Community Structure and Distribution of Fishes in an Enclosed High Island Lagoon in Guam[1]

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Abstract

Cocos lagoon is described as a barrier reef enclosed ecosystem located at the foot of the southern mountain range on the island of Guam. The lagoon is shown to comprise a diverse array of environments and is considered to be an important natural recreation and fishery resource to the island.

Six distinct fish communities in six biotopes are investigated. One biotope is included from outside the barrier for comparing lagoon communities with an open ocean reef community. The lagoon biotopes discussed are the coral-rich walls of Mamaon and Manell channels, the lagoon patch reefs, the barrier reef flat, the seagrass beds including *Halodule* and *Enhalus* species, and the sand bottoms of the lagoon floor and channels.

Visual fish counts are conducted within the six biotopes to characterize the community structure of each. Results of 42 transects along with an equal number of random (qualitative) counts are discussed. Importance values, linear biomass and, where possible, actual biomass figures are calculated for each species within the biotopes. Shannon-Wiener diversity indices are computed along with coefficients of community for each biotope and the results used to compare species diversity and community structure between biotopes.

INTRODUCTION

The island of Guam, Mariana Islands, has a variety of marine biotopes including both fringing and barrier reef systems, extensive reef flats and lagoons, patch reefs, seagrass beds, mangrove swamps and estuaries. At the extreme southern end of the island, all the above biotopes occur in one single complex ecosystem, the Cocos Lagoon (Fig. 1). Not only is this geographic area unique with regard to its environmental diversity, but it is also one of the prime centers of water-related recreational activities on the island. The Cocos Lagoon has recently been the subject of an extensive baseline ecological survey funded by the U.S. Army Corps of Engineers (Randall *et al.*, 1975). A component part of the survey was a

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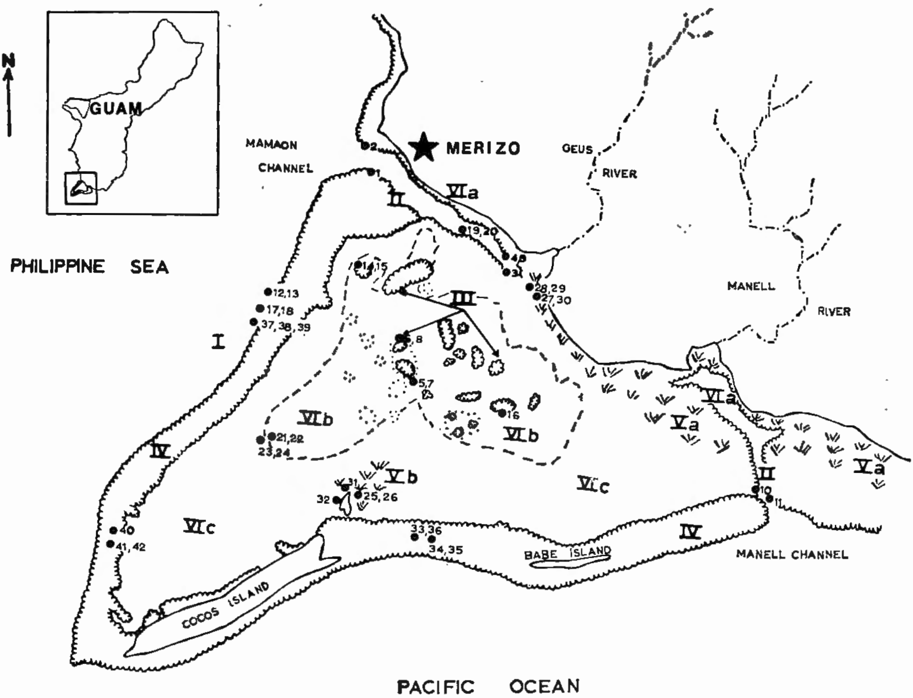

Fig. 1. Map of Cocos Lagoon study area. The black spots show the approximate locations of the transect stations, the arabic numerals indicate the transect numbers, and the dashed line is the boundary between the lagoon terrace and the lagoon floor. The number of patch reefs and shoals shown is considerably less than the number that actually occur in the lagoon. I-Biotope outside the barrier; II-Channel wall biotope; III-Lagoon patch reef biotope; IV-Barrier reef flat biotope; V-Seagrass biotope, a-*Enhalus acoroides*, b-*Halodule uninervis*; and VI-Sand bottom biotope, a-channel bottoms, b-lagoon floor, and c-lagoon terrace.

study of the marine fish community inhabiting the lagoon.

This paper provides a list of the tropical marine shore fishes found in the lagoon, considers the community structure, and discusses the biotopes in which the species are commonly found. Similar studies have been completed by Chave and Eckert (1974) at Fanning Island, in the Line Islands, and Smith *et al.* (1973) at Kaneohe Bay in the Hawaiian Islands. It is also our intention to briefly compare the relative diversity of the ichthyofauna inside the lagoon with transects outside the barrier reef.

Previous work on the fishes of Guam includes checklists of species known from the island by Kami *et al.* (1968) and Kami (1971). The Guam Division of Fish and Wildlife has established two artificial reefs in the lagoon, made from old tires, and has two transect stations for general fish surveys there. Their data are reported in a series of annual reports from 1965 to 1974 and are available on request.

Cocos Lagoon is a heavily used tourist attraction at the present time. Large numbers of tourists are transported daily to Cocos Island (Fig. 1) and view the lagoon patch reefs and associated organisms from glass-bottomed boats. The lagoon is popular as a recreation site for snorkeling, SCUBA diving, sailing and water skiing. It is fished regularly by line, net, and spear-fishermen, and there are a series of government-licensed fish traps in the lagoon. The area is, therefore, an important natural resource from several points of view.

Data included within this paper are expected to serve not only as basic research but may also be useful in the future as a baseline study for evaluating the impact of the rapidly urbanizing Merizo municipality (Fig. 1). It should be possible to duplicate the study at a later date for the purpose of measuring potential degradation of biotopes within this valuable resource area. For this reason, considerable space has been devoted to methodology.

Wittaker *et al.* (1973) note that the terms biotope and habitat have been used almost interchangeably. However, when distinction is desired then biotope should apply to the community's environment and habitat to the species' environment (Udvardy, 1959). This distinction is appropriate to the fish communities studied in this paper.

The study was conducted from 28 March to 20 May 1974.

METHODS

Description of the Study Area

GENERAL

The Cocos Lagoon is described in detail by Randall *et al.* (1975). In general, the lagoon is surrounded along its northwestern and southeastern margins by a barrier reef (Fig. 1). The northeastern margin of the lagoon is mainland Guam. The lagoon lies at the end of a rugged volcanic mountain range that makes up the southern half of the island. Cocos Island is the largest land mass on the lagoon barrier. The lagoon floor varies in depth from 3 to 12 m and is penetrated, at its northern end, by Manell Channel on the east and Mamaon Channel on the west. These natural channels range in depth from 3 to 30 m. Seawater circulation in the lagoon is via these channels and by wave and tidal transport over the barrier. Primary input of freshwater into the lagoon is from the Geus and Manell Rivers and a series of small creeks that drain the nearby, steep mountain slopes. The contribution of these freshwater sources is confined mostly to the fringing reef and channels and rarely, if ever, influences the main part of the lagoon.

Seven major biotopes (Fig. 1) were recognized *a priori* as distinct for the ichthyofauna.

I. OUTSIDE REEF

The combined lower reef margin and reef front, submarine terrace, and upper seaward slope to the west of the Cocos Lagoon barrier reef (terminology of Tracey *et al.*, 1964) were used as one biotope in order to compare the diversity of the fish community (by biotope) inside the lagoon with that outside. Seven transects were made in this biotope parallel to depth contours (NE to SW). Four were run on the submarine terrace, two on the reef margin/front and one on the seaward slope. Had more time been available to the investigators, we would have increased the number of transects and treated each of the above zones as separate biotopes.

II. CHANNEL WALLS

The walls of both Mamaon and Manell channels vary from sand slopes to steep or overhanging coral developmental features. The latter form excellent cover for fish species. Transects were deliberately concentrated in the coral areas and were oriented parallel to channel margins at varying depths (vertical zig-zag). They included seven in all, five in Mamaon Channel and two in Manell. Transects were run at both the seaward (western) and lagoon (eastern) ends of Mamaon Channel.

III. LAGOON PATCH REEFS

Numerous patch reefs of various sizes occur in the Cocos Lagoon at nearly all possible depths. Four separate patch reefs were investigated and seven transects run on them, normally along the longest axis of each reef. Transect lines were woven to include both sides and tops of patch reefs. Duplicate transects were run on three of these reefs. All the reefs rise to within one-half meter of the surface, at mean low tide, and all have live corals, usually dominated by dense thickets of branching species in the genus *Acropora*. Fishes seek cover primarily among these coral branches.

IV. BARRIER REEF FLAT

This area is frequently exposed at low spring tides. During such times the fishes that occur here must migrate to deeper waters adjacent to the barrier or seek shelter in tide pools or in holes that connect with the water surface investing the reef framework. Primary cover for fishes includes holes and cracks in the coral framework and rubble tracts along the barrier. Four transects were run on the southeast barrier and three on the west. The transects were oriented perpendicular to the barrier axis and were normally parallel to water flow over the barrier.

V. SEAGRASS BEDS

Two species of seagrasses occur in Cocos Lagoon. They are *Halodule uninervis* (Forsk.) Ascherson and *Enhalus acoroides* (L.f) Royle. The *Halodule* beds are located along a small sand spit northeast of Cocos Island. The *Enhalus* beds are concentrated more around the channels and fringing reef adjoining the mainland. Four transects were run in the *Enhalus* beds and three in the *Halodule* bed. All transects were allowed to meander at random through the grass beds. The seagrasses themselves form the basic cover for fishes living there.

VI. SAND BOTTOM

The sand bottom biotope includes channel floors, the floor of the lagoon proper, and the lagoon terrace. Three transects were run on the shallow (1 m) lagoon terrace floor, two on the lagoon bottom, and two on the channel bottom. Transect direction was random in each case. These virtually featureless habitats offered no cover for fishes except burrowing forms.

VII. ESTUARINE AND FRESHWATER

The heavily silted fringing reef/mud flats, concentrated around river and creek mouths along the shore of mainland Guam, are essentially estuarine systems and often characterized by a mangrove community. No attempt was made to investigate this biotope because we chose to concentrate on the primary marine system. The freshwater and estuarine fauna is included in a report prepared by the Guam Division of Fish and Wildlife and appears in Kami *et al.* (1974).

Transects

Forty-two transects were run as noted above, seven in each biotope. Of these, 35 were run inside the lagoon and seven outside (Fig. 1). Each transect was arbitrarily set at 100 m in length. The transect line was unreeled in the biotope to be sampled. Some attempt was made to lay the transect lines in a random fashion. However, a deliberate bias was also introduced in order to compare the sand bottom, grass flat, and coral dominated biotopes. For example, transect lines in sand areas were set to avoid all grass flat and coral features, while coral transects were set to avoid sand bottoms and grass flats, and so forth.

All fishes seen by SCUBA-equipped observers within 1 m to either side of the transect line and 2 m above it were counted and their total lengths estimated in mm. It usually required about 20 minutes to complete one transect count. This was immediately followed by a 20-minute random count in the vicinity of, but not restricted to, the transect line. We considered this necessary because many of the ubiquitous species in a given transect area failed to appear on the transect. This is due not only to the natural non-random distribution of the fishes but also because many of them are wary of approaching SCUBA divers and move away from the transect line during the count.

It was obvious that many of the smaller species were territorial or adhered to restricted home ranges. These species (largely pomacentrids) tended to remain on the transect while larger species, even those with territories, had a tendency to leave the count zone (at least temporarily) when approached by the observers. This resulted in our transect data being biased in favor of smaller species. The random counts were somewhat helpful, if examined intuitively, in alleviating this bias. These counts frequently added as much as 30% more species to the transect station, thus considerably increasing species richness (Table 2). However, the random counts only enumerated the species and not individuals, because it is virtually impossible to keep accurate counts of the swarms of fishes that surround a diver (360°) on a tropical reef. Duplicate counts are inevitable unless the observer confines himself to a control transect line or other devices.

Highly cryptic and nocturnal species were not sought out. Therefore, the transect data and random counts are relative instead of absolute indicators of fish community structure within the biotopes. No attempts were made to use chemical fish poisons to collect cryptic species because of the constant use of the lagoon as a recreational area.

Underwater tape recorders were used for recording observations because we found that a great many species were missed when we tried to use writing slates. Too much time is spent looking down at a slate, whereas with a recorder, the observer's eyes do not leave the transect.

The normal variability encountered in such visual counts, made it necessary to combine the seven transects in each of the six biotopes rather than consider the transects separately.

For each biotope, data on the species were treated and analyzed as follows:

DENSITY

The total number of individuals of each species on the seven transects within a biotope were summed and the number per unit area computed in the normal manner:

$$\text{density (d)} = \frac{\text{number of individuals for a species}}{\text{area sampled}}$$

The area sampled in this case is 1400 m^2 (7 transects $\times$200 m^2)

From these values, relative densities were computed as:

$$\text{relative density (rd)} = \frac{\text{density for a species}}{\text{total density for all species}} \times 100$$

DOMINANCE AND LINEAR BIOMASS

As is true of many organisms, small fish species often occur in much greater numbers than larger species. Therefore, density figures based on enumeration tend to be heavily biased toward the more numerous small species. It is obvious that it would be more appropriate if the large fishes (e.g., *Scarus sordidus*) could be weighted in some way to equal a number of individuals of a smaller species (e.g., *Chromis caeruleus*). We attempted to handle this bias by computing a dominance value similar to that used by plant ecologists. Such values usually consider, for example, the total area covered by a given plant, divided by the total area sampled. Fishes, however, being uncooperative and mobile organisms, are impossible to measure in this way. Instead, we estimated the combined lengths (in mm) of the individuals of each species in a given biotope. This number (total species length) was then related to the total length of the transects in each biotope (7 transects $\times$ 100 m $\times$ 1000 mm/m $= 7 \times 10^5$ mm). In addition, Porter (1972) used a similar technique for studying reef corals and referred to it as a "linear biomass measurement". We calculated these values as:

$$\text{dominance (dm)} = \frac{\text{sum of individual lengths for a species}}{\text{total length of the transects } (7 \times 10^5 \text{ mm})}$$

These values were then converted to relative dominance figures:

$$\text{relative dominance (rdm)} = \frac{\text{dominance for a species}}{\text{total dominance for all species}} \times 100$$

And:

$$\text{linear biomass (lbm)} = \frac{\text{sum of individual lengths for a species}}{\text{total length of all species combined}} \times 100$$

Since the data derived in each above case are linear only, and do not consider the actual physical bulk of each animal on a unit area basis, it is obviously not the best method of reducing the bias introduced by the large numbers of smaller species (e.g., a trumpetfish and a parrotfish of equal lengths differ considerably as to weight). It would be better to use some value based on actual fish weight (biomass) rather than length alone. Such estimations are possible from length measurements and predetermined length/weight constants (see below). However, since we did not have necessary conversion constants for all the species observed, we were forced to work with the lengths alone to determine dominance and linear biomass values. The lengths are also obviously subject to observer error.

IMPORTANCE VALUE

The above two relative parameters (rd, rdm) were summed to give a single importance value (Cox, 1972):

$$\text{importance value (I.V.)} = \text{rd} + \text{rdm}$$

Importance values are considered useful in comparing community structure between biotopes. The relative density (rd) value by itself is, as noted above, biased by inclusion of large numbers of small species. By adding relative dominance (rdm), some additional weight (numerical) is applied to the larger (longer) species.

OVERALL IMPORTANCE VALUE

It became evident, early in the study, that the community structure of lagoon biotopes II–IV (all reef biotopes) were quite similar, as would be expected *a priori*, and differed considerably from lagoon biotopes V and VI (grass flats and sand bottoms). The raw data from lagoon biotopes II–IV were pooled and an overall importance value computed for the species occurring in these coral-dominated biotopes. The 21 transects were essentially treated as one large transect crossing all three of the major lagoon reef biotopes (4200 m^2). This analysis was done to ascertain the relative numerical importance of each species for combined coral biotopes.

FISH BIOMASS

Estimation of fish biomass was the third method of obtaining the relative contribution of each species within each biotope.

Brock (1954), in one of the pioneering works on visual fish transects conducted by SCUBA divers, used a standard fishery conversion of length to weight via a constant computed for each species observed. The transformation equation is:

$$W = A(L)^3$$

where: W = the weight of the fish
A = the constant for the species
L = the length of the fish

The estimates of weights for all individuals of one species thus obtained, were then summed to obtain the total weight of that species. The weights were converted to kilograms-per-hectare (kg/ha) for each species. The work was hindered somewhat in that length/weight constants were not available for all species. Fortunately, the Guam Division of Fish and Wildlife was able to furnish the constants for some of the more dominant species.

SHANNON-WIENER DIVERSITY INDEX

The sums of individuals for each species in each biotope as well as their linear biomass values were used to compute Shannon-Wiener diversity indices (Pielou, 1966) using the equation:

$$H' = -\sum_{i=1}^{S} p_i \log p_i$$

where: p_i = the proportion of some measure of the i th species in a population.

Since H' is the diversity for the entire population, which we were unable to measure, it must be approximated by:

$$H'' = -\sum \frac{N_i}{N} \log e \frac{N_i}{N}$$

where: N = the total number of individuals, or total linear biomass for all species in a sample biotope and
N_i = the number of individuals, or linear biomass for the i th species.

Since diversity depends not only upon the number of species but also the equitable distribution of individuals (or lbm.) among the species, the population evenness (Pielou, 1966) was estimated as:

$$E\ (\text{evenness}) = \frac{H''}{\log_e S}$$

where: S = the total number of species observed in the biotope. This includes both random and transect species (Table 2) and is a better measure of S than transect species alone. Herein lies another value of the random counts.

COMMUNITY COMPARISONS

Importance values were used to compute coefficients of community or similarity (Oosting, 1956) for each biotope compared with every other biotope after the formula:

$$C = \frac{2w}{a + b}$$

where: w = the sum of the lower of the two I.V.'s for each species shared by the two communities (biotopes)
a = the sum of all I.V.'s for the first community
b = the sum of all I.V.'s for the second community

These data were placed in a matrix of similarity coefficients. Dissimilarity coefficients were then computed as the difference between the calculated coefficients of similarity and the maximum possible value. These values are calculated because the ordination (below) depends on the difference between communities (biotopes) rather than similarities. The maximum value would theoretically be 1.0, however, as Cox (1972) points out, a maximum value of 0.85 more readily approximates a true community upon which replicate samples have been drawn. These dissimilarity coefficients (0.85—C) are placed in the mirror image of the above matrix and used in a simple community ordination procedure such as that shown by Cox (1972). The result is a two dimensional ordination of fish communities (biotopes) on the basis of x ("the greatest component of community variation") and y ("the greatest component of the remaining community variation") coordinates (Fig. 2). The degree to which the spacing of the communities (biotopes) on the ordination accounts for variations in community composition is estimated by correlation of ordination interval with observed dissimilarity between community pairs (Cox, 1972).

RESULTS AND DISCUSSION

Table 1 is a list of fish species known from Cocos Lagoon and the outside reef biotope. The table shows distribution of species among biotopes and provides some insight as to the most common species in each. Kami *et al.* (1968) and Kami (1971) record a total of 598 fish species from Guam. The list of species in Table 1 includes a total of 276 species, 42 of which were observed only outside of the lagoon (biotope I) during this study. Thus, a total of 234 species are now recorded from the lagoon proper. This constitutes about 40 percent of the species known from Guam. Use of ichthyocides might well have added 50 or more species to the list. However, we chose to rely on visual counts to determine the most important of the ubiquitous fishes without regard to cryptic species. The latter, we suspect, comprise a small part of the total ichthyofauna. Of the 234 species recorded from the lagoon, 189 were actually observed on the transects and random counts, while another 45 were reported from other sources (Table 1).

Table 2 is a summary of observations made in this study. The combined area of the 42 transects was equal to 8400 m^2. Transect areas for each biotope amounted to 1400 m^2. A total of 10,032 individual fishes representing 181 species were counted on the transects.

On the basis of individuals and total species observed (Table 2), it is apparent

Table 1. Checklist of the fishes. Fishes recorded from the lagoon by previous workers are shown in the first column and coded as 1—Kami *et al.* (1968); 2—Kami (1971); 3—University of Guam Museum; 4—Jones and Randall (1973); 5—Randall *et al.* (1973); 6—Collections or incidental observations, in the lagoon during the study. Fishes observed by the present authors on random counts are shown as (+) under the pertinent biotope. Numbers refer to the actual number of a species seen on seven combined transects. I—Outside of Lagoon, II—Channel Walls, III—Lagoon Patch Reefs, IV—Barrier Reef Flat, V—Seagrass Beds, and VI—Sand Bottoms. *—Fishes observed or recorded only outside of lagoon.

Family/Species		I	II	III	IV	V	VI
ACANTHURIDAE							
Acanthurus glaucopareius Cuvier		2	+	6	—	—	—
A. lineatus (Linnaeus)		1	+	—	—	—	—
A. mata Valenciennes	2						
A. nigrofuscus (Forskal)	1	19	15	1	6	—	—
A. olivaceous (Bloch & Schneider)	1						
A. pyroferus Kittlitz		+	+	—	—	—	—
A. thompsoni (Fowler)	*	+	—	—	—	—	—
A. triostegus (Linnaeus)		—	+	10	26	—	—
A. xanthopterus (Cuvier & Valenciennes)		+	5	2	—	6	—
Ctenochaetus binotatus Randall		4	5	—	—	—	—
C. striatus (Quoy & Gaimard)		56	89	57	23	—	—
Naso brevirostris (Cuvier & Valenciennes)	*	+	—	—	—	—	—
N. hexacanthus (Bleeker)	*	+	—	—	—	—	—
N. lituratus (Bloch & Schneider)	1	5	+	3	+	—	—
N. unicornis (Forskal)		+	1	1	2	—	—
Zebrasoma flavescens (Bennett)	1	+	9	9	—	—	—
Z. scopas (Cuvier)		—	1	+	—	—	—
Z. veliferum (Bloch)	1	+	4	2	—	—	—
APOGONIDAE							
Apogon exostigma (Jordan & Starks)		—	1	—	—	—	—
A. leptacanthus Bleeker	1						
A. mydrus (Jordan & Starks)	1						
A. novemfasciatus Cuvier & Valenciennes		—	—	—	14	—	—
A. robustus (Smith & Radcliffe)	1						
A. trimaculatus Cuvier & Valenciennes	5						
A. sp.		—	200	—	—	—	—
Cheilodipterus macrodon (Lacepede)		—	2	2	—	—	—
C. quinquelineata (Cuvier & Vilenciennes)		—	34	33	—	3	—
ATHERINIDAE							
Pranesus insularum (Jordan & Evermann)	1						
AULOSTOMIDAE							
Aulostomus chinensis (Linnaeus)		+	6	2	—	1	—
BALISTIDAE							
Balistapus undulatus (Mungo Park)	1	+	1	—	—	—	—
Balistoides niger (Bloch)	*	+	—	—	—	—	—
Melichthys niger (Bloch)	*	+	—	—	—	—	—
M. vidua (Solander)	*	1	—	—	—	—	—

Table 1. (continued)

Family/Species		I	II	III	IV	V	VI
Pseudobalistes flavomarginatus (Ruppell)	1	—	—	+	—	—	—
Rhinecanthus aculeatus (Linnaeus)		—	—	—	+	—	—
R. rectangulus (Bloch & Schneider)		—	—	—	+	—	—
Sufflamen bursa (Bloch & Schneider)	1	1	—	—	—	—	—
S. chrysoptera (Bloch & Schneider)		3	+	—	—	—	—
BLENNIIDAE							
Aspidontus taeniatus Quoy & Gaimard		6	6	4	1	—	—
Cirripectes sebae Fowler	*	12	—	—	—	—	—
C. variolosus (Cuvier & Valenciennes)		47	+	—	3	—	—
Ecsenius bicolor (Day)	*	2	—	—	—	—	—
E. opsifrontalis Chapman & Schultz	*	4	—	—	—	—	—
Exallias brevis (Kner)	*	+	—	—	—	—	—
Istiblennius coronatus (Gunther)		1	—	—	1	—	—
Meiacanthus atrodorsalis (Gunther)	3	73	122	45	—	—	—
Petroscirtes mitratus (Ruppell)		—	—	—	—	+	+
Plagiotremus tapeinosoma (Bleeker)		6	2	—	1	—	—
P. sp.	*	+	—	—	—	—	—
Salarias fasciatus (Bloch)		+	—	—	4	—	—
BOTHIDAE							
Bothus mancus (Broussonet)		—	2	—	—	—	—
CANTHIGASTERIDAE							
Canthigaster amboinensis (Bleeker)	*	1	—	—	—	—	—
C. coronatus (Randall)	1	2	1	7	—	—	—
C. janthinopterus (Bleeker)		4	1	—	—	—	—
C. solandri (Richardson)		12	19	3	8	—	—
CARACANTHIDAE							
Caracanthus maculatus (Gray)	*	3	—	—	—	—	—
CARANGIDAE							
Carangoides malabaricus (Bloch & Schneider)	1						
Caranx melampygus Cuvier & Valenciennes		+	—	+	—	—	+
Gnathanodon speciosus (Forskal)	1						
CARAPIDAE							
Carapus homei (Richardson)	1						
CHAETODONTIDAE							
Centropyge bispinosus (Gunther)	*	9	—	—	—	—	—
C. flavissimus (Cuvier)	1	5	2	+	+	—	—
C. heraldi Woods & Schults	*	+	—	—	—	—	—
Chaetodon auriga Forskal	1	1	2	11	5	—	—
C. bennetti Cuvier		+	1	+	—	—	—
C. citrinellus Cuvier	1	9	5	3	11	—	—
C. ephippium Cuvier		+	4	4	+	—	—
C. falcula Bloch		+	12	6	—	—	—
C. kleini Bloch		—	4	—	—	—	—
C. lunula (Lacepede)		+	4	1	3	—	—
C. melannotus Schneider	1	—	4	3	—	—	—

Table 1. (continued)

Family/Species		I	II	III	IV	V	VI
C. mertensii Cuvier	1	2	7	1	—	—	—
C. ornatissimus Solander	1	3	2	—	—	—	—
C. punctato-fasciatus Cuvier & Valenciennes	1	20	4	+	—	—	—
C. quadrimaculatus Gray	*	3	—	—	—	—	—
C. reticulatus Cuvier	1	11	1	+	—	—	—
C. strigangulus (Gmelin)		1	—	4	—	—	—
C. trifasciatus Mungo Park	1	+	23	14	+	—	—
C. unimaculatus Bloch	1	7	1	—	—	—	—
Forcipiger flavissimus Jordan & McGregor	2	4	—	—	—	—	—
Heniochus permutatus Cuvier	1	6	4	5			
H. varius (Cuvier)	1	—	—	—	—	—	—
H. monoceros Cuvier		+	4	+	+	—	—
Holacanthus trimaculatus Cuvier	*	+	—	—	—	—	—
Pomacanthus imperator (Bloch)	1	—	+	—	1	—	—
Pygoplites diacanthus (Boddaert)	1	—	1	—	—	—	—
CIRRHITIDAE							
Cirrhitus pinnulatus (Schneider)	*	+	—	—	—	—	—
Neocirrhites armatus Castelnau	*	8	—	—	—	—	—
Paracirrhites arcatus (Cuvier & Valenciennes)		8	—	1	—	—	—
P. forsteri (Bloch & Schneider)	1	16	+	—	—	—	—
P. hemistictus (Gunther)	*	+	—	—	—	—	—
DASYATIDAE							
Dasyatis kuhlii (Müller & Henle)	3						
DIODONTIDAE							
Diodon hystrix (Linnaeus)	1						
ENGRAULIDAE							
Thrissina baelama (Forskal)	1						
FISTULARIDAE							
Fistularia petimba Lacepede	1	—	—	—	1	—	—
GOBIIDAE							
Acentrogobius belissimus Smith	5	—	12	11	—	—	—
A. triangularis Weber	4						
Amblygobius albimaculatus (Rupell)	1	—	+	4	+	+	+
A. decussatus (Bleeker)	4						
A. sp.		—	—	—	—	—	86
Asterropteryx semipunctatus Ruppell		—	—	—	2	10	63
Bathygobius fuscus (Ruppell)	6						
Eleotriodes strigata (Bleeker)	1	30	—	—	2	—	—
Eviota prasites Jordan & Seale	5						
Gnatholepis deltoides (Seale)		—	+	—	3	+	—
Gobius ornatus Ruppell		—	—	—	—	+	+
Nemateleotris magnificus Fowler	*	25	—	—	—	—	—
Obtortiophagus koumansi (Whitely)	5	—	—	—	—	7	—
Oxyurichthys guibei Smith	3	—	—	—	—	—	2
Periopthalmus koelreuteri Eggert	3						

Table 1. (continued)

Family/Species		I	II	III	IV	V	VI
Pogonoculius zebra Fowler	*	5	—	—	—	—	—
Ptereleotris tricolor Fowler	*	28	—	—	—	—	—
Rhinogobius decoratus Herre	3						
Trimma caesiura Jordan & Seale	4						
HEMIRAMPHIDAE							
Hyporhamphus laticeps (Gunther)	1						
HOLOCENTRIDAE							
Adioryx caudimacula (Ruppell)	*	10	—	—	—	—	—
A. microstomus (Gunther)		1	—	—	2	—	—
A. spinifer (Forskal)	1	+	3	—	2	—	—
A. tiere (Cuvier & Valenciennes)	1	3	—	—	—	—	—
A. lacteoguttatus (Cuvier)	6						
A. sp.		1	5	—	+	—	—
Flammeo sammara (Forskal)		—	92	11	5	—	—
Myripristis amaenus (Castelnau)		—	65	+	—	—	—
M. kuntee (Cuvier & Valenciennes)		—	1	—	—	—	—
M. micropthalmus Bleeker	1						
M. murdjan (Forskal)		6	46	+	1	—	—
KUHLIIDAE							
Kuhlia taeniura (Cuvier & Valenciennes)	1						
KYPHOSIDAE							
Kyphosus cinerascens (Forskal)	1						
LABRIDAE							
Anampses caeruleopunctatus Ruppell	*	+	—	—	—	—	—
Cheilinus celebicus Bleeker	1						
C. chlorourus (Bloch)		—	+	2	2	1	—
C. fasciatus (Bloch)	1	1	9	19	13	+	—
C. rhodochrus Gunther		2	5	2	—	—	—
C. trilobatus Lacepede		+	1	+	+	—	—
C. undulatus Ruppell		+	+	3	1	—	—
Cheilio inermis (Forskal)		—	—	+	2	41	—
Cirrhilabrus temmincki Bleeker	*	15	—	—	—	—	—
Coris aygula Lacepede	1						
C. gaimardi (Quoy & Gaimard)	1	2	—	—	1	—	—
Epibulus insidiator (Pallas)	1	2	9	1	1	—	—
Gomphosus varius Lacepede		5	3	8	+	—	—
Halichoeres biocellatus Schultz	*	4	—	—	—	—	—
H. hortulanus (Lacepede)		4	1	—	1	—	—
H. margaritaceus (Cuvier & Valenciennes)		1	+	—	82	3	—
H. marginatus Ruppell	1	3	2	—	3	—	—
H. trimaculatus (Quoy & Gaimard)	1	—	+	34	388	135	—
Hemigymnus fasciatus (Bloch)		+	+	—	—	—	—
H. melapterus (Bloch)	1	1	5	3	1	—	—
Hemipteronotus sp.		+	—	—	—	+	+
Labrichthys unilineata Bleeker		—	6	6	—	—	—
Labroides bicolor Fowler & Bean	1	+	+	—	—	—	—
L. dimidiatus (Cuvier & Valenciennes)		22	16	15	20	—	—

Table 1. (continued)

Family/Species		I	II	III	IV	V	VI
Macropharyngodon meleagris Seale		—	+	—	—	—	—
M. pardalis (Kner)		2	3	—	4	—	—
Pseudocheilinus hexataenia (Bleeker)	2	1	1	—	—	—	—
Pteragogus guttatus (Fowler & Bean)		—	3	—	—	—	—
Stethojulis (axillaris) bandanensis Bleeker	1	2	21	3	214	3	—
S. strigiventer (Bennett)		—	5	2	—	537	—
Thalassoma amblycephalus (Bleeker)		9	3	—	—	—	—
T. hardwickei (Bennett)		+	6	27	28	—	—
T. lutescens (Lay & Bennett)	1	12	4	2	9	—	—
T. purpureum (Forskal)	1	+	—	—	1	—	—
T. quinquevittata (Lay & Bennett)	1	93	—	—	12	—	—
Xyrichthys taeniourus (Lacepede)	1	1	—	—	12	—	—
LUTJANIDAE							
Aphareus furcatus (Lacepede)	1	+	+	1	—	—	—
Aprion virescens Valenciennes	*	+	—	—	—	—	—
Caesio caerulaureus Lacepede	1						
Gnathodentex aureolineatus (Lacepede)	1	—	1	—	—	—	—
Lethrinus reticulatus Cuvier & Valenciennes	1						
L. rhodopterus Bleeker		+	+	+	2	18	+
L. sp.		—	—	+	—	16	—
Lutjanus argentimaculatus (Forskal)		+	+	—	—	—	—
L. (vaigiensis) fulvus (Bloch & Schnieder)		1	4	2	+	—	—
L. kasmira (Forskal)	6						
L. monostigmus (Cuvier & Valenciennes)	*	+	—	—	—	—	—
Macolor niger (Forskal)	1						
Scolopsis cancellatus (Cuvier & Valenciennes)	1	—	—	+	+	—	—
MALACANTHIDAE							
Malacanthus latovittatus (Lacepede)	1						
MONACANTHIDAE							
Alutera scripta (Gmelin)	2						
Amanses carolae Jordan & McGregor	*	+	—	—	—	—	—
A. sandwichiensis (Quoy & Gaimard)	1	1	+	+	—	—	—
Oxymonacanthus longirostris (Bloch & Schneider)	1	+	2	22	+	—	—
Paraluteres prionurus Bleeker	2	—	5	—	—	—	—
Pervagor melanocephalus (Bleeker)	1						
MONODACTYLIDAE							
Monodactylus argenteus (Linnaeus)		—	2	—	—	—	—
MUGILIDAE							
Chelon vaigiensis (Quoy & Gaimard)	1						
Crenimugil crenilabis (Forskal)	1						
Mugil cephalus Linnaeus	1						
MUGILOIDIDAE							
Parapercis cephalopunctatus (Seale)		+	1	—	—	—	—
P. clathrata Ogilby	1	1	1	—	+	—	—

Table 1. (continued)

Family/Species		I	II	III	IV	V	VI
MULLIDAE							
Mulloidichthys auriflamma (Forskal)		—	—	2	—	—	—
M. samoensis (Gunther)		—	3	+	4	2	+
Parupeneus barberinus (Lacepede)	1	+	+	+	2	76	—
P. bifasciatus (Lacepede)		1	—	—	3	—	—
P. cyclostomus (Lacepede)	1	3	1	+	+	—	—
P. multifasciatus (Quoy & Gaimard)	1	8	22	2	22	21	—
P. pleurostigma (Bennett)		—	3	—	+	+	—
P. porphyreus (Jenkins)	4	—	+	+	—	117	—
Upeneus vittatus (Forskal)		—	—	—	—	—	2
MURAENIDAE							
Echidna nebulosa (Ahl)		—	1	—	+	—	—
E. zebra (Shaw)	6						
Gymnothorax gracilicaudus Jenkins	2						
G. javanicus (Bleeker)	2	—	+	—	—	—	—
G. pictus (Ahl)	1						
G. undulatus (Lacepede)	*	+	—	—	—	—	—
Uropterygius concolor Ruppell	1						
MYLIOBATIDAE							
Aetobatus narinari (Euphrasen)	2	—	—	—	—	—	+
OPHICHTHIDAE							
Leiuranus semicinctus (Lay & Bennett)	1						
OSTRACIONTIDAE							
Lactoria cornutus Linnaeus	1						
Ostracion cubicus Linnaeus		—	3	3	—	—	—
O. meleagris camurum (Randall)	1	1	+	1	—	—	—
PEMPHERIDAE							
Pempheris oualensis Cuvier & Valenciennes		—	5	—	—	—	—
POMACENTRIDAE							
Abudefduf amabilis (de Vis)	1	10	+	—	1	—	—
A. curacao (Bloch)		—	172	278	—	—	—
A. dicki (Lienard)		171	6	—	—	—	—
A. glaucus (Cuvier & Valenciennes)		—	—	—	266	—	—
A. imparipinnis (Sauvage)	*	+	—	—	—	—	—
A. johnstonianus (Fowler & Ball)	*	52	—	—	—	—	—
A. lacrymatus (Quoy & Gaimard)	1	60	68	8	2	—	—
A. leucopomus (Lesson)		55	+	—	5	—	—
A. leucozona (Bleeker)		—	—	—	39	—	—
A. saxatilis (Linnaeus)	*	+	—	—	—	—	—
A. septemfasciatus (Cuvier & Valenciennes)		+	—	—	+	—	—
A. sexfasciatus (Lacepede)		—	—	18	—	—	—
Amphiprion bicinctus Ruppell	1						
A. chrysopterus Cuvier	3	8	—	—	3	—	—
A. melanopus Bleeker	1	—	8	4	5	—	—
A. perideraion Bleeker	*	+	—	—	—	—	—

Table 1. (continued)

Family/Species		I	II	III	IV	V	VI
Chromis atripectoralis Welander & Schultz		—	1	+	3	—	—
C. caeruleus (Cuvier & Valenciennes)	1	—	222	544	158	—	—
C. (*dimidiatus*) *hanui* Randall & Swerdloff		78	1	—	—	—	—
C. leucurus Gilbert	*	3	—	—	—	—	—
C. vanderbilti (Fowler)	*	5	—	—	—	—	—
C. xanthochir (Bleeker)	*	+	—	—	—	—	—
C. sp.		5	+	—	—	—	—
Dascyllus aruanus (Linnaeus)	1	—	143	131	112	—	—
D. reticulatus (Richardson)	1	277	3	—	—	—	—
D. trimaculatus (Ruppell)	1	22	5	—	15	—	—
Pomacentrus albofasciatus Schlegel & Muller		—	—	—	380	—	—
P. amboinensis Bleeker		—	5	—	—	—	—
P. jenkinsi Jordan & Evermann		274	+	—	3	—	—
P. lividus (Bloch & Schneider)	1	—	10	36	+	—	—
P. nigricans (Lacepede)	1	—	8	211	24	—	—
P. pavo (Bloch)		—	1	2	—	—	—
P. traceyi Schultz		133	61	2	—	—	—
P. vaiuli Jordan & Seale		225	205	1	83	—	—
P. sp.	*	255	—	—	—	—	—
PSEUDOCHROMIDAE							
Plesiops corallicola Bleeker	1						
SCARIDAE							
Calatomus spinidens (Quoy & Gaimard)		—	+	—	+	—	—
Chlorurus bicolor (Ruppell)	1	—	1	+	—	—	—
C. gibbus (Ruppell)	2	—	—	+	—	—	—
Leptoscarus vaigiensis (Quoy & Gaimard)		—	—	—	—	2	—
Scarus dubius Bennett		+	+	4	—	3	—
S. lepidus Jenyns		9	+	+	+	—	—
S. sordidus Forskal		45	50	192	13	139	—
S. venosus Cuvier & Valenciennes		6	20	12	10	—	—
SCORPAENIDAE							
Pterois antennata (Bloch)	1						
P. volitans (Linnaeus)		+	+	—	—	—	—
Scorpaenopsis gibbosa (Bloch & Schneider)	1						
SERRANIDAE							
Cephalopholis argus Bloch & Schneider	1						
C. urodelus (Bloch & Schneider)	*	16	—	—	—	—	—
Epinephelus emoryi Schultz	*	+	—	—	—	—	—
E. merra Bloch	1	—	2	+	2	—	—
Grammistes sexlineatus (Thunberg)	*	+	—	—	—	—	—
SIGANIDAE							
Siganus argenteus (Quoy & Gaimard)		—	—	—	—	+	—
S. punctatus (Bloch & Schneider)	1	—	—	+	—	—	—
S. spinus (Linnaeus)	1	—	—	—	+	+	—

Table 1. (continued)

Family/Species		I	II	III	IV	V	VI
SPARIDAE							
Monotaxis grandoculis (Forskal)	1	+	3	+	+	—	—
SPHYRAENIDAE							
Sphyraena sp.		—	—	—	—	+	—
SYNGNATHIDAE							
Corythoichthys intestinalis waitei (Jordan & Seale)	1	—	8	2	—	2	—
C. sp.		—	—	—	3	—	—
SYNODONTIDAE							
Saurida gracilis (Quoy & Gaimard)	1	—	1	—	—	—	1
Synodus variegatus (Lacepede)	1	—	2	2	+	—	1
TETRAODONTIDAE							
Arothron alboreticulatus (Tanaka)	3	+	+	—	—	—	—
A. immaculatus (Bloch & Schneider)	1	—	—	—	—	+	—
ZANCLIDAE							
Zanclus cornutus (Linnaeus)		2	13	20	2	—	—

Table 2. Summary of data by biotope (based on seven combined transects for each biotope).
N = Number of individuals observed on transects.
Ts = number of species observed on transects.
Rs = number of random species observed in 140 minutes (7×20 min.).
S = combined transect and random species or total species observed.
H″ = Shannon-Wiener diversity index (based on N and Ts; and linear biomass and *Ts*).
E = evenness values based on S (E = 1 would show perfect equitability).
Biomass ≐ total kg/ha values, all species combined less those with values under 0.5 kg.

	Area Sampled (Transects)	N	Ts	Rs	S	Biomass kg/ha	H″(N)	E(N)	H″(lbm)	E(lmb)
I Outside Reef	1400 m²	2397	94	147	150	43.07	3.338	0.666	3.590	0.716
II Channel Walls	1400 m²	2044	104	133	138	167.89	3.367	0.683	3.622	0.735
III Patch Reefs	1400 m²	1859	67	92	94	85.80	2.562	0.564	2.936	0.646
IV Barrier Reef Flats	1400 m²	2084	67	84	91	25.29	2.722	0.603	2.817	0.624
V Grass Flats	1400 m²	1489	22	29	32	14.79	1.916	0.553	2.047	0.591
VI Sand Bottom	1400 m²	159	7	11	14	3.38	0.966	0.366	1.059	0.401

that biotope I (outside) is "richer" than any of the lagoon biotopes. Lagoon biotope II follows in a close second and is itself approached by biotope IV only by virtue of the fact that IV has more individuals, although considerably fewer species. It is clear that while the first four (reef) biotopes are not widely separated in terms of individuals, biotopes I and II differ considerably from III and IV in number of species. Biotope V, although lower than the other biotopes in numbers of individuals, is still well represented. Biotope VI remains well below the range for other biotopes.

The picture changes somewhat when the biotopes are viewed in terms of biomass and the Shannon-Wiener diversity index. Biotope II supports the greatest biomass (Table 2). Biotope III is in a distant second place with about half the value of II and biotope I falls to third place. Biotopes III and IV showed the same number of transect species and IV had more individuals than III, yet III had a biomass value of more than triple that of biotope IV. This suggests that larger species make a stronger contribution to biotopes II and III than to the other biotopes. The biomass value of biotope V represents a large number of the juveniles of larger species which apparently use the grass flats as nursery grounds. The reader should bear in mind the fact that conversion constants were not available for all species. Therefore the biomass figures in Table 2 are only for the more common species, in each case the number should be higher.

The Shannon-Wiener diversity index (based on individuals, N) shows the highest diversity value for biotope II, closely followed by I (Table 2). The fact that biotope I has a greater number of individuals (N=2397) and total number of species (S = 150) than biotope II (N = 2044, S = 138) is offset by the fact that the calculations for the diversity index consider only the number of transect species and does not include random species (Ts = 94 for biotope I and 104 for biotope II). Moreover, the Shannon-Wiener function describes the degree of uncertainty in predicting the species of an individual picked at random from the community. The uncertainty, and therefore the value of the index, increases not only as the number of species increases but also as the individuals are distributed more evenly among the species present (Table 2). As expected, from the lower numbers of species and lower equitability, (evenness) biotopes III and IV show considerably lower indices than I and II. Biotope IV has a slightly higher diversity index than III, which indicates that although biotopes III and IV have the same number of species (Ts = 67), the individuals are more equitably distributed among the species in IV than those in III (Table 2).

The linear biomass values for each species in each biotope were also used to calculate the Shannon-Wiener function. These data are found in Table 2 and follow the same general pattern as the indices based on individuals and number of species, with the primary exceptions being the higher overall diversity values and the reversal of positions of biotopes III and IV. In the latter case there is an increase in the evenness in biotope III over biotope IV. Moreover, as noted above with biomass, there is a greater preponderance of large species in biotope III than IV. Since H'' based on linear biomass takes into consideration the relative size of the species and the distribution of size among them, biotope III is the more diverse. The percent differences are not great in the latter case and may not be significant.

Figure 2 is a plot of community ordination based on the dissimilarity coefficients. The relationships of the communities of each biotope and the validity of these relationships are obvious from the figure and associated correlation coefficient. Communities of biotopes I–IV form a rather tight grouping when compared to V and VI, which are in turn widely separated from each other. It is apparent that the

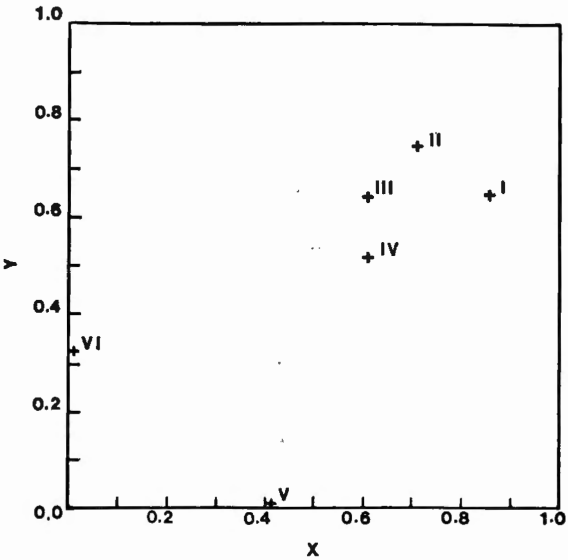

Fig. 2. Plot of community ordination between biotopes using species importance values. (r=0.87).

I–IV grouping is based on the one principal unifying factor that all four biotopes have in common, they are coral reef structures. Biotopes V and VI obviously are structurally different from the above. The separation between V and VI is no doubt based on the more adequate cover provided by the grass beds for the fishes themselves as well as the organisms the fishes feed upon. As pointed out above, the grass flats have a preponderance of juvenile fishes in temporary residence while awaiting maturity. The sand bottom fishes are either transients or burrowing forms. It comes as no surprise that the greater diversity of microhabitats available to reef dwelling species results in a much greater biological diversity and species richness.

Further inspection of Figure 2 reveals that the greatest similarity is between lagoon biotopes II and III. Moreover, biotopes I and II, and III and IV, have a fairly high degree of similarity or community concordance. This is of interest because it may indicate that the channel biotope (II) bridges, in part, the gap between the lagoon communities and those outside the barrier reef.

Table 3 compares for combined transects of biotopes II–IV, the rank order of the 20 species with the highest index values for each of the four indicated techniques used in estimating species value. For example, the rank order of the top 20 species is shown for number of individuals (N), for overall importance values (O.I.V.), for linear biomass (lbm.) and for actual biomass (kg/ha). The table not only compares the four methods but also shows the relative importance of each species in the three lagoon reef biotopes based on each method.

It is evident from Table 3 that only small differences exist between the rank orders of species listed by N, O.I.V. and lbm. Spearman's rank correlation coefficient indicated that the ranks of these three methods are highly correlated with

Table 3. Comparison of rank order of top 20 species from reef biotopes II–IV using all four evaluation techniques (N, O.I.V., lbm and kg/ha).

Species	N	Species	O.I.V.	Species	lbm	Species	kg/ha
C. caeruleus	924	*C. caeruleus*	22.6	*C. caeruleus*	7.9	*S. sordidus*	50.8
A. curacao	450	*A. curacao*	14.1	*S. sordidus*	7.6	*M. amaenus*	33.0
H. trimaculatus	422	*H. trimaculatus*	13.0	*A. curacao*	7.2	*P. nigricans*	25.3
D. aruanus	386	*P. albofasciatus*	11.7	*H. trimaculatus*	6.4	*C. striatus*	24.4
P. albofasciatus	380	*S. sordidus*	11.5	*P. nigricans*	6.0	*M. murdjan*	12.0
P. vaiuli	288	*D. aruanus*	10.7	*P. albofasciatus*	5.5	*F. sammara*	13.4
A. glaucus	266	*P. nigricans*	9.6	*C. striatus*	4.6	*S. venosus*	9.1
S. sordidus	255	*P. vaiuli*	7.8	*D. aruanus*	4.5	*A. curacao*	9.0
P. nigricans	243	*C. striatus*	7.0	*F. sammara*	3.5	*P. albofasciatus*	8.8
S. bandenensis	238	*S. bandenensis*	7.0	*S. bandenensis*	3.4	*E. insidiator*	7.4
Apogon sp.	200	*A. glaucus*	6.8	*P. vaiuli*	3.3	*P. lividus*	6.5
C. striatus	169	*Apogon* sp.	5.7	*M. amaenus*	2.9	*H. trimaculatus*	6.3
M. atrodorsalis	167	*F. sammara*	5.4	*A. glaucus*	2.6	*D. aruanus*	5.3
F. sammara	108	*P. traceyi*	5.2	*Apogon* sp.	2.4	*Z. cornutus*	4.9
H. margaritaceus	82	*M. atrodorsalis*	4.6	*M. murdjan*	1.9	*C. trifasciatus*	3.6
A. lacrymatus	78	*M. amaenus*	4.1	*M. atrodorsalis*	1.7	*P. multifasciatus*	3.4
C. quinquelineata	67	*M. murdjan*	2.6	*C. quinquelineata*	1.3	*A. xanthopterus*	3.3
M. amaenus	65	*A. lacrymatus*	2.5	*P. lividus*	1.3	*S. bandenensis*	3.0
P. traceyi	63	*C. quinquelineata*	2.3	*S. venosus*	1.3	*A. chinensis*	2.9
T. hardwickei	61	*T. hardwickei*	2.2	*T. hardwickei*	1.2	*C. caeruleus*	2.9

each other (N vs O.I.V., rs = 0.91; N vs lbm., rs = 0.81; O.I.V. vs lbm., rs = 0.90; in all cases $p < .0005$). Therefore, in this study and for these biotopes and fishes, any one of the three methods would have given similar results. There is some evidence to indicate that linear biomass provided more weighting to larger fishes (e.g., the advancement of *Scarus sordidus* from eighth and fifth places for N and O.I.V. to second for lbm) to better equate them to the more numerous smaller species than did N and O.I.V. Biomass on the other hand provides an obvious across-the-board difference in rank order of the top 20 species. *Chromis caeruleus* which ranked number one in the first three techniques was last in kg/ha. Moreover, several species occur in the top 20, based on biomass, that did not rank high enough in the other techniques to make the lists. Likewise, several species dominant in the first three lists are absent from the biomass list. Spearman's rank order correlation indicates little or no correlation between the rank of the biomass technique and the other three (N vs kg/ha, rs = 0.03; O.I.V. vs kg/ha, rs = 0.20; lbm vs kg/ha, rs = 0.35; and the probability values are $p > .10$, $p > .10$, and $p > .01$, respectively). Of the above three, lbm most closely approximates biomass.

We are left with the usual, perhaps rhetorical question, of whether a large number of individuals of small species are more "important" to a community than fewer individuals of larger species. They are no doubt both equally important to the community structure but the question plays havoc with sampling techniques. The first four species in the biomass list account for more than 50% of the total weight of the top 20 species (Table 3).

CONCLUSIONS

Although the channel-wall biotope (II) of Cocos Lagoon proved to be more diverse than the biotope outside the barrier (biotope I) in terms of transect species, diversity, and biomass, it seems that the lagoon as a whole is not supporting an exceptionally rich ichthyofauna. Even with the use of ichthyocides, we doubt that the total number of species in the lagoon would amount to much more than half of the nearly 600 species known from Guam to date. Moreover, if random species are also considered, then biotope I would exceed biotope II in species richness (150 to 138). We account for the higher diversity and biomass in biotope II by the fact that the steep lagoon slopes with their dense, and at times cavernous or overhanging, coral structures are a concentrating feature not duplicated in the outside reef biotope investigated.

Were it not for the reef development within the lagoon, as well as the rubble tracts and seagrass beds, the lagoon would be considerably more depauperate. Comparison of biotope VI (sand bottoms) with the other biotopes makes this point obvious. Unfortunately, the sand-dominated biotope makes up considerably more of the total lagoon than those areas (biotopes II–V) that provide more adequate cover and possibly a food supply for the fishes (Randall *et al.* 1975).

Qualitative observations as well as many of our transect counts indicated that large numbers of juvenile reef fish species occurred in the lagoon. This was true both in areas with reef cover and in the seagrass beds. These observations lead us to believe that the lagoon's enclosed nature, coupled with the natural cover available, makes Cocos Lagoon an invaluable nursery for many of the species. For example, large numbers of juvenile rabbitfishes, goatfishes, and snappers were observed in the *Halodule* beds and equally large numbers of juvenile parrotfishes were observed in the *Enhalus* beds. On one occasion, we saw enormous (too numerous to count) schools of juvenile surgeonfishes, *Ctenochaetus striatus*, swarming among the coral colonies of the channel walls (biotope II). All these species form important components of Guam's sport and commercial fishery.

The lagoon as a whole and the areas of natural cover within the lagoon do, therefore, make a significant contribution to the local fish fauna, both adults and juveniles. Physical disruption to the seagrass beds or the coral reefs and rubble tracts in the lagoon could affect, seriously, the fish populations of the lagoon as well as the rate of recruitment of subadults to nearby reef areas outside the lagoon.

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