.7
<i>Abudefduf notatus</i> (Day)			1		1		2	33.3
<i>A. septemfasciatus</i> (Cuvier)	2						1	16.7
<i>A. sexfasciatus</i> (Lacépède)				1			1	16.7
<i>A. sordidus</i> (Forsskål)	1		2	1			3	50.0
<i>A. vaigensis</i> (Quoy & Gaimard)	1		4	3	2	2	5	83.3
<i>Amblyglyphidodon aureus</i> (Cuvier)	3	9	4	2	3	1	6	100.0
<i>A. curacao</i> (Bloch)	3	12	1		1		4	66.7
<i>A. leucogaster</i> (Bleeker)		1	2		3	1	3	66.7
<i>A. ternatensis</i> (Bleeker)			2			1	2	33.3
<i>Cheiloprion labiatus</i> (Day)	5		1		1		3	50.0
<i>Chrysiptera biocellata</i> (Quoy & Gaimard)			2				3	50.0
<i>C. cyanea</i> (Quoy & Gaimard)	2	6	3		1	1	5	83.3
<i>C. glauca</i> (Cuvier)	1		1				2	33.3
<i>C. leucopoma</i> (Lesson)	1	2	2	2		1	5	83.3
<i>C. leucopoma amabilis</i> (Lesson)	2	2	1				4	66.7
<i>C. oxycephala</i> (Bleeker)	2	4	2	3	4	2	6	100.0
<i>C. rex</i> (Snyder)	1	3	1				3	50.0
<i>C. talboti</i> (Allen)		2	1				2	33.3
<i>C. traceyi</i> (Woods & Schultz)			1				2	33.3
<i>C. unimaculata</i> (Cuvier)	1	2	1				3	50.0
<i>Dischistodus chrysopoecilus</i> (Schlegel & Müller)	1	4	1				3	50.0
<i>D. melanotus</i> (Bleeker)	1	2					2	33.3
<i>D. perspicillatus</i> (Cuvier)	1	5					2	33.3
<i>Hemiglyphidodon plagiometapon</i> (Bleeker)		4					1	16.7
<i>Neopomacentrus violascens</i> * (Bleeker)		1					2	33.3

## APPENDIX (continued)

FAMILY/SPECIES	LOCALITY <sup>a</sup>						TOTAL	%
	T	H	M	P	S	F		
<i>Neoglyphidodon melus</i> (Cuvier)	1	9					2	33.3
<i>N. nigroris</i> (Cuvier)		1					1	16.7
<i>Plectroglyphidodon dickii</i> (Lienard)	6	12	6	2	5	4	6	100.0
<i>P. imparipennis</i> (Vaillant & Sauvage)	1		1				2	33.3
<i>P. johnstonianus</i> (Fowler & Ball)			1		4	1	3	50.0
<i>P. lacrymatus</i> (Quoy & Gaimard)	5	4	4	2	6	2	6	100.0
<i>P. leucozona</i> (Bleeker)	4	2		1			3	50.0
<i>Pomacentrus amboinensis</i> Bleeker		4		1	3		3	50.0
<i>P. bankanensis</i> (Bleeker)	3	8	7	2	6	4	6	100.0
<i>P. brachialis</i> Cuvier	1	6	4		1		4	66.7
<i>P. burroughi</i> Fowler		1					1	16.7
<i>P. coelestis</i> Jordan & Starks	1	1	2				4	66.7
<i>P. grammorhynchus</i> Fowler	1	4					2	33.3
<i>P. moluccensis</i> Bleeker	3	5					2	33.3
<i>P. nigromanus</i> Weber	1	7					2	33.3
<i>P. pavo</i> (Bloch)		3			1		2	33.3
<i>P. philippinus</i> Evermann & Seale		7	3		1		4	66.7
<i>P. reidi</i> Fowler & Bean		1			1		2	33.3
<i>P. simsiang</i> Bleeker	1	5					2	33.3
<i>P. vaiuli</i> Jordan & Seale	1	1				1	3	50.0
<i>Pomacentrus</i> sp. 2						1	1	16.7
<i>Stegastes albifasciatus</i> (Schlegel & Müller)	1						2	33.3
<i>S. fasciolatus</i> (Ogilby)	3	3	5	2	6	2	6	100.0
<i>S. lividus</i> (Bloch & Schneider)	1	1					2	33.3
<i>S. nigricans</i> (Lacépède)	1		1				2	33.3
Mugilidae								
<i>Crenimugil crenilabris</i> (Forsskal)							1	16.7
<i>Liza ceramensis?</i> (Bleeker)		1	1				2	33.3
<i>Oedalechilus labiatus?</i> (Valenciennes)			1				1	16.7
Labridae								
<i>Bodianus axillaris</i> (Bennett)	4	3	5	2	5	3	6	100.0
<i>B. bimaculatus</i> Allen			1				1	16.7
<i>B. diana</i> (Lacépède)	5	8	6	4	4	3	6	100.0
<i>B. mesothorax</i> (Schneider)	2	4		1	2		4	66.7
<i>Choerodon fasciatus</i> ** (Günther)		1					1	16.7
<i>Pseudodax moluccanus</i> (Valenciennes)	2	1			1		3	50.0
<i>Cheilinus chlorourus?</i> (Bloch)		1					1	16.7
<i>C. fasciatus</i> (Bloch)		14	2	1		1	4	66.7
<i>C. oxycephalus</i> Bleeker		4	1		1	1	4	66.7
<i>C. trilobatus</i> Lacépède	2	2	1				3	50.0
<i>C. undulatus</i> Rüppell	4	7	3	2	3	1	6	100.0
<i>Oxycheilinus arenatus</i> (Valenciennes)		4	5		2	1	5	83.3
<i>O. celebicus</i> (Bleeker)	2	6	2				3	50.0
<i>O. diagrammus</i> (Lacépède)	1	4		1			3	50.0
<i>O. orientalis</i> (Günther)		3					1	16.7
<i>O. unifasciatus</i> (Streets)	6	6	4	3	3	2	6	100.0
<i>Epibulus insidiator</i> (Pallas)	3	14	4		2		4	66.7
<i>Epibulus</i> sp. 2							1	16.7
<i>Novuculichthys taeniorus</i> (Lacépède)			1	1		1	3	50.0
<i>Cirrhilabrus cyanopleura</i> (Bleeker)	3	2		2			3	50.0
<i>C. exquisitus</i> Smith	2	2	4		6	3	5	83.3
<i>C. rubrimarginatus</i>		3					1	16.7
<i>Pseudochellinus evanidus</i> Jordan & Evermann		8	1			1	3	50.0
<i>P. hexataenia</i> (Bleeker)	4	6	6	3	5	4	6	100.0
<i>P. octotaenia</i> Jenkins	1	2					2	33.3
<i>Anampses caeruleopunctatus</i> Rüppell	3	2	5	2		3	6	100.0

## APPENDIX (continued)

FAMILY/SPECIES	LOCALITY <sup>a</sup>						TOTAL	%
	T	H	M	P	S	F		
<i>A. geographicus</i> Valenciennes						1		16.7
<i>A. melanurus</i> Bleeker	4	2	1	3	3	2	6	100.0
<i>A. meleagrides</i> Valenciennes	2	1				1	4	66.7
<i>A. twisti</i> Bleeker	3	9	4	1	3	1	6	100.0
<i>Coris aygula</i> Lacépède				1	1		2	50.0
<i>C. gabnardi</i> (Quoy & Gaimard)			4		4	3	5	83.3
<i>C. variegata</i> (Rüppell)		3	2		1		3	50.0
<i>Gomphosus varius</i> Lacépède	6	12	5	3	6	4	6	100.0
<i>Halichoeres biocellatus</i> * Schultz	1						2	33.3
<i>H. chloropterus</i> (Bloch)			1	2			2	33.3
<i>H. chrysus</i> Randall	3	4	5	1	4	2	6	100.0
<i>H. hortulanus</i> (Lacépède)	5	11	5	4	6	3	6	100.0
<i>H. margaritaceus</i> (Valenciennes)		6	1	1			3	50.0
<i>H. marginatus</i> Rüppell	1	5	1				3	33.3
<i>H. melanurus</i> (Bleeker)	4	6	3	3	3	2	6	100.0
<i>H. melasmapomus</i> Randall	1	2	1				3	50.0
<i>H. prosopion</i> (Bleeker)							3	50.0
<i>H. richmondi</i> Fowler & Bean		4					1	16.7
<i>H. scapularis</i> (Bennett)	1	3	1		1		4	66.7
<i>H. trimaculatus</i> (Quoy & Gaimard)	2	4	2		4	2	5	83.3
<i>Halichoeres</i> sp.		3	3		2	1	4	66.7
<i>Halichoeres</i> sp. 2	1			1			2	33.3
<i>Hemigymnus fasciatus</i> (Bloch)	3	5	5	2	2	1	6	100.0
<i>H. melapterus</i> (Bloch)	1	7	1				3	50.0
<i>Hologymnosus doliatus</i> (Lacépède)				1		1	2	33.3
<i>Macropharyngodon meleagris</i> (Valenciennes)	1	1	4	1	2	2	6	100.0
<i>Pseudocoris yamashiroi</i> (Schmidt)			1		1		3	50.0
<i>Stethojulis bandanensis</i> (Bleeker)	2	4					3	50.0
<i>S. strigiventor</i> (Bennett)	1		1	1	4	3	6	100.0
<i>Thalassoma amblycephalum</i> (Bleeker)	7	12	4	3	6	3	6	100.0
<i>T. hardwicki</i> (Bennett)	6	14	4	3	5	4	6	100.0
<i>T. janseni</i> (Bleeker)	1	2	3	3	1		6	100.0
<i>T. lunare</i> (L.)	3	7	2	3	1	3	6	100.0
<i>T. lutescens</i> (Lay & Bennett)			2		4	2	4	66.7
<i>T. purpureum</i> (Forsskal)	2	1					2	33.3
<i>T. quinquevittatum</i> (Lay & Bennett)	5	6	5	3	6	4	6	100.0
<i>T. trilobatum</i> (Lacépède)	2		1				3	50.0
<i>Diproctacanthus xanthurus</i> (Bleeker)		7		1			5	83.3
<i>Labrichthys unilineatus</i> (Guichenot)		5	3		2		4	66.7
<i>Labroides bicolor</i> Fowler & Bean	5	12	5	3	5	3	6	100.0
<i>L. dimidiatus</i> (Valenciennes)	5	12	4	2	4	3	6	100.0
<i>L. pectoralis</i> Randall & Springer	7	5	3	2	2	2	6	100.0
<i>Labropsis micronesica</i> Randall		2	8	1	1		4	66.7
<i>L. xanthonota</i> * Randall		3					1	16.7
Scaridae								
<i>Calatomus carolinus</i> (Valenciennes)	1						1	16.7
<i>C. spinidens</i> (Quoy & Gaimard)		1					2	33.3
<i>Bolbometopon muricatum</i> (Valenciennes)		3					1	16.7
<i>Cetoscarus bicolor</i> (Rüppell)		8	3	1	4	1	6	100.0
<i>Hipposearus longiceps</i> (Valenciennes)		15	2	4		1	5	83.3
<i>Scarus altipinnis</i> (Steindachner)		4					1	16.7
<i>S. atropectoralis</i> Schultz	1	1		1	3	2	5	83.3
<i>S. bleekeri</i> (deBeaufort)	1	7	1	1			5	83.3
<i>S. bowersi</i> (Snyder)		9					1	16.7
<i>S. chaemeleon</i> Choat & Randall		4			1		2	33.3

## APPENDIX (continued)

FAMILY/SPECIES	LOCALITY*						TOTAL	%
	T	H	M	P	S	F		
<i>S. dimidiatus</i> Bleeker	4	10	2	3	3		5	83.3
<i>S. festivus</i> Valenciennes	1	6	1		1		5	83.3
<i>S. flavopectoralis</i> * Schultz		8			1		4	66.7
<i>S. forsteni</i> (Bleeker)	5	2	2	4	4	2	6	100.0
<i>S. frenatus</i> Lacépède	2	2	3	2			5	83.3
<i>S. ghobban</i> Forsskål		4	1		1		3	50.0
<i>S. globiceps</i> Valenciennes	1	7					2	33.3
<i>S. hypselopterus</i> Bleeker		2	1				2	33.3
<i>S. microrhinos</i> Bleeker	1	4			4	2	6	100.0
<i>S. niger</i> Forsskål	4	14	5		5	3	6	100.0
<i>S. oviceps</i> Valenciennes	3	2	2			2	4	66.7
<i>S. prasioignathos</i> Valenciennes		5	2				3	50.0
<i>S. psittacus</i> Forsskål		1					1	16.7
<i>S. quoyi</i> Valenciennes	3		1		2		3	50.0
<i>S. rivulatus</i> Valenciennes		1					1	16.7
<i>S. rubroviolaceus</i> (Bleeker)	3	9	6	3	5	4	6	100.0
<i>S. schlegeli</i> (Bleeker)		6	3	1			4	66.7
<i>S. sordidus</i> Forsskål	7	16	6	2	3		5	83.3
<i>S. spinus</i> Kner		2	1				2	33.3
<i>Scarus</i> sp*	1						1	16.7
<b>Pinguipedidae</b>								
<i>Parapercis clathrata</i> * Ogilby					2	2	2	33.3
<i>P. cylindrica</i> (Bloch)						1	1	16.7
<i>P. tetracantha</i> * (Jordan & Seale)	1						1	16.7
<i>P. xanthozona</i> (Bleeker)	1						1	16.7
<b>Trichonotidae</b>								
<i>Trichonotus</i> sp.*							1	16.7
<b>Tripterygiidae</b>								
<i>Helcogramma capitata</i> Rosenblatt					1		1	16.7
tripterygid 1							1	16.7
<b>Blenniidae</b>								
<i>Atrosalarius fuscus holomelas</i> (Günther)		1					1	16.7
<i>Cirripectes castaneus</i> (Valenciennes)	1	1					2	33.3
<i>C. perustus</i> Smith					1		1	16.7
<i>C. polyzona</i> (Bleeker)		1					1	16.7
<i>C. quagga</i> Fowler & Ball					1		1	16.7
<i>C. variolosus</i> (Valenciennes)	3		2		3		3	50.0
<i>Ecsenius bicolor</i> (Day)					1		1	16.7
<i>E. opsifrontalis</i> Chapman & Schultz		2					1	16.7
<i>E. yaeyumaensis</i> (Aoyagi)		1					1	16.7
<i>Ecsenius</i> sp.*		1					1	16.7
<i>E. sp. 2**</i>		1					1	16.7
<i>Entomacrodus caudofasciatus</i> (Regan)	2						1	16.7
<i>Entomacrodus</i> sp. ( <i>brevis</i> ?)		1					1	16.7
<i>Meiacanthus atrodorsalis</i> (Günther)		2					1	16.7
<i>M. grammistes</i> (Valenciennes)		5	1				2	33.3
<i>Petrosirtes mitratus</i> Rüppell		1					1	16.7
<i>P. xestus</i> Jordan & Seale			1				1	16.7
<i>Plagiotremus laudanus laudanus</i> (Whitley)		1					1	16.7
<i>P. rhynorhynchus</i> (Bleeker)	2	5					3	50.0
<i>P. tapeinosoma</i> (Bleeker)	3	7	1	2	2		5	83.3
<b>Callionymidae</b>								
<i>Diplagrammus goraensis</i> (Bleeker)		1					1	16.7
<b>Microdesmidae</b>								
<i>Nemaeleotris magnifica</i> Fowler	2	2	1	1	3	1	6	100.0

## APPENDIX (continued)

FAMILY/SPECIES	LOCALITY <sup>a</sup>						TOTAL	%	
	T	H	M	P	S	F			
<i>Parioglossus formosus</i> (Smith)		4					1	16.7	
<i>Ptereleotris evides</i> (Jordan & Hubbs)		3	1	3	4	2	6	100.0	
<i>P. zebra</i> (Fowler)				1				16.7	
Gobiidae									
<i>Amblyeleotris perioptalma</i> Bleeker							1	16.7	
<i>A. randalli</i> Hoesc & Steene		1					1	16.7	
<i>A. steinitzi</i> * (Klausewitz)		2					1	16.7	
<i>Cryptocentrus cinctus</i> (Herre)		1					1	16.7	
<i>C. octofasciatus</i> * Regan		1						16.7	
<i>Ctenogobius pomastictus</i> Lubbock & Pulonin							1	16.7	
<i>Lotilia graciliosa</i> Klausewitz		1					1	16.7	
<i>Amblygobius hectori</i> (Smith)		1					1	16.7	
<i>A. phalaena</i> (Valenciennes)		4					1	16.7	
<i>A. rainfordi</i> (Whitley)		3					1	16.7	
<i>Opolomus opolomus</i> (Valenciennes)		1						16.7	
<i>Signigobius biocellatus</i> Hoese & Allen							1	16.7	
<i>Valenciennesa strigata</i> (Broussonet)			7			2	1	3	50.0
<i>Valenciennesa</i> sp.	1								16.7
<i>Vanderhorstia ambanoro</i> * Fourmanoir		1							16.7
<i>Bathygobius fuscus fuscus</i> (Rüppell)							1		16.7
<i>Bryaninops amplus</i> Larson		1					1		16.7
<i>B. erythrops</i> * (Jordan & Seale)		1					1		16.7
<i>B. youngei</i> (Davis & Cohen)							1		16.7
<i>Eviota afeli</i> ?* (Jordan & Seale)			1				1		16.7
<i>E. bifasciata</i> Lachner & Karnella		1					1		16.7
<i>E. lachnbredert</i> Giltay	1						1		16.7
<i>E. melasma</i> Lachner & Karnella			1				1		16.7
<i>E. prasina</i> (Klunzinger)		1					2		33.3
<i>E. prasites</i> * Jordan & Seales		1	1				2		33.3
<i>E. queenslandica</i> ? Whitley		1					1		16.7
<i>Eviota</i> sp. ( <i>storthynx</i> ?)							1	1	16.7
<i>Eviota</i> sp. green spot		1	1	1	1			4	66.7
<i>Eviota</i> sp. green		4	1					2	33.3
<i>Eviota</i> sp. white		1	1		1			3	50.0
<i>Eviota</i> sp. white spotted		1						1	16.7
<i>Eviota</i> sp. orange/gold stripes		1						1	16.7
<i>Eviota</i> sp. gold spots		1						1	16.7
<i>Eviota</i> sp. black head/white spot		1						1	16.7
<i>Eviota</i> sp. yellow head		1						1	16.7
<i>Eviota</i> sp. pale orange/white spots		1						1	16.7
<i>Eviota</i> sp. orange head		1						1	16.7
<i>Eviota</i> sp. clear orange		1	2		2			4	66.7
<i>Exyrias belissimus</i> (Smith)		1						1	16.7
<i>Fusigobius neophytus</i> (Günther)			1					1	16.7
<i>Gnatholepis</i> sp. ( <i>anjerenensis</i> ?)*	1	1						1	33.3
<i>Gnatholepis</i> sp.*	3	5	2		1			4	66.7
<i>Gobiodon okinawae</i> Sawada, Arai & Abe		5						1	16.7
<i>Istigobius decoratus</i> * (Herre)						1	1	2	33.3
<i>I. ornatus</i> (Rüppell)	1	1						2	33.3
<i>I. rigilius</i> * (Herre)			1					1	16.7
<i>Paragobiodon echinocephalus</i> (Rüppell)	2	2					2	5	83.3
<i>P. lacunicolus</i> * (Kendall & Goldsborough)		1						1	16.7
<i>Trimma naudei</i> * Smith	1							1	16.7
<i>T. okinawae</i> * (Aoyagi)		1						1	16.7
<i>Trimma</i> sp.	1	1						2	33.3



## APPENDIX (continued)

FAMILY/SPECIES	LOCALITY <sup>a</sup>						TOTAL	%
	T	H	M	P	S	F		
Bothidae								
<i>Bothus</i> sp.*		1						16.7
Balistidae								
<i>Balistapus undulatus</i> (Mungo Park)	6	11	5	4	6	2	6	100.0
<i>B. conspicillum</i> (Bloch & Schneider)	2	3	5	3	2	2	6	100.0
<i>B. viridescens</i> (Bloch & Schneider)	6	6	6	3	4	3	6	100.0
<i>Melichthys niger</i> (Bloch)	4	7	4	2	2	3	6	100.0
<i>M. vidua</i> (Solander)	5	6	5	4	5	1	6	100.0
<i>Odonus niger</i> (Rüppell)	2	2	5	3	3	4	6	100.0
<i>Pseudobalistes flavimarginatus</i> (Rüppell)	2	2	3	2	1	2	6	100.0
<i>Rhinecanthus aculeatus</i> (L.)	1	1					2	33.3
<i>R. rectangularis</i> (Bloch & Schneider)	4	2		1			3	50.0
<i>Sufflamen bursa</i> (Bloch & Schneider)	1	1	3	4	4	3	6	100.0
<i>S. chrysoptera</i> (Bloch & Schneider)		1			1	2	4	66.7
<i>Xanthichthys auromarginatus</i> (Bennett)	2		2	1	1			83.3
Monacanthidae								
<i>Ahlueterus scriptus</i> (Osbeck)		1		1			2	33.3
<i>Cantherhines damerilii</i> (Hollard)			2			1	2	33.3
<i>C. pardalis</i> (Rüppell)					1		1	16.7
<i>Parahuterus prionurus</i> (Bleeker)	1						1	16.7
<i>Pervagor janthinosoma</i> (Bleeker)		1				1	2	33.3
Ostraciidae								
<i>Ostracion cubicus</i> L.	1	3			1		4	66.7
<i>O. meleagris meleagris</i> Shaw	4		1	1	3		4	66.7
<i>O. solorensis</i> Bleeker		1					2	33.3
Tetraodontidae								
<i>Arothron mappa</i> (Lesson)					1		1	16.7
<i>A. nigropunctatus</i> (Bloch & Schneider)	1	1		1			3	50.0
<i>A. nigropunctatus</i> (gold) (Bloch & Schneider)		1		1	1		3	50.0
<i>A. stellatus</i> (Bloch & Schneider)						1	1	16.7
<i>Canthigaster bennetti</i> (Bleeker)		1					1	16.7
<i>C. valentini</i> (Bleeker)		1					1	16.7
Diodontidae								
<i>Diodon hystrix</i> L.	1					1	2	33.3
<i>Chilomycterus reticulatus</i> * 1.			1				1	16.7

<sup>a</sup>T, Tobi; H, Helen Reef; M, Merir; P, Pulo Anna; S, Sonsorol; F, Fanna.

\*, New record.

\*\*, New record for Micronesia.

#, Species observed other than on transects and not included in analyses.

Values indicate the number of transects where the species was observed at each locality. Total is the number of localities where the species was observed. Percent is the proportion of localities where the species was observed × 100.