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High islands versus low islands: a comparison of fish faunal composition of the Palau Islands

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Synopsis

High islands, with potentially greater habitat diversity, are expected to have greater species richness and diversity compared to low islands, typically atolls and coral islands of lower habitat diversity, within the same geographical area. Patterns of species similarity, richness, and diversity were compared among coral reef fishes between the low island of the Southwest Palau Islands (SWPI), and the low and high islands of the Main Palauan Archipelago (MPA). Data from diurnal visual transects accounted for approximately 64% and 69% of the shorefish faunas known from the SWPI and MPA, respectively. Two distinct fish faunas were representative of low and high islands. The first was confined to the coral islands of the SWPI. The second was partitioned into both low and high islands of the MPA, and Helen Reef, a large atoll in the SWPI. The second type was clustered into atolls, low islands with atoll-like barrier reef systems, a coral island, and three high island systems, one with an extensive barrier reef system. Contrary to the prediction that high islands, with relatively greater habitat diversity, would have greater species richness and diversity, species richness and diversity were greatest at Kossol, a large atoll-like 'low island' locality at the northern end of a high island in the MPA, followed by two atolls, Kayangel (MPA, north of Kossol) and Helen Reef. In contrast, species richness and diversity were lower at high island localities and lowest at small coral islands. These results suggest that habitat diversity for reef fishes increases as a function of increasing area regardless of whether the locality is a high or low island.

Introduction

The Palau Islands (Republic of Belau, Micronesia) are a remarkably diverse assemblage of tropical high islands, low coral islands, atolls, and submerged, relatively shallow offshore reefs. Two distinct archipelagos are within this group: the Main Palauan Archipelago (MPA) and the Southwest Palau Islands (SWPI) (see Donaldson 1996, figure 1). The MPA extends from Velasco Reef south to Angaur Island, a distance of approximately 125 km. This group consists of 580 islands. The SWPI are located ca. 300–600 km southwest of the MPA and about 250 km northeast of Halmahera, Indonesia. The SWPI consist of one atoll, Hotsarihie or Helen Reef, and five low-lying coral islands. Together, the MPA and SWPI support a highly diverse fish fauna and certainly the richest in all of Micronesia (Myers 1999, Donaldson 1996). This diversity is a likely consequence of the island's geographical position at the margin of the Philippine and Pacific plates, the presence of the MPA within the Belau–Caroline Islands Corridor (Springer 1982, Myers 1989, 1999) and their proximity, particularly the SWPI, to the Indo-Malayan area. This area, the so-called 'Indo-Malayan Center of Diversity', consists of a highly diverse region bound by the Malay

Peninsula, the Philippines, Indonesia, and New Guinea (Briggs 1974, Woodland 1983, Donaldson 1986).

Ecological theory predicts that species diversity increases with increased habitat complexity or diversity and greater numbers of habitat types (Ricklefs 1973, Roughgarden 1996). Alternately, species diversity may increase as a function of area or some effect of scale (e.g., Anderson et al. 1981, Williams 1991), geographical location (Thresher 1991) or random processes (see review in Sale 1991). The MPA has greater area, greater numbers of habitat types, and relatively greater habitat diversity compared with the SWPI (Donaldson 1996). The diversity of habitat types in the MPA is rather exceptional, and includes fringing, barrier and patch reefs, reef walls, mangrove forests, sea grass flats, mud flats, sand and rubble flats, emergent limestone islets (i.e., 'Rock Islands'), estuaries, freshwater streams, and freshwater and marine lakes. The SWPI, however, has fewer habitat types, and these are consistent with atolls or low coral islands. Habitat types associated with high islands, e.g., mud flats, extensive mangrove forests, estuaries, and well-developed freshwater lakes and streams, are absent. Species richness and diversity are predicted to be greater in the MPA than in the SWPI. Within the SWPI however, a single locality, Hotsarihie Atoll (Helen Reef), has a large area of approximately 105 km^2 (Donaldson 1996). Here, relatively high levels of species richness and diversity exist that are certainly higher than other localities within the SWPI (Donaldson 1996). Levels of species richness and diversity are comparable with or may exceed those found in some geographically distinct areas within the MPA.

The fishes of the SWPI were surveyed earlier during the Southwest Palau Islands Expedition (Maragos,[1] Donaldson 1996). Two subsequent surveys were conducted in the MPA, both part of the Palau Islands Rapid Ecological Assessment (summarized in Maragos & Cook 1995). These surveys provided an opportunity to measure biodiversity of non-cryptic largely diurnal fish species and compare levels of species richness, diversity, and similarity between low and high island localities. Results of these surveys are presented here and compared with those obtained from the SWPI.

[1] Maragos, J.E. (ed.) 1993. Natural and cultural resources survey of the Southwest Palau Islands. Part 1: Rapid ecological assessment of Palau. Report submitted to the Ministry of Resources and Development, Republic of Belau, The Nature Conservancy, Honolulu. 62 pp.

Materials and methods

Surveys

Fishes were surveyed visually with the 'Rapid Ecological Assessment' (REA) technique (Maragos 1993, Maragos & Cook 1995, Donaldson 1996) to determine the presence–absence of species. This method consisted of timed swims (visual transects) with scuba or by snorkeling along a depth gradient at each station. Generally, transect surveys were 30 min, commenced at a depth of 20–25 m, rarely at 40 m, and ascended at a steady pace until the shallowest possible depth was reached. Usually, the first 15 min were spent below 10–15 m and the second between 10–15 m and the surface. For stations surveyed by snorkeling, depths ranged between 0.5 and 1.5 m. Two inshore reef flat stations at the island of Merir (SWPI) could be surveyed only by walking at low tide and observing fishes sheltering in tide pools and pockets. Reef topography, currents, and surface conditions ultimately determined overall length and actual depths at the onset and completion of each transect. Occasionally, reef margins could not be surveyed because of heavy surf.

A total of 132 stations at 13 localities was surveyed. Six localities and 56 stations were surveyed in the SWPI during June 1992 (Donaldson 1996). Seven localities were arbitrarily designated for the MPA, from which a total of 76 stations was surveyed during two expeditions in August and September–October 1992. High and low island designations followed Maragos & Cook (1995). In the MPA, three high island and four low island localities were recognized. All localities within the SWPI were considered low islands. Some localities were easily delineated (i.e., SWPI and Angaur). Boundaries of others were arbitrarily designated under the REA survey plan. Consequently, stations at Kayangel also included Ngeruangl Atoll and Velasco Reef. Kossol consisted of reefs north Ngerechur-Ngerkeklau (east) and Ebil Passage (west) at the northern tip of Babeldoab Island. Eastern Babeldoab extended along the barrier reef and inner reef flats south of Ngerechur-Ngerkeklau as far as the bay at Ngeream. Western Babeldoab included the barrier reef, passes, selected patch reefs, and reef flats south as far as Aimeliik. Koror/Rock Islands included patch reefs, rock islands, reef flats, passes, and barrier reefs from Koror south to the Marine Lakes area of the Southern Rock Islands. Peliliu/South consisted of the barrier reef, passages, channels, and reef flats south of Denges Passage in the east and Mutkebesang in the

west to the reef at the tip of Peliliu. Details are given in Maragos (1993) and Maragos & Cook (1995).

Data were recorded on underwater paper and by underwater photography. Species were identified to the lowest taxon possible. Identifications were confirmed from Masuda et al. (1984), Smith & Heemstra (1986), Myers (1989), Randall et al. (1990), Allen (1991), Randall & Heemstra (1991), and Kuiter (1992). Subsequently, name changes were made following Eschmeyer (1998) and Myers (1999).

Physical and logistical limitations prevented making accurate counts of each species observed on a transect. Large numbers of species and individuals were encountered at many stations. Therefore, only presence–absence data for each species at each station in a given locality were obtained. Some taxa (e.g., Cirrhitidae, Labridae of the genera *Cheilinus* and *Oxycheilinus*, Pinguipedidae, Pomacanthidae, Scorpaenidae, and Serranidae) were quantified, however, by enumerating all individuals on a given transect. These data will be presented elsewhere (Donaldson unpublished). Logistics also dictated that surveys be undertaken during daylight hours (7:00–18:30 h), and so nocturnal species were poorly sampled. Because surveys were confined to relatively shallow waters (<40 m) and were conducted without the use of ichthyocides or other capture techniques, pelagic, deep reef, and cryptic species also were poorly sampled, and freshwater species not at all.

Analyses

Presence–absence data limit hypothesis testing. Therefore, analyses were simple but adequate to reflect patterns of species richness, species diversity, evenness, and similarity in species composition between localities. These patterns have utility in comparisons between low and high islands.

Similarity of species composition between localities was measured by pair-wise 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 similarity) to 1.0 (complete similarity). This index is considered the most robust for presence–absence data (Magurran 1988), although some caution should be used in its interpretation because strict criteria for its evaluation remain to be well defined (Sale 1991). Relationships between localities were examined by subjecting a matrix of locality similarity values to cluster analysis (Complete linkage, CLUSTER procedure, SYSTAT vers. 7[2]).

Species richness (SR) was measured as the number of species at each station and the total number of species for each locality. Values within and between localities were analyzed with pair-wise chi-square tests. The null hypothesis in each instance was that values of species richness between stations or localities were equivalent. Because accurate measures of the area of localities sampled could not be made, the number of stations sampled per locality was an indirect measure of locality size. The relationship between this measure and species richness was determined by calculation of Spearman's non-parametric correlation coefficient (Sokal & Rohlf 1981).

Species diversity was measured with the Shannon Index of Diversity (Magurran 1988), modified to reflect proportional representation of a species at each locality and based upon the number of stations within the locality where the species occurred. Thus, the index was 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 differences in pair-wise comparisons of H' between localities. The null hypothesis was that H' was equivalent between localities. The relationship between H' and the number of stations per locality was examined by calculation of the Spearman's non-parametric correlation coefficient (Sokal & Rohlf 1981).

Results

Faunal composition

A total of 823 species of fishes was observed on transects in the MPA and SWPI combined. This number comprised 64.4% of the known reef fish fauna and 59.3% of the total fish fauna for the Palau Islands (Myers 1999). Of these, 733 species (57.4% reef and 52.9% total) were observed in the MPA and 596 species

[2] SYSTAT, vers. 7.0. 1997. SPSS Inc., Chicago.

(46.6% reef and 43% total) were observed in the SWPI. Again, most cryptic, nocturnal, deep slope, and pelagic species were largely absent from transects. Freshwater species were not surveyed. A spreadsheet of species presence–absence at each station and each locality is available from the author.

Species similarity

Patterns of association between localities are indicated in a dendrogram (Figure 1) generated from the cluster analysis of the index matrix (Table 1). Two major clusters, representing fish faunas of high and low islands, were indicated. The first cluster consisted of low coral islands of the SWPI. The second consisted of high and low islands of the MPA, plus Helen Reef of the SWPI. The second cluster was partitioned as follows: a high island with an extensive barrier reef system (West Babeldoab), a large atoll (Helen Reef), and two high islands (East Babeldoab and Koror/Rock Islands); a low coral island (Angaur), and three low islands sites consisting of an atoll (Kayangel) an 'atoll-like' barrier reef and lagoon system (Kossol), and an extensive barrier reef–coral island system (Peleliu/South).

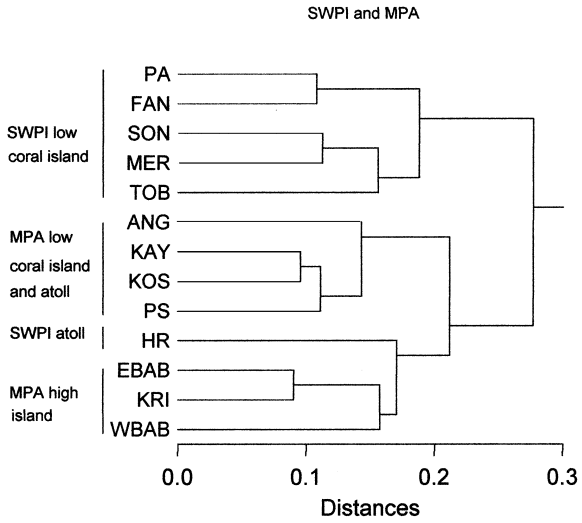

Figure 1. Clustering of SWPI and MPA fish faunas. Locality codes are defined in Table 1.

Geographical patterns of species richness and diversity

Species richness for MPA and SWPI localities is summarized in Table 2. Species richness was greatest at Kossol, an atoll-like 'low island' locality at the northern end of a high island in the MPA, followed by two atolls, Kayangel (MPA, north of Kossol) and Helen Reef. In contrast, species richness and diversity were lower at high island localities and lowest at small coral islands. Differences between high MPA and SWPI localities were significant in all but 22.2% of pair-wise comparisons (Table 3). Differences between high MPA and low MPA localities were significant in all but 25% of pair-wise comparisons. Differences between low MPA and SWPI localities were significant in all but 12.5% of pair-wise comparisons.

Table 1. Matrix of Sorenson Qualitative Similarity Index values from pair-wise comparisons of species composition between SWPI and MPA localities.

	Locality												
	TOB	HR	MER	PA	SON	FAN	ANG	PS	KOS	KAY	KRI	EBAB	WBAB
TOB	X	0.62	0.69	0.60	0.64	0.58	0.63	0.65	0.64	0.62	0.53	0.63	0.53
HR		X	0.59	0.49	0.57	0.49	0.58	0.68	0.69	0.65	0.61	0.66	0.59
MER			X	0.63	0.74	0.61	0.61	0.62	0.59	0.60	0.50	0.59	0.53
PA				X	0.69	0.73	0.56	0.54	0.48	0.51	0.44	0.52	0.49
SON					X	0.71	0.61	0.58	0.56	0.57	0.47	0.57	0.49
FAN						X	0.59	0.52	0.51	0.52	0.44	0.52	0.49
ANG							X	0.68	0.69	0.71	0.54	0.62	0.59
PS								X	0.74	0.73	0.64	0.74	0.66
KOS									X	0.77	0.67	0.70	0.68
KAY										X	0.62	0.65	0.65
KRI											X	0.85	0.64
EBAB												X	0.65
WBAB													X

Locality abbreviations are: TOB = Tobi, HR = Helen Reef, MER = Merier, PA = Pulo Anna, SON = Sonsorol, FAN = Fanna, ANG = Angaur, PS = Peleliu/South, KOS = Kossol, KAY = Kayangel, KRI = Koror/Rock Islands, EBAB = East Babeldoab, WBAB = West Babeldoab.

Species richness within high islands (Table 2) was greatest at Western Babeldoab and least at Eastern Babeldoab. Differences between localities were not significant in pair-wise comparisons of the three high island localities (Table 3). At low MPA islands, species richness was greatest at Kossol and least at Angaur. Differences between localities were significant in all pair-wise comparisons except for Kayangel–Kossol and Kayangel–Peleliu/South. In the low SWPI, species richness was greatest at Helen Reef and least at Fanna. Differences between localities were significant in all pair-wise comparisons except for Tobi–Merir, Merir–Sonsorol, and Pulo Anna–Fanna. There was a significant rank correlation between SR and the number of stations per locality ($r = 0.7777$, $p < 0.01$).

Mean species diversity (H', $+/-$ SD; data pooled for each locality type) was $H' = 1.4868$ (SD $= 0.1602$) for high MPA islands, $H' = 1.8605$ (SD $= 0.3282$) for low MPA islands, and $H' = 1.5738$ (SD $= 0.2725$) for the SWPI (Table 2). As with species richness, species diversity was greatest at Kossol, followed by two atolls, Kayangel and Helen Reef. Species diversity was lower at the remaining high and low island MPA localities, and lowest at the low coral islands of the SWPI. Differences were significant for all pair-wise comparisons between localities, except for Merir–Sonsorol, and Pulo Anna–Fanna (Table 4). Species diversity of specific localities in high islands (Table 2) was greatest at Eastern Babeldoab and least at Koror-Rock Islands. In the low MPA localities, species diversity was greatest at Kossol and least at Peleliu/South. In the low SWPI localities, species diversity was greatest at Helen Reef and least at Pulo Anna. There was a significant rank correlation between H' and the number of stations sampled per locality ($r_S = 0.9087$, $df = 12$, $p < 0.05$).

Fish species in the MPA and the SWPI varied proportionally in their distribution among islands within groups (Table 5). In the MPA, 22.7% of all species recorded were from the seven localities in this group, while 15.2% were recorded from a single locality. In the SWPI, 17.5% of all species were recorded from all six localities, while 35.6% were found at only a

Table 2. Summary of fish community composition at localities in the SWPI and MPA.

Locality	A	N	SR	H'	%
KAY	MPA	16	467	2.05	36.5
KOS	MPA	16	495	2.21	38.7
EBAB	MPA	11	337	1.67	26.4
WBAB	MPA	6	374	1.41	29.3
KRI	MPA	6	343	1.38	26.8
PS	MPA	7	424	1.49	33.2
ANG	MPA	8	346	1.68	27.1
HR	SWPI	22	488	1.99	38.2
TOB	SWPI	8	317	1.55	24.8
MER	SWPI	10	294	1.68	23.0
PA	SWPI	5	198	1.27	15.5
SON	SWPI	6	250	1.66	19.6
FAN	SWPI	5	195	1.29	15.3
High islands	MPA	23	351.3	1.49	
SD			19.9	0.16	
Low islands	MPA	47	433.0	1.86	
SD			64.9	0.33	
Low islands	SWPI	56	290.3	1.57	
SD			108.6	0.27	

A = archipelago, SR = species richness, H' = Shannon index of species diversity, and % = percentage of the total fauna known from the Palau Islands. SWPI data are from Donaldson (1996). SR and H' are mean values for high and low islands; SD is the standard deviation. Locality codes are defined in Table 1.

Table 3. Chi-square tests of pair-wise comparisons of species richness values between localities.

	Locality												
	KAY	KOS	EBAB	WBAB	KIR	PS	ANG	TOB	HR	MER	PA	SON	FAN
KAY	X												
KOS	0.8	X											
EBAB	21.0[a]	30.0[a]	X										
WBAB	10.3[b]	16.9[a]	1.9	X									
KRI	18.9[a]	27.6[a]	0.05	1.3	X								
PS	2.2	5.7[c]	9.7[b]	3.0[c]	8.4[b]	X							
ANG	18.0[a]	26.4[a]	0.01	1.1	0.01	7.7[b]	X						
TOB	14.4[a]	39.0[a]	0.6	4.7[c]	1.0	15.2[b]	1.3	X					
HR	0.5	0.1	27.6[a]	15.1[b]	25.3[b]	4.6[c]	24.2[a]	35.4[a]	X				
MER	39.3[a]	51.0[a]	2.9	9.6[b]	3.8	23.2[a]	4.9[c]	0.8	47.6[a]	X			
PA	108.8[a]	127.3[a]	36.1[a]	54.2[a]	38.9[a]	81.5[a]	40.3[a]	27.5[a]	122.6[a]	18.7[a]	X		
SON	65.7[a]	80.6[a]	12.9[b]	24.6[a]	81.5[a]	44.5[a]	15.5[b]	7.9[b]	76.8[a]	3.6	6.0[b]	X	
FAN	111.8[a]	130.4[a]	37.9[a]	56.3[a]	40.3[a]	84.1[a]	42.2[a]	29.1[a]	125.7[a]	20.0[a]	0.02	6.8[b]	X

Levels of significance are [a]$p < 0.001$, [b]$p < 0.01$, and [c]$p < 0.05$. Locality codes are defined in Table 1.

Table 4. Matrix of values for pair-wise comparisons of Shannon species diversity indices (H′) between localities.

	Locality												
	KAY	KOS	EBAB	WBAB	KIR	PS	ANG	TOB	HR	MER	PA	SON	FAN
KAY	X	958	795	812	794	842	812	729	907	712	653	714	661
KOS	2.6[b]	X	810	819	801	888	839	731	909	715	665	734	685
EBAB	6.6[a]	9.4[a]	X	706	678	678	673	636	812	616	534	586	529
WBAB	10.4[a]	13.0[a]	4.4[a]	X	716	678	693	686	860	664	570	615	557
KRI	11.2[a]	13.9[a]	4.9[a]	0.4	X	670	670	651	826	630	540	588	531
PS	10.5[a]	13.7[a]	3.4[a]	1.6	2.1[c]	X	729	590	768	574	539	612	573
ANG	6.7[a]	9.6[a]	0.2	4.8[a]	5.4[a]	3.9[a]	X	615	792	596	532	592	540
TOB	8.1[a]	10.6[a]	10.9[a]	3.1[b]	2.6[b]	0.9	2.3[c]	X	803	610	506	546	489
HR	0.8	3.3[a]	4.8[a]	8.3[a]	8.8[a]	7.9[a]	4.8[a]	6.3[a]	X	781	681	721	664
MER	6.2[a]	8.2[a]	0.2	4.4[a]	4.9[a]	3.4[a]	0.1	2.1[c]	4.5[a]	X	536	525	468
PA	14.8[a]	18.1[a]	7.9[a]	2.4[c]	2.1[c]	5.0[a]	8.5[a]	4.9[a]	11.5[a]	7.6 [a]	X	445	388
SON	7.3[a]	10.4[a]	0.2	4.5[a]	5.2[a]	3.6[a]	9.4[a]	2.0[c]	5.2[a]	0.4	8.5[a]	X	444
FAN	15.0[a]	18.4[a]	7.8[a]	2.2[c]	1.9	4.9[a]	8.6[a]	4.8[a]	11.5[a]	7.6[a]	0.4	8.6[a]	X

Lower numbers are t-test values; upper numbers are degrees of freedom. Levels of significance are [a]$p < 0.001$, [b]$p < 0.01$, and [c]$p < 0.05$. Locality codes are defined in Table 1.

Table 5. Proportional distribution of fish species in the SWPI (n = 6 localities; 596 species observed on transects) and the MPA (n = 7 localities; 745 species observed on transects). SWPI data are from Donaldson (1996).

Archipelago	No. of localities	No. of species	Percent total
SWPI	1	212	35.6
	2	102	17.1
	3	79	13.3
	4	54	9.1
	5	50	8.4
	6	104	17.5
MPA	1	166	22.7
	2	97	13.2
	3	90	12.3
	4	79	10.8
	5	82	11.2
	6	107	14.6
	7	112	15.2

single locality. In both cases, families having species with wide ranges of distribution (i.e., the Gobiidae) also had species with extremely narrow ranges.

Discussion

The fish faunas of the MPA and SWPI are highly diverse, with relatively low levels of endemism, and consist of over 96% of the Micronesian and 35% of all Indo-Pacific inshore fish species (Donaldson 1996, Myers 1999); factors that contribute towards explaining faunal composition at these localities are discussed in these articles. The fish faunas of the SWPI, especially Helen Reef, share a number of species with the MPA, but the archipelago, especially Helen Reef, also supports species with closer affinities to Indonesia in the south than to the MPA in the north or Micronesia to the east (Donaldson 1996).

Habitat heterogeneity has been shown previously to be a predictor of species richness (Boecklen 1986, Kulbicki et al. 1994). Greater diversity of habitats in the Palau Islands and SWPI should correspond to greater species richness and diversity (Donaldson 1996). Islands in relatively close geographical proximity to one another, and with similar degrees of habitat diversity, should also have similar fish faunas (Donaldson 1996) or suites of fishes (i.e., life history classes; Kulbicki 1996), while shifts in habitat structure from one area to the next should have corresponding changes in fish faunal structure (Anderson et al. 1981, Williams 1982, 1991, Williams & Hatcher 1983, Grimaud & Kulbicki 1998). High islands (i.e., Eastern Babeldoab and Koror/Rock Islands) have relatively greater habitat diversity, occur only in the MPA, and have similar fish faunas. Low islands, with relatively less habitat diversity, occur in both the MPA and the SWPI. Low island localities and their respective fish faunas include those characterized by barrier reef systems, i.e., Helen Reef, Kossol, Kayangel, and Peleliu/South, or coral island systems, i.e., Angaur, Sonsorol, Tobi, Merir, Fanna, and Pulo Ana. Western Babeldoab, with a broad barrier system and lagoon instead of broad fringing reef flats that are found in much of Eastern Babeldoab, has a fauna that appears

to bridge the gap between high islands and barrier reef-type low islands.

Central to this analysis is the assumption that the diversity of habitats increases with increased area surveyed. Although this relationship remains to be demonstrated here, a larger area, with a greater diversity of habitat types, would be expected to support a greater diversity of fish species (Ormond & Roberts 1997). The data presented here indicate that both SR and H′ increase with the number of stations surveyed in a given area and that this increase may be related to an inferred increase in habitat diversity within that area. This was especially true of larger low island areas with extensive reef development, such as Helen Reef, Kossol, Kayangel, and Pelelieu/South, and less so with high island localities, which were predicted to have greater species richness and diversity. In contrast, Donaldson (1996) found a significant rank correlation between fish species diversity and locality size but no correlation between diversity and the number of stations sampled within SWPI localities. The latter result differs from the analysis presented here and might be a consequence of a smaller sample size. Only six localities were sampled in the SWPI study. With the addition of seven MPA localities to the data set, the number of localities more than doubled. Further, with the exception of Helen Reef, the islands of the SWPI are relatively small, have relatively lower habitat diversity, and are surrounded by deep oceanic water compared to the localities surveyed in the MPA. Thus, greater area likely accounts for greater levels of habitat diversity and, hence, greater species richness and diversity. Truly quantitative analyses of the relationships between area, habitat diversity, and species richness and diversity between same-archipelago high and low islands, however, remain to be made.

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