

## Comparative Analysis of Reef Fish Distribution Patterns in the Northern and Southern Mariana Islands

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**Abstract** Distributions of reef fishes from the older (>35 myp) Southern (SMI) and younger (1-1.5 myp) Northern Mariana Islands (NMI) were compared. The SMI were distinguished by extensive habitat development, including barrier reefs, well-defined fringing reefs, lagoons, estuaries, mangrove stands, and freshwater streams and ponds. The NMI were distinguished by relatively poor reef development (except at western Anatahan, southern Sarigan, and parts of Pagan) on steep slopes, narrow but well-defined rocky reefs, and no estuaries, mangrove and freshwater habitats, although Pagan has two lacustrine bodies supporting a non-native tilipianine cichlid. Species and family richness were greatest in the SMI. Species composition was moderately similar, with a Sorenson Qualitative Similarity value of  $C_s=0.6371$ . Endemism was relatively low in both island groups. Differences in faunal composition and development are likely a function of the degree of habitat development in each group.

**Key words:** distribution, endemism, fauna, guild, macrohabitat, similarity, trophic, Mariana Islands.

The Mariana Islands are located in the Western Pacific between 12.6°-20.6°N latitude. They consist of 15 high islands, numerous small islets, banks, seamounts, and pinnacles stretching north to south over a distance of some 800 km (Myers, 1988). The islands occur along the margin of the Pacific and Philippine Plates and are bordered to the east by the Marianas Trench, and the west by seamounts of the West Marianas Ridge. The Marianas anchor the southern end of an arc that extends northward through the Volcano or Iwou Islands, the Ogasawara Islands, and the Izu Islands, the latter rising south and east of the Izu Peninsula of southern Honshu, Japan. For the purposes of this paper, the Marianas may be partitioned into two chains: the Southern (SMI—ca. 13°-16°N) and Northern Mariana Islands (NMI—ca. 16°-20.6°N).

The fish faunas of both have been documented previously, with most effort directed towards the more accessible SMI (*e.g.*, Kami *et al.*, 1968; Kami, 1971, 1975; Shepard and Myers, 1980; Myers and Shepard, 1980; Myers, 1988, 1989, in press; Myers and Donaldson, in press; see review in Myers, 1988). Recently, zoogeographic relationships of fishes of the Mariana

Islands and the faunas of the Ogasawara and Izu islands were examined (Donaldson *et al.*, 1994).

In this paper, I will argue that island group faunal composition is related to island group macrohabitat (=zone) complexity, which provides a greater arena for stochastic recruitment of larval forms. These forms settle and become members of different macrohabitat guilds. Thus, the number of macrohabitat types present in a group should be equivalent to the number of macrohabitat guilds of fishes occurring at that locality. There should, then, be a positive relationship between the number of guilds at a locality and species richness.

Further, greater macrohabitat complexity also provides potentially increased diversity in available food sources, thus offering the opportunity for greater trophic complexity and diversity in feeding guilds. This increased complexity and diversity likely also promotes increased species richness.

I predict that the SMI will have greater species richness because these islands have a greater age, a greater number of macrohabitats, and hence, greater trophic complexity, compared to the NMI. Greater species richness

in the SMI has already been demonstrated (Donaldson *et al.*, 1994). Here, additional taxa are included along with data on macrohabitat and trophic guild membership.

I will first summarize patterns of species richness, family richness, endemism, and faunal similarity between fish faunas of the SMI and NMI. I shall then provide a comparison of the representation of SMI and NMI fishes in macrohabitat and feeding guilds in relation to patterns of species richness.

### The Islands

The SMI are >35 myp (million years before present) in age, and largely consist of coralline limestone laid over volcanics. Their geology relevant to fishes is discussed in Myers (1988). Macrohabitat development is extensive, particularly on Guam and Saipan. Guam supports two barrier reefs, extensive fringing reefs, lagoons (Cocos and Apra Harbor) and protected embayments, patch reefs, cliff and cave habitats, estuaries, mangroves, sea grasses, and freshwater streams and ponds. Saipan supports a large barrier reef and lagoon, inshore and offshore patch reefs, fringing reefs, cliffs and caves, and seagrass beds, but estuaries, mangrove, and freshwater macrohabitats, though present, are much less well developed compared to Guam's. Rota, Tinian, Aguigan, and Farallon de Mendinilla are even less well developed, although fringing reefs are important at Rota and Tinian, with wave-swept pavement immediately offshore, and a well-developed reef slope occurs at Rota's protected Sasanhaya Bay. Cliff and cave development is variable from island to island, but cliffs are especially common on windward and exposed coasts. The SMI also includes offshore coral reefs or banks (*e.g.*, Galvez, Santa Rosa, and Marpi).

The NMI dates from 1–1.5 myp, and consists of four active volcanos (*e.g.*, Pagan, Uracus), apparently dormant volcanos (*e.g.*, Guguan), and the partially submerged remains of a caldera (Maug). NMI geology relevant to fishes is discussed in Myers (1988). Reef development is poor or non-existent, except below a depth of 25 m at western Anatahan and southern Sarigan, and at portions of Pagan, all more or

**Table 1.** Assignment of islands and offshore reefs or banks to the Southern (SMI) and Northern Mariana Islands (NMI). Scheme follows Donaldson *et al.* (1994), with slight modification.

Southern Mariana Islands	Northern Mariana Islands
Galvez Banks	Anatahan
Santa Rosa Banks	Sarigan
Guam	Guguan
Rota	Alamagan
Aguigan (Goat Island)	Zealandia Banks
Tinian	Pagan
Saipan	Agrihan
Marpi Reef	Asuncion
Farallon de Mendinilla	Maug
	Uracus
	(Farallon de Pajaros)

less southerly in distribution within the NMI. Most islands have macrohabitats distinguished by steep slopes, some limestone pavement (*e.g.*, Anatahan, Sarigan, Pagan, Alamagan), and rocky reefs. The latter often consist of submerged lava flows or clusters of large boulders, with some coral growth. Cliff and cave development is variable, but includes a relatively large open cave, some 20 m deep, on the southeast coast of Sarigan (*pers. obs.*).

Island assignments to either the SMI or the NMI are given in Table 1.

The islands are in the westward flow of the North Equatorial Current (Myers and Shepard, 1980) from the Pacific Plate, but seasonally are influenced by the Subtropical Counter Current, a southern extension of the Kuroshio that transports waters of the Luzon Strait to the northern-most NMI (Uda, 1971; Myers and Shepard, 1980).

### Methods

Patterns of species richness, family richness, endemism, and similarity in faunal composition are drawn from Donaldson *et al.* (1994), with some additions. Values of species richness, family richness, and endemism were compared between SMI and NMI with Chi-square tests. The null hypothesis was given that values of each were equivalent between localities.

Faunal similarity was calculated with the Sorenson Qualitative Similarity Index ( $C_s$ ),

which considers only presence-absence data but is the most robust of qualitative measures (Magurran, 1988). Values could range from 0.0 (no similarity) to 1.0 (complete similarity).

A checklist of SMI and NMI fishes (Donaldson *et al.*, 1994, appendix II), with additions, was partitioned into separate guilds according to known general macrohabitat preference and trophic designation of each species. This partition was based upon comments from the literature (*e.g.*, Hiatt and Strasburg, 1960; Hobson, 1974; Sano *et al.*, 1984; Myers, 1989; Schupp *et al.*, in prep., *etc.*) and personal observations.

Macrohabitat designations were kept simple and some were pooled (*e.g.*, barrier and fringing reef) to avoid excessive duplication from overlap. Since multiple macrohabitat associations were common for a number of taxa, each species was scored for all those known. Macrohabitat designations were: barrier-fringing reef, reef flat, rocky reef (rock of recent volcanic origin with or without some coral growth), lagoon, mangrove, sea grass-algal bed, nearshore pelagic, and freshwater-estuaries. Caves, cliffs, and patch reefs were not included because of incomplete faunal knowledge of the former and potential overlap with barrier-fringing reef, and potential overlap with lagoon or reef flat for the latter two.

Trophic guilds were designated as: pelagic carnivore, benthic carnivore, omnivore, planktivore, benthic herbivore, detritivore, and corallivore. Each species was assigned only to one guild.

The number of SMI and NMI fishes in each macrohabitat and each trophic guild were calculated separately. Chi-square tests were run to determine significance in values between SMI and NMI guilds. The null hypothesis was given that the number of species in each habi-

tat or trophic guild were equivalent, respectively.

## Results

### 1. Species richness, endemism, and similarity

Species richness and family richness were both greater in the SMI compared to the NMI (Table 2). There was no significant difference in endemism, however (Table 2). Endemic species of the SMI appear also in the NMI, as well. Species assemblages were moderately similar, with a Sorenson Qualitative Similarity value of  $C_s = 0.6371$ , and 445 shared species.

### 2. Macrohabitat guilds

Fishes were distributed in seven macrohabitats in the SMI but only four in the NMI (Table 3 and Fig. 1). In the SMI, the greatest number of species were found on barrier-fringing reefs, followed by lagoons, reef flats, sea grass and algal beds, nearshore pelagics, freshwater-estuaries, and mangroves. There were 76 species whose habitat affinities were classified as unknown. In the NMI, the greatest number occurred on rocky reefs, followed by barrier-fringing reefs, flats, and nearshore pelagics. There were just two species with unknown macrohabitat affinities. Differences between

**Table 2.** Species richness, family richness, and endemism of fish faunas from the Southern (SMI) and Northern Mariana Islands (NMI).

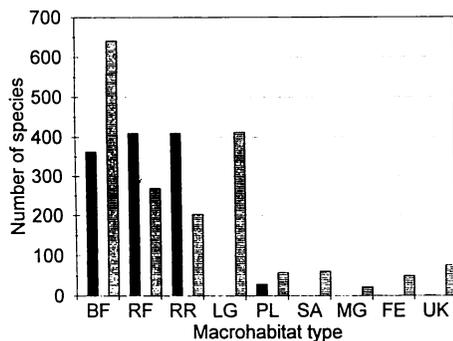
Variable	Island Group			Significance
	SMI	NMI	$X^2$	
Species richness	934	471	152.7	$p < 0.001$
Family richness	100	74	4.5	$p < 0.05$
Endemism (%)	<1.0	<1.0	nt	ns

$df = 1$ ; nt = no test; ns = no significant difference.

**Table 3.** Distribution of fishes in macrohabitat types in the SMI and NMI. Abbreviations are: BF—barrier-fringing reef; RF—reef flat; RR—rocky reef; LG—lagoon; PL—nearshore pelagic; SA—sea grass-algal bed; MG—mangrove; FE—freshwater-estuaries; UK—unknown; N—number of species for which information is available.

Locality	N	BF	RF	RR	LG	PL	SA	MG	FE	UK
NMI	471	363	140	410	0	29	0	0	0	2
SMI	934	642	269	0	411	58	62	22	50	76
$X^2$		77.5**	40.7**	nt	nt	9.7*	nt	nt	nt	70.2**

$df = 1$ ; \*\* $p < 0.001$ ; \* $p < 0.01$ ; nt = no test.



**Fig. 1.** Distribution of species in macrohabitat types of the NMI (dark bars) and SMI (striped bars). See Table 3 for abbreviations.

**Table 4.** Summary of species richness in relation to the number of macrohabitats and the number of trophic guilds at each locality. NMI—Northern Mariana Islands; SMI—Southern Mariana Islands.

Variable	Locality	
	NMI	SMI
Number of species	471	934
No. of macrohabitats	4	7
No. of trophic guilds	7	7

**Table 5.** Pattern of species distribution among NMI and SMI macrohabitats. Values are the number of species.

Locality	Number of habitats						
	1	2	3	4	5	6	7
NMI	104	267	98	0	0	0	0
SMI	304	318	144	67	8	1	2
$X^2$	98***	4.5*	8.7**	nt	nt	nt	nt

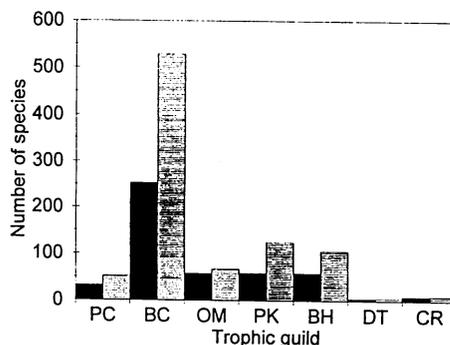
$df=1$ ; \*\*\* $p < 0.001$ ; \*\* $p < 0.01$ ; \* $p < 0.05$ ; nt=no test.

the NMI and SMI were pronounced, especially on rocky reefs (NMI=410; SMI=0) and lagoons (SMI=411; NMI=0), because of the absence of one or the other from a respective locality. Additionally, sea grass-algal beds, mangroves, and freshwater-estuaries were absent from the NMI. The presence of two lakes of volcanic origin on Pagan were not taken into consideration since native fishes were absent from these bodies of water. Species richness and the number of macrohabitats at a locality appear related (Table 4).

**Table 6.** Proportional distribution (as percent) of species in each trophic guild in the SMI and NMI.  $N$ =number of species for which information is available.

Trophic guild	Island group			Significance
	NMI	SMI	$X^2$	
Pelagic carnivore	6.8	4.9	0.31	ns
Benthic carnivore	53.9	59.6	0.29	ns
Omnivore	12.3	7.6	1.11	ns
Planktivore	12.1	14.2	0.17	ns
Benthic herbivore	12.3	12.0	0.003	ns
Detritivore	0.8	0.6	0.03	ns
Coralivore	1.9	1.1	0.21	ns
$N$	473	883		

$df=1$ .



**Fig. 2.** Distribution of species in trophic guilds of the NMI (dark bars) and SMI (striped bars). Abbreviations are: PC—pelagic carnivore; BC—benthic carnivore; OM—omnivore; PK—planktivore; BH—benthic herbivore; DT—detritivore; and, CR—corallivore.

Species were distributed in one or more macrohabitats (Table 5). In the NMI, they ranged from 267 species in two macrohabitats to 98 species in three. In the SMI, they ranged from 318 species in two macrohabitats to 2 in seven. Tests of significance between the NMI and SMI were possible only for species distributed in 1–3 macrohabitats, and differences were all significant (Table 5).

### 3. Trophic guilds

Species richness does not appear to be positively related to the number of trophic guilds present at a given locality (Table 4). Proportional representation of trophic guilds were remarkably similar between localities, with no significant differences in distribution (Table 6).

This indicates that although species numbers in each guild may vary between localities, the proportion of species in each guild does not.

Significant differences in absolute numbers of species (Fig. 2) were found in three guilds: benthic carnivores, planktivores, and benthic herbivores. The absolute number of benthic carnivores in the SMI were nearly twice that of the NMI ( $X^{-2}=94.0$ ,  $df=1$ ,  $p<0.001$ ). Similarly, the absolute number of planktivores ( $X^{-2}=25.4$ ,  $df=1$ ,  $p<0.001$ ) and benthic herbivores ( $X^{-2}=14.1$ ,  $df=1$ ,  $p<0.001$ ) from the SMI were about twice that of those of the NMI. Absolute numbers in other trophic guilds were also greater in the SMI compared to the NMI but the differences were not significant (Fig. 2).

## Discussion

### 1. Species richness, macrohabitats, and trophic complexity

Ecological theory predicts an increase in species diversity with increased habitat complexity and greater numbers of habitat types (Ricklefs, 1973; Roughgarden, 1979). This theory is applied here in terms of increased species richness with increased numbers of macrohabitats and, in turn, an increased number of available trophic levels. Indeed, the SMI, with a greater number of available macrohabitats compared to the NMI, had nearly twice the numbers of species found in the NMI. These differences are analogous to instances of complexity within habitats. For example, the diversity of reef fishes at Kaneohe Bay, Hawaii, and on fringing reefs in the Red Sea, is correlated both with coral diversity and bottom relief (Smith *et al.*, 1973; Roberts and Ormond, 1987).

The SMI also had greater family richness, but the difference was not nearly as pronounced, with the NMI having only 26 fewer families. The composition of these missing families is instructive. Fifteen (ca. 58%) are strongly associated with freshwater-estuarine or sea grass-algal bed macrohabitats (see Donaldson *et al.*, appendix I, in press, for comparison; the addition of Myliobatidae to the NMI has since occurred). These macrohabitats are absent from the NMI. An additional ten (38%) are families with cryptic or nocturnal

species which may turn up with further collecting, and the remainder are nearshore pelagics yet to be encountered.

A greater number of macrohabitats available for fishes should lead to a greater number of possible food sources, providing an increase in the number of potentially available trophic guilds, and hence, greater species richness. This scenario was borne out in macrohabitat diversity, only. The SMI, with greater numbers of macrohabitats but equal numbers of trophic guilds, had greater species richness compared to the NMI. Interestingly, proportional differences in trophic guild representation were not significant despite differences in available macrohabitats. This contrasts with the results of Sale (1991), who compared trophic guilds between similar patch reefs on the Great Barrier Reef and in the U.S. Virgin Islands and found differences in trophic composition. In the NMI-SMI comparison, the lack of differences is especially telling with respect to benthic herbivores. The sea grass-algal bed macrohabitat was absent from the NMI, yet the proportion of benthic herbivores was virtually the same as in the SMI. This disparity may be reconciled when one considers that no clear direct relationship between macrohabitat type and trophic guild was made *a priori*. NMI benthic herbivores likely target emergent benthic algae on rocky reef substrata and on dead corals, as well as algae symbiotic with corals, rather than sea grasses and lush algal beds, which were both absent from this island group. In the SMI, benthic herbivores target one or more of these plant sources, depending upon macrohabitat location and time of day *e.g.*, dietary descriptions in Myers, 1989). The SMI has greater numbers of benthic herbivores because of the presence of sea grasses and algal beds, in addition to the possible plant sources listed above. The exact relationship between macrohabitat, diet, and species richness cannot be ascertained until feeding preferences and macrohabitat associations among herbivorous species have been adequately quantified.

### 2. Historical considerations

Two general hypotheses may account for the present pattern of fish distributions in the NMI

and SMI:

*Hypothesis 1*—Specific macrohabitat types were either present or absent in each island group, according to the geological development of the islands, and thus, current fish species composition generally reflects the current macrohabitat composition of those groups. Ecological refugia may exist in one or both groups.

*Hypothesis 2*—Both island groups possessed the same macrohabitats, and hence, the same species at one time, but vicariant events, notably changes in sea level, eliminated certain macrohabitats from the NMI, and with their elimination, species richness declined. Ecological refugia do not exist.

Given the age of the SMI relative to that of the NMI, the first hypothesis seems much more likely than the second. The SMI has had >35 my to develop diverse macrohabitats, and in turn, to “accept” or “capture” colonists carried historically by the action of plate tectonics (*e.g.*, northeastward migration from the Kyushu-Palau Ridge) or oceanic currents. Changes in sea level doubtless eliminated some macrohabitat types from the SMI (Myers, 1988). Ecological refugia, *e.g.*, in the form of freshwater or estuarine areas, account for a number of species absent from the NMI (Myers, 1988; pers. obs.).

The NMI has too little time to follow suit. Rocky reefs and some limited coral reef development on lower terraces and reef slopes of the southern-most islands exist (pers. obs.). No barrier reefs, sea grass-algal beds, mangroves, streams or estuaries have developed in the NMI; the twin lakes of Pagan are of recent origin and lack a native fish fauna, although one or more species of *Tilapia* (Cichlidae) have been introduced (pers. obs.).

Endemism does not differ significantly between the SMI and NMI despite the relative potential for endemism in the SMI. Endemic species appear to be distributed in both groups (Donaldson *et al.*, 1994). The Mariana Islands have only about one percent endemism, and this low percentage is attributed to the relative lack of geographic isolation of the archipelago (Myers, 1989; Randall, 1992; Donaldson *et al.*, 1994). Low levels of endemism also attest to

the dispersal capabilities of many species, whose larvae have adapted for oceanic transport (*e.g.*, Brothers and Thresher, 1985; Thresher and Brothers, 1985), and are able to traverse the Pacific Plate, the Philippine Sea via the Subtropical Counter current, or along the Philippines-Carolines conduit (Springer, 1982; Myers, 1988, 1989) before settling in the Marianas. The faunas have strong affinities with these of the Pacific Plate (Springer, 1982; Myers, 1988), but those species found with limited distributions share affinities with the Indo-West Pacific (Myers, 1988).

The fish faunas of the NMI and the SMI are moderately similar in composition. With the addition of new species to the NMI, the value reported here is less than  $C_S = 0.6681$  reported in Donaldson *et al.* (1994). Most species observed in the NMI also occur in the SMI but the converse is not true. (Donaldson *et al.*, 1994). The faunas of both groups are strongly tropical, although the NMI does have a small component of warm-temperate species absent from the SMI (Donaldson *et al.*, 1994).

In conclusion, my data support the hypothesis of increased species richness as an outcome of increased macrohabitat diversity, which provides a wider spectrum for potential colonization. My data lend only some support to the hypothesis that increased trophic guild diversity, a function of greater macrohabitat diversity, leads to greater species richness. Greater absolute numbers of species in some guilds are demonstrable for the SMI versus the NMI, but proportional representation of guilds is approximately the same. The exact relationship between macrohabitat type and trophic guild, and its influence upon species richness, cannot be elucidated until a determination is made of the proportional utilization of macrohabitat types (*e.g.*, time budgets in each type utilized by a species) and food sources (*e.g.*, proportion of diet relative to its source in a given macrohabitat) by each species.

#### Acknowledgments

I'm grateful to R. F. Myers, P. J. Schupp, J. T. Moyer, and J. E. Randall for their kind assistance. This paper was prepared while I was a Japan Society for the Promotion of Science

Foreign Research Fellow at Kyushu University. Portions were delivered at the *International Symposium on the Natural History of the Izu-Mariana Arc*, held at Chiba, Japan (11–12 February, 1994), while I was a Distinguished Visiting Scientist of the Natural History Museum and Institute, Chiba (CBM). My thanks to A. Asakura and the curators and staff of the CBM for their kind hospitality. Thanks also to J. M. Fitzsimons who kindly read and improved the manuscript. This is Contribution No. 91 of the Tatsuo Tanaka Memorial Biological Station and Contribution No. 359 of the University of Guam Marine Laboratory.

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(Accepted on 13 October 1994)

## 北マリアナ諸島と南マリアナ諸島における、 リーフにすむ魚類の比較分析

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3500 万年以上の地史をもつ南マリアナ諸島と、100～150 万年の地史をもつ北マリアナ諸島における魚類相の比較をおこなった。南マリアナ諸島には、魚類にとってのさまざまな生息地をみいだすことができる。たとえば、裾礁、堡礁、礁原、河口域、マングローブ、河川、池沼などである。北マリアナ諸島は急斜面が多く（アナタハン島の西海岸、サリガン島の南海岸、バガン島の一部を除く）、狭い岩礁があるものの、河口域、マングローブや淡水域は無い。ただし、バガンには2つの湖があるが、移入されたティラピアがいるだけである。種と科の多様性は、南マリアナ諸島が高い。種組成はやや似ていて、ソーレンソンの類似度指数は  $C_s = 0.6371$  である。固有率は、両諸島とも低い。種組成とその多様性のちがいは、生息地の発達程度の違いと、考えられた。