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THE ISLAND AND MAINLAND BIOGEOGRAPHY OF RESIDENT ROCKY-SHORE FISHES IN THE GULF OF CALIFORNIA

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THE ISLAND AND MAINLAND BIOGEOGRAPHY OF RESIDENT ROCKY-SHORE FISHES IN THE GULF OF CALIFORNIA

by

Matthew Reid Gilligan

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In the Graduate College

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As members of the Final Examination Committee, we certify that we have read the dissertation prepared by Matthew Reid Gilligan

entitled THE ISLAND AND MAINLAND BIOGEOGRAPHY OF RESIDENT ROCKY-SHORE FISHES IN THE GULF OF CALIFORNIA

and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy.

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Date

Date

Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copy of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

D A Thomson
Dissertation Director

2/19/80
Date

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SIGNED: Matthew R Gilligan

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TABLE OF CONTENTS

TABLE OF CONTENTS--Continued

LIST OF TABLES

LIST OF TABLES--Continued

LIST OF ILLUSTRATIONS

LIST OF ILLUSTRATIONS--Continued

Figure | Page

ABSTRACT

Resident rocky-shore fishes were quantitatively sampled and visually censused on islands and mainlands in the Gulf of California. Patterns of biogeographic distribution were investigated in relation to the MacArthur-Wilson model of island biogeography, and the lottery hypothesis of reef fish community structure.

Analyses of the collections show regular patterns of distribution and relative abundance of rocky-shore fishes. Most of the variation in species number and species diversity is explained by latitude and the associated gradient of physical and oceanographic parameters. The correlation of species number and diversity is higher for island than for mainland samples.

The best graphical (numerical clustering) evidence of distinct biogeographic regions in the Gulf is obtained using a similarity measure which includes proportional abundance of species (Horn's measure). Groups corresponded to upper, central, and lower Gulf areas.

Greater species number, biomass, and numerical (H'_n) and biomass (H'_b) species diversity on islands is paralleled by greater water clarity and volume of ocean near collecting sites. This is true for the entire Gulf, the central Gulf, and for Isla San Pedro Nolasco versus the adjacent mainland rocky shoreline in the central Gulf. Community differences between island and mainland areas were greatest in the upper Gulf.

'Gamma' diversity, a proposed measure of community variance (site to site species turnover within habitats) is highest for mainlands and lowest for islands indicating more predictable community species composition on islands. Visual censuses show a good species-area curve for patch reefs and very small nearshore islands and lower species turnover in more exposed near shore habitats.

There is a trend toward smaller body size of fishes on islands and an increase in body size with latitude. It is suggested that both phenomena are the result of thermally regulated growth rather than genetic population differences.

High endemism in the resident rocky-shore community (the small sedentary, blennioid and gobioid fishes) is attributed to their relatively poorer means of dispersal (demersal eggs and short-lived pelagic larvae) as compared to the more mobile larger resident reef fishes with greater means of dispersal (pelagic eggs and long-lived pelagic larvae).

Insular biogeographic processes in marine reef habitats are mediated by physical and biological oceanographic conditions and processes. Distance appears to be no significant barrier to dispersal for Gulf rocky-shore fishes. Immigration rates may be high in rocky habitats in general, but in inshore mainland areas physical and biological disturbance suggest higher extinction rates and consequent lower diversities.

The results of these studies do not agree well with either the MacArthur-Wilson model of island biogeography or the lottery hypothesis of reef fish community structure, however, disturbance does seem to play some role in regulating diversity. Considering dispersal and colonization, oceanographic conditions (e.g., water quality, current patterns) may be important ecological factors that influence the evolution of this community.

CHAPTER 1

INTRODUCTION

Many of the principles that have become the dogma of evolutionary ecology and biogeography are based mainly upon terrestrial patterns of distribution, abundance, and resource allocation (MacArthur and Wilson 1967; Leigh 1971; MacArthur 1972; Pianka 1974; Cody and Diamond 1975; Roughgarden 1979). Marine reef fishes, and perhaps fishes in general, differ remarkably from most other vertebrates and terrestrial organisms in important aspects of their life histories, growth, patterns of food and space resource utilization, species interactions, and population dynamics. Because the processes of dispersal and colonization in marine shoreline and reef communities are so strikingly different, it has become apparent that some current models of biogeography and community structure may not provide a realistic framework for their study. In fact, that marine systems have provided so little empirical or theoretical support for models based on the provocative terrestrial patterns (e.g., MacArthur-Wilson model of island biogeography, species-packing and optimal foraging theory) questions the general nature of these formulations.

Mechanisms of diversity regulation and community evolution in reef fishes are poorly understood. Essentially descriptive studies suggest that species are not randomly distributed within habitats and that a certain kind of order exists (Hiatt and Strasburg 1960; Tyler 1971; Collette and Talbot 1972; Smith and Tyler 1972; Bradbury and Goeden 1974; Chave and Eckert 1974; Goldman and Talbot 1976; Clarke 1977; C. L. Smith 1978). However, some experimental studies (Sale and Dybdahl 1975; Sale 1977, 1978; Talbot, Russell and Anderson 1978) suggest unpredictable distributions and community structure which is largely the result of stochastic processes. Helfman (1978) suggests that the relative roles of deterministic and random processes may be different in different systems.

Life histories of marine reef species and marine fishes in general usually involve large numbers of small pelagic (planktonic) eggs and larvae; parental care of young is practically nonexistent. It appears that this kind of strategy of reproduction and dispersal has evolved in response to high predation on early life stages and the distribution of and need to colonize post-larval habitats (Johannes 1978). Reef-fish communities reflect continuous colonization processes where only slight differences in percent survival of propagules may produce large fluctuations in adult populations (Cushing 1973; Larkin 1978) and where, since most reproduction is exported, population growth of reef species is more or less independent of local population sizes.

Flexibility in growth and in species interaction have been stressed as important considerations in fishes (in relation to ecology and community structure) (Werner 1977; Helfman 1978; Larkin 1978). Growth in fishes is not indeterminate but growth rates are quite variable and can be influenced by temperature (Kinne 1963), feeding and diet (Martin 1966), and by intra- and interspecific social control

(Allen 1972; see also C. L. Smith 1978). Smith (1978) has suggested that a certain amount of community organization, reflected in the smooth progression of size of largest individuals of infaunal reef fish species may be a result of behavioral growth limitation. Age- and size-specific shifts in trophic relationships (Helfman 1978, p. 136; Larkin 1978, p. 60) and habitat selection, combined with behavioral plasticity, result in wide niches in fishes and create difficulties in studying resource allocation and overlap implicit in species packing theory. Niche complementarity (Werner 1977) is apparently one mechanism associated with these peculiarities in fishes that allows coexistence of species that are separated by less than the theoretically predicted minimum distance along a resource axis.

Related to dispersal and population processes in reef fishes are questions of whether marine islands are 'biogeographic islands' to shore fishes as they are to terrestrial plants and animals and how biogeographic distributions in reef fishes are related to environmental predictability.

Marine islands represent potentially isolated habitats for shoreline-restricted marine organisms, yet it is not clear that they have impoverished biotas relative to adjacent mainland shores as do their terrestrial counterparts. Additionally, it is not clear that colonization rates based on distance from propagule sources, and extinction rates based on island size (as suggested by MacArthur and Wilson 1967), play a substantial role in determining the number of species that may occur there.

Although adults and juveniles of most marine shore fishes cannot readily cross the deep waters separating land masses, eggs and larvae are often found at great distances from shore (Leis and Miller 1976). Certain families of teleostean fishes (e.g., the blennioids and gobiioids) have demersal eggs that are attached to the substrate and only the larvae are dispersed by ocean currents. Some of these have short-lived larvae which normally are found only close to shore. Apparently that distance over open water must be some sort of barrier to dispersal in shore and reef fishes as it is to terrestrial species. In fact, shore fish faunas of oceanic islands show high degrees of endemism, e.g., 23% in Galapagos shore fishes (Walker 1960), 29% and 27% in Hawaiian and Easter Island fishes, respectively (Randall 1976). The first part of this study concentrates upon the biogeographic distribution of rocky-shore fish species with restricted dispersal ability; the species for which distance is most likely to be a barrier to dispersal.

The well known MacArthur-Wilson (M-W) model of island biogeography (MacArthur and Wilson 1963, 1967; Diamond 1969; Simberloff and Wilson 1969, 1970) predicts that the number of species of plants or animals on islands or in isolated habitats reaches an equilibrium that is the result of a balance between the opposing rates of immigration and extinction. The immigration rate is inversely related to the number of species on the island and extinction rate is directly related to the number of species. Colonization and extinction are continuous (the equilibrium is dynamic) and species' identities change (species turnover occurs). Modifications of the M-W model have been suggested (Brown and Kodric-Brown 1977) and other explanations (Roughgarden's 'ecological algorithm' /n.d./, and Rosen's 'vicariance model' /Rosen 1975/) have been proposed to account for the distributions of plants and animals on islands. The first alternative view essentially predicts that dispersal into a region will continue until habitats are saturated and, beyond this, continued immigration will have little effect on species composition and will not cause significant species turnover. The other view invokes historical explanations related to dynamic geological processes (tectonics and barrier formation) rather than dispersal to account for distributional patterns.

Most aquatic studies of insular biogeography have used small scale insular habitats (Schoener 1974a, 1974b). Results indicate that marine colonization processes may be fundamentally different than those in terrestrial systems. Experimental studies of fishes on artificial patch reefs in the Gulf of California (Molles 1978), the Great Barrier Reef of Australia (Talbot et al. 1978) and in Florida (Bohnsack 1979) showed patterns of immigration and extinction which fit predictions of the M-W model. In apparent contradiction to these, G. Smith (1979) studying recolonization of Gulf of Mexico patch reefs after natural defaunation by a red tide showed that fish communities developed according to a well-defined successional sequence and not by primarily stochastic processes. Although some different species were initially successful on the reefs a "climax" community formed rather than a dynamic species equilibrium affected by continued species turnover. Bohnsack (1979) suggests that contradictory impressions or interpretations of reef fish communities may arise from the variable sampling intervals in different experimental studies and the sensitivity of turnover values to interval length (Diamond and May 1977). Longer time intervals between censuses fail to detect many colonizations and extinctions resulting in a lower estimated rate of species turnover than if a shorter census interval had been used.

On a larger scale, it is well known that marine insular environments differ considerably from mainland or 'continental' environments (Robins 1971). Essentially, the former are characterized by a more stable, predictable physical regime with fluctuations in physical factors (e.g., sea temperature, salinity, turbidity) moderated and buffered by larger current volumes, whereas the latter usually have wider and more unpredictable fluctuations. Starck (1968), Robins (1971) and Gilbert (1972) have all noted that the differences in the identities of families, genera, and species of shore fishes between insular and continental areas of the western Atlantic are related to these physical characteristics. They feel that these distributional distinctions are more the result of 'ecological' barriers rather than barriers to dispersal *per se*.

Similar differences in patterns of distribution in offshore vs. inshore environments have been noted in fossil assemblages of benthic invertebrates (Valentine and Moores 1974; Bambach 1977) and for benthic and demersal carnivores (Bakus 1969, p. 353). Continental and insular patterns of distribution of coral reef asteroid species noted in the Indo-Pacific appear to be related to larval swimming behavior (Yamaguchi 1977).

Studies of island-mainland reef-fish distributions and biogeography intersect with current hypotheses and investigations in reef fish community structure. The lottery hypothesis or 'chaos' view of reef fish diversity maintenance and community structure (Sale and Dybdahl 1975; Sale 1977, 1978) invokes stochastic processes in the settlement or recruitment and in the elimination of individuals from the reef. In this scheme the earliest larvae to settle in an unoccupied space, regardless of identity, will have an advantage and effectively exclude late arrivals. This model assumes uniformly high dispersal and colonization rates and competitive equality among species and a high degree of resource overlap of which space is considered to be the only limiting resource. This view predicts that reef-fish communities will be unstable and not resilient (i.e., unlikely to return to a similar composition if disturbed), and that community composition should vary stochastically from patch to patch within habitats and from time to time within habitats.

An alternate deterministic or 'order' view maintains that after defaunation successional events will rapidly and ultimately result in a community composition not unlike that of the original community (C. L. Smith 1978; Thomson and Lehner 1976; G. Smith 1979). This implies that habitat selection, competitive superiority, and species-specific rates of colonization and immigration play a major role in community organization. Apart from seasonal compositional changes, this view predicts lower species turnover from site to site and within sites and that species composition and community structure should be relatively constant within similar habitats in a biogeographic region. In this view communities should reflect habitat characteristics (e.g., reef structure species pool, island size and distance to colonizing source, resource spectra).

Within the framework of these different views or hypotheses it should be noted that M-W equilibria require stochastic immigration and extinction with competitive interactions influencing the extinction rate, whereas the lottery hypothesis, which also involves random recruitment and extinction, maintains that competitive processes are unimportant in community development and organization.

In these studies I examine the biogeographic and community patterns of rocky shoreline fishes in the Gulf of California, Mexico, to determine how well they conform to existing models and hypotheses of biogeography and community structure in reef fishes. The Gulf of California and eastern tropical Pacific are dominated by rocky rather than coral reef habitats yet this area supports a diverse, primarily tropical (Panamic) reef-fish fauna (Walker 1960; Thomson, Findley and Kerstitch 1979; Thomson and Gilligan n.d.). I focus upon the regularity and predictability of compositional change throughout the Gulf and discuss the patterns which emerge in relation to studies on a smaller scale, within a peninsular shoreline habitat gradient in the central Gulf. I explore mechanisms of diversity regulation in this community which help explain island-mainland phenomena in marine systems. Understanding the patterns of distribution and change in species diversity is essential to sorting out the important ecological factors that influence the evolution of these communities.

CHAPTER 2

MATERIALS AND METHODS

A total of 28 island and 22 mainland sites in the Gulf of California (Fig. 1 and Appendix A) were sampled between June 1973 and July 1976, usually during the summer and fall months of highest sea temperature. Quantitative collections of fishes were made along the shorelines of small protected rocky coves of similar substrate topography and complexity (e.g., crevices, ledges, loose rock) and depth profile. This type of habitat is commonly found along steeply sloping rocky coastlines in the Gulf (Fig. 2). The collections were standardized by spreading 500 ml of Pro-noxfish, a rotenone base ichthyocide (Meyer, Schnick and Cumming 1976), over an area not smaller than 10 m^2, bounded on one side by the shoreline. In most cases the slope of the substrate below the sea surface was nearly 45 degrees and the maximum depth was three meters. All fishes in the area that were partially or totally immobilized by the toxicant were collected using hand nets (Fig. 3) and a modified "slurp gun" device (Gilligan 1976). All fishes could be collected by a diver using SCUBA in 1.5 to 2 hours. The more mobile resident species that usually were able to escape the ichthyocide (e.g., damselfishes) and transient species (e.g., mullets, anchovies, etc.) were collected but not included in the analysis. All resident reef fishes that were judged to be quantitatively sampled by

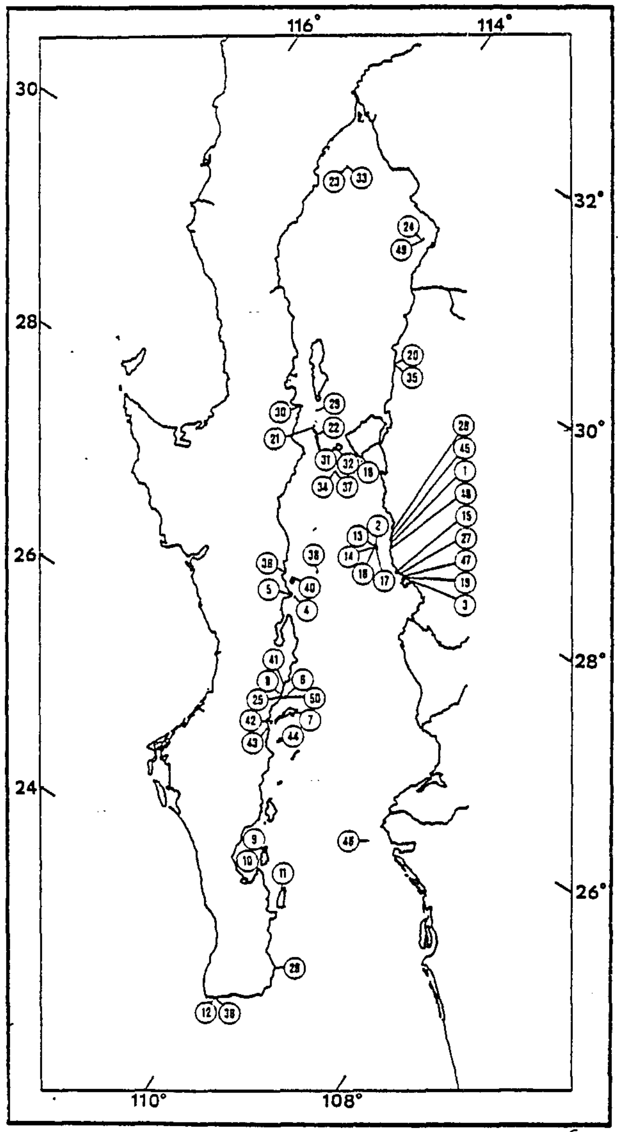


Figure 1. Location of ichthyocide collections of rocky-shore fishes in the Gulf of California. -- Map numbers correspond to collection numbers in Appendix A and Tables 1 and 2.

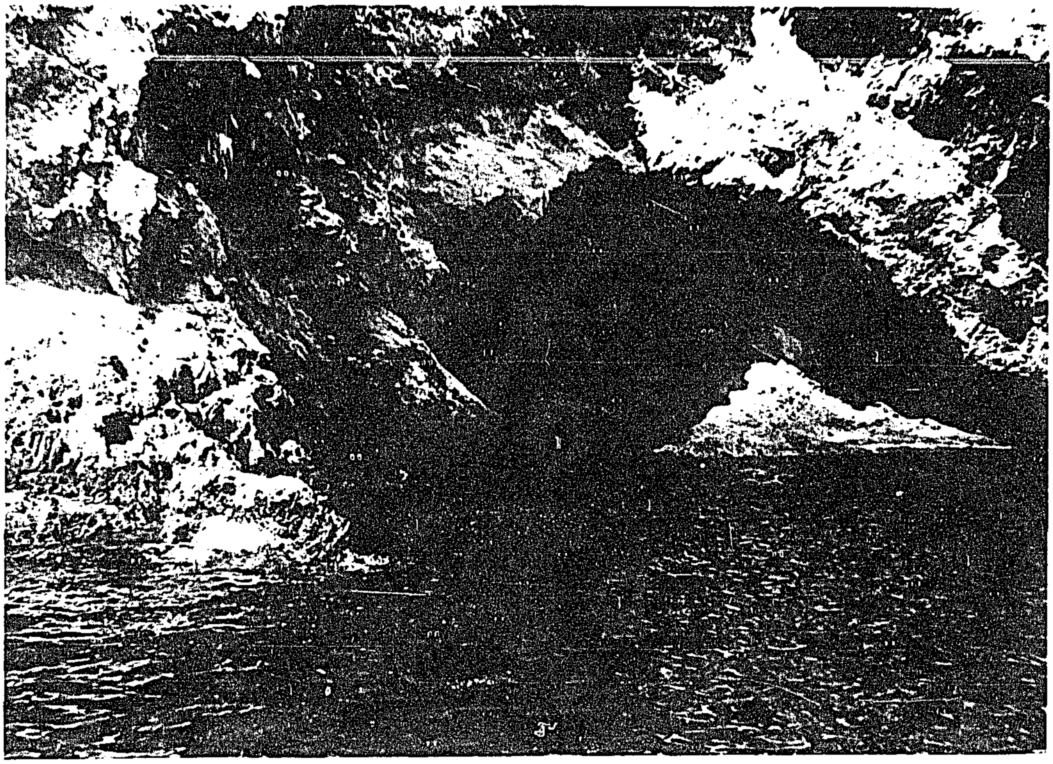


Figure 2. Protected rocky shoreline (collection #37, Isla San Pedro Martir) typical of areas sampled on islands and the mainland coastlines in the Gulf of California.

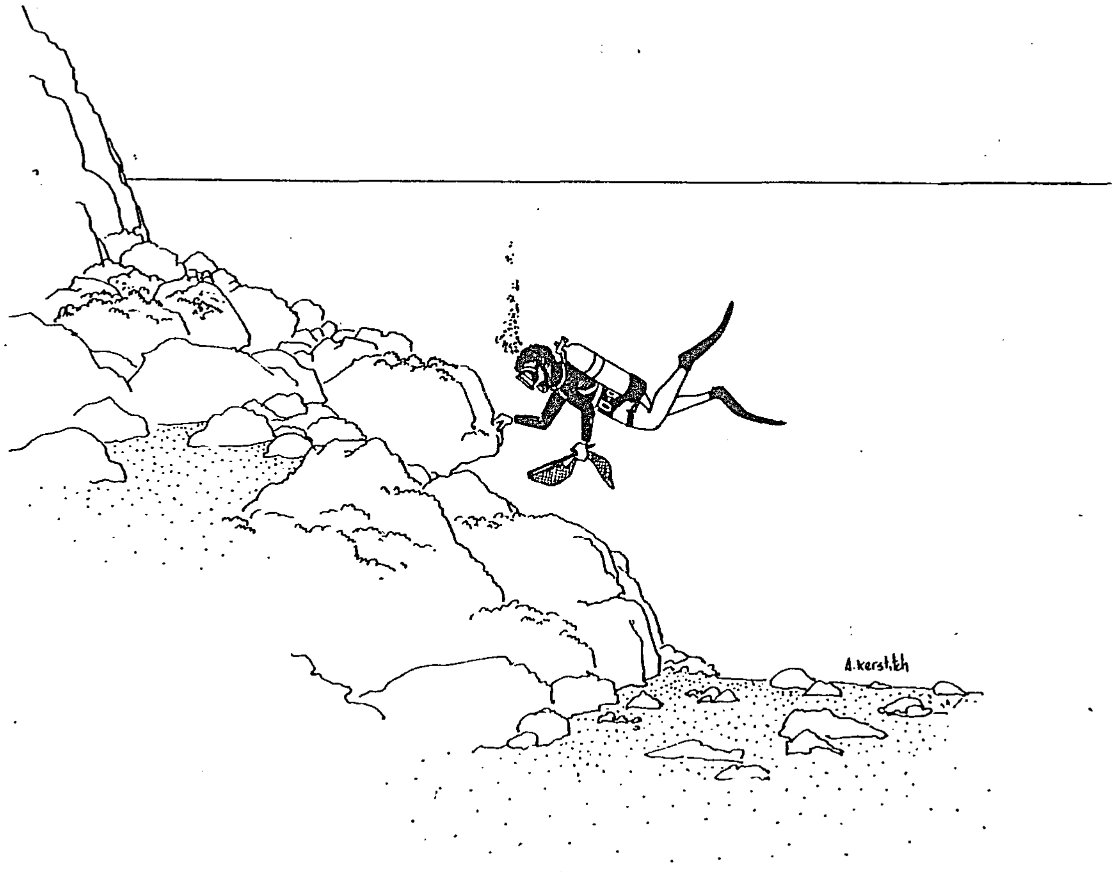


Figure 3. Nearshore (shoreline) depth profile and collecting technique typical of collections made on rocky reefs in the Gulf of California.

this method (i.e., species that are unable to avoid or escape from the toxicant due to their strong degree of association with hard substrates and limited mobility were included in the analyses.

Samples were preserved in 10% formalin, stored in 40% isopropyl alcohol, identified, counted, and weighed by species lots to ± 0.05 gm on a Mettler K7T top-loading balance after blot-drying. All specimens are deposited in The University of Arizona Fish Collection.

Sea surface temperature (1 m below the surface and several meters offshore) and secchi disk depth (a measure of water transparency) were recorded at the time of each collection. Latitude, mean monthly sea surface temperature, island area and perimeter, distance of islands to the nearest mainland rocky shore and ocean volume within 20 km were determined for each site (Tables 1 and 2).

Ancillary studies involving visual observation census methods of reef fish species on small nearshore islands and along a mainland shoreline habitat gradient in the central Gulf were made in conjunction with the present study. The former methods are outlined below and the latter are given elsewhere (Gilligan in press).

Visual methods were used to obtain species number only for the small nearshore islands in the Guaymas-San Carlos area of the central Gulf (see Fig. 4 and Table 3). Each fish species that was observed while snorkling three meters from the rocky shoreline on a path that circumscribed the entire island was recorded on a data sheet. Habitat area of each island was estimated by the circumference of each island. This was used since the nearshore rocky reef habitats of these islands and most Gulf islands generally form a ring around the island, bounded

Table 1. Physical data of mainland areas sampled in the Gulf of California.

Name of Area	No. of Collections	Sample Numbers[1]	Rocky Coastline[2] (km)	Mean Monthly Min. Temp.[3] (°C)	Mean Monthly Max. Temp.[3] (°C)	Vol. of Water Within 20 km (km^3)[4]
South of Libertad	2	20, 35	20	16	30	43
Punta Que Malo	1	30	98	14	28	334
Guaymas vicinity	9	28, 45, 1, 48, 15, 27, 47, 19, 3	45	16	30	73 to 132
Santa Rosalia	1	39	98	16	31	460
Punta Chivato	1	5	5	17	31	470
North of Loreto	3	41, 8, 25	98	18	31	478
South of Loreto	1	42	98	18	31	478
La Paz	1	10	27	19	31	483
Cabo Pulmo	1	26	5	20	30	490
Cabo San Lucas	2	12, 36	10	21	29	483

[1] Sample numbers listed in Appendix A and in Figure 1.

[2] Km of a major rocky coastline contiguous with a collection or collections.

[3] Mean monthly minimum and maximum sea surface temperatures from Robinson (1973).

[4] Volume of water within a 20-km radius of collection sites; calculated from areas between major depth isoclines measured with a planimeter from Chart I in Fisher, Rusnak and Shepard (1964).

It should be pointed out that those temperatures were taken from isotherm charts that were constructed using interpolation, space-smoothing and time-smoothing computer analyses of temperature data collected (on oceanographic cruises) from 1949 to 1966. Consequently, maximum and minimum inshore temperatures may be expected to be underestimated and overestimated, respectively.

Table 2. Physical data of islands sampled in the Gulf of California.

Name	No. of Collections	Collection Nos.[1]	Area[2] (km^2)	Perimeter[3] (km)	Distance to Mainland[4] (km)	Mean Monthly Min. Temp[5] (°C)	Mean Monthly Max. Temp.[5] (°C)	Vol. of Water within 20 km[6] (km^3)
Roca Consag	2	23, 33	0.6	2.8	31	15	30	33
San Jorge	2	24, 49	2.4	5.5	13	16	31	25
Partida Norte	1	29	1.2	3.9	17	15	29	446
Tiburon	1	18	1208.0	123.2	2	15	30	82
San Lorenzo	2	21, 22	7.5	9.7	18	14	29	538
San Esteban	2	31, 32	43.0	23.2	37	15	29	447
San Pedro Martir	2	34, 37	1.9	4.9	48	15	30	550
San Pedro Nolasco	5	2, 13, 14, 16, 17	3.2	6.3	10	16	30	360
Tortuga	1	38	6.3	8.9	37	16	31	467
San Marcos	1	40	32.0	20.1	5	16	31	464
Santa Ines	1	4	0.4	2.2	2	17	31	470
Coronado	2	6, 50	8.5	10.3	2	18	31	477
Carmen	1	7	151.0	43.6	6	18	31	477
Danzante	1	43	4.9	7.8	1	17	31	477
Monserrate	1	44	19.4	15.6	13	18	31	479

Table 2--Continued.

Name	No. of Collections	Collection Nos.[1]	Area[2] (km²)	Perimeter[3] (km)	Distance to Mainland[4] (km)	Mean Monthly Min. Temp[5] (°C)	Mean Monthly Max. Temp.[5] (°C)	Vol. of Water within 20 km[6] (Km³)
Farallon	1	46	0.7	3.0	20	18	30	479
Espiritu Santo	1	9	99.0	35.3	6	18	31	483
Cerralvo	1	11	160.0	44.8	11	19	31	479

[1] Sample numbers listed in Appendix A and in Figure 1.

[2] Island area from Case (personal communication 1979).

[3] Perimeter of island calculated from area assuming circular islands.

[4] Distance to nearest mainland from Case (personal communication 1979) or measured by M. Gilligan.

[5] Mean monthly minimum and maximum sea surface temperature from Robinson (1973).

[6] Volume of water within a 20-km radius of collection sites; calculated from areas between major depth isoclines measured with planimeter from Chart I in Fisher, Rusnak and Shepard (1964).

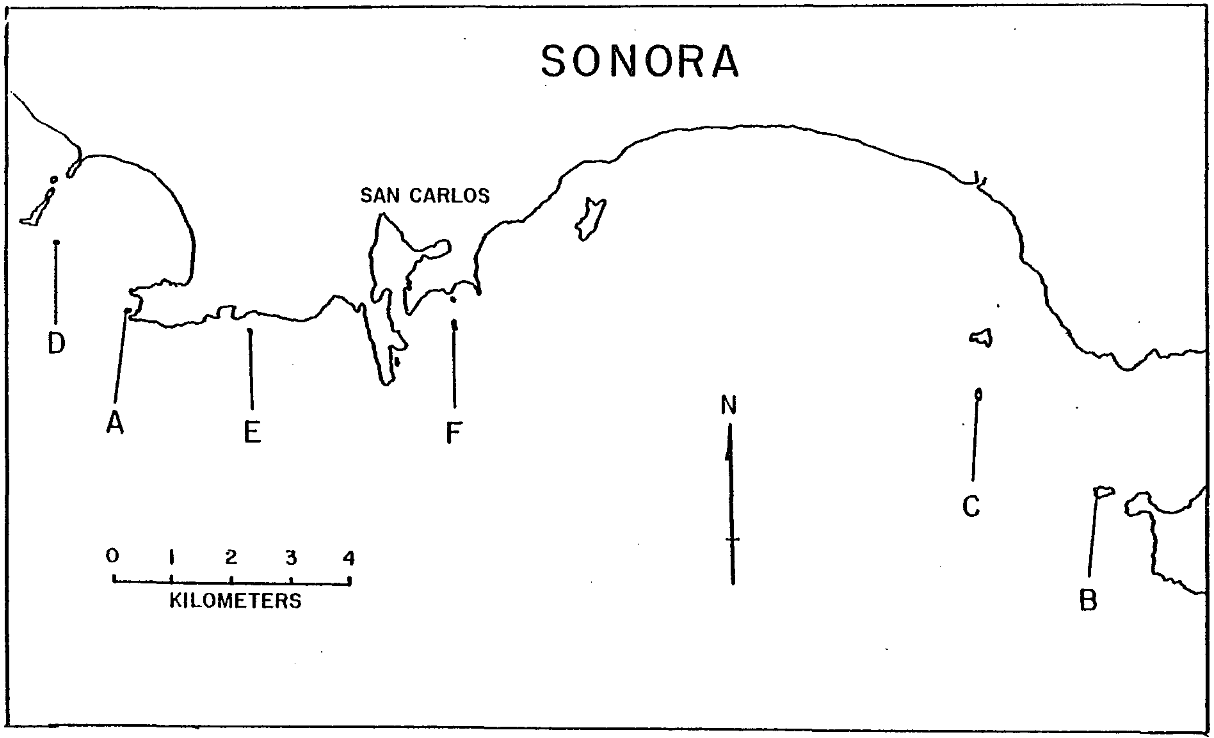


Figure 4. Small nearshore islands near San Carlos, Sonora, Mexico in the Gulf of California where species counts were made.

Table 3. Sampling date, subsurface reef area, and species counts for small islands and rocks in the San Carlos area in the Gulf of California. -- Letters refer to Figure 4.

Island/Rock Name		Date*	Area (m^2)	Species
A	Punta San Antonio rock	18 Oct. 1976	2800	33
B	Isla Blanca (Peruano)	19 Oct. 1976	7900	42
C	Isla Candelero	19 Oct. 1976	4300	40
D	Isla Venado rock	20 Oct. 1976	800	31
E	Lalo rock	20 Oct. 1976	2000	40
F	Isla San Nicholas	21 Oct. 1976	4300	34

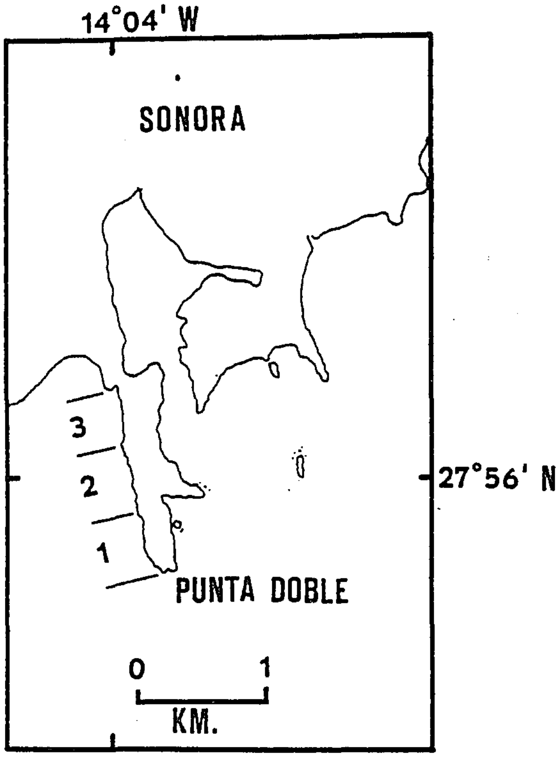
*Sea surface temperature in all areas was 28°C.

by the shoreline landward and sandy bottom seaward only a few meters offshore. Visual census methods used along a rocky shoreline habitat gradient in the San Carlos area (Gilligan in press) have also involved recording the frequency of encounter of each species in each of three segments of the shoreline (Fig. 5). It should be noted that visual census methods include many resident reef fish species that cannot be sampled quantitatively with a fish toxicant due to their larger sizes and greater mobility (e.g., wrasses, surgeonfish, parrotfish, angelfish) but are nevertheless reef residents. Likewise, many reef residents that can be quantitatively sampled by ichthyocide methods are small, cryptic, and secretive species (e.g., blennioids and gobioids) that are underestimated by visual methods.

Methods Measuring Species Diversity

The biological literature is replete with discussions of the distribution of individuals among species in ecological communities and biological collections. The methods that were chosen to quantify these properties in this study are presented here without detailed discussion of their requisite properties. However, references that were important in choosing appropriate measures will be cited in this and the following section.

Measures used to quantify the variety and abundance distributions of species into a single number are collectively referred to as diversity and evenness indices. The first and oldest concept of species diversity is simply species number or richness (S). From the generalization that a community with N individuals distributed evenly



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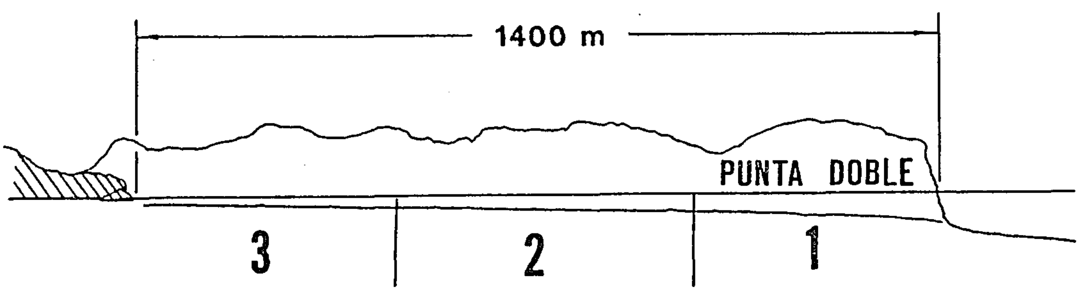

b

Figure 5. Rocky shoreline study areas of the Punta Doble peninsula near Puerto San Carlos, Sonora, Mexico in the Gulf of California. -- a, Map of the San Carlos, Sonora area showing Punta Doble and the study area segments (1 = point, 2 = middle, 3 = bay); b, Vertical profile of west side of peninsula and shoreline study segments (from Gilligan in press).

among S species should have a higher diversity value (measure or index) than one in which the N individuals are disproportionately distributed among the S species, several measures of species diversity have been introduced. These indices combine information regarding both richness and evenness or equitability of the abundance distributions. Their properties have been reviewed by several authors (Lloyd and Chelardi 1964; Sheldon 1969; Pielou 1966, 1975; Hurlburt 1971; Fager 1972; Hill 1973; Heip 1974; Peet 1974, 1975; DeJong 1975). Heip and Engels (1974) present a summary of most of the common indices. The Shannon-Weaver index (equation 1)

$$H' = -\sum_{i=1}^{S} \frac{n_i}{N} \ln \frac{n_i}{N} \quad (1)$$

was used in this study where S = the total number of species in a collection, n_i = the numerical abundance or biomass total of the ith species, and N = the total number or total biomass of all species.

Evenness is variously described as the ratio of H' (Shannon-Weaver in this case) diversity to a hypothetical maximum value. Maximum diversity (H_{max}) is the H' diversity that would be calculated if all individuals were evenly distributed among the species in a collection. H_{max} is equal to ln S and therefore evenness (J) is equal to H'/H_{max}. The antilog of J is $e^{H'}/S$ and represents the number of species evenly distributed that has the same diversity value as the collection for which it was calculated. Both species numerical diversity H'_n and species biomass diversity H'_b (Wilhm 1968) were calculated for each collection in this study.

Methods Measuring Similarity or Overlap

Collections were compared directly using several numerical methods in order to identify biogeographic patterns. Three measures of similarity between collections were used. The Simple Matching Coefficient (SMC) and the Jaccard Coefficient (JA) use information regarding only presence or absence of species and their identity. Figure 6a shows how presence-absence is tallied and Figure 6b shows how the coefficients are calculated. Both SMC and JA vary from zero when two collections are maximally dissimilar (e.g., no species in common between two collections) to one when the species lists are identical. The definition of maximum dissimilarity varies between these two measures. The SMC measure includes co-absence information in both the numerator and denominator (Fig. 6b) of the expression but the JA measure neglects co-absence information in both the numerator and denominator. Under certain assumptions it would be difficult to justify high similarities based on the absence of many species from two collections (sites) using the SMC measure but on the other hand, one might want to include co-absence information in order to get high enough similarity to reflect what might be ecologically important situations that result in species-poor communities. For discussions of these and other binary similarity coefficients see Clifford and Stephenson (1975), Anderberg (1973) and Sneath and Sokal (1973).

Horn's measure (Horn 1966) is a similarity coefficient that utilizes species abundance proportion information. It was chosen from among several like it (Mountford 1962; Hummon 1974; Grassle and Smith 1976) on the basis of its general use in ecology, statistical

A)

		collection X	
		present	absent
collection Y	present	a	b
	absent	c	d

B)

Simple Matching (SM)

$$SM = \frac{a + d}{a + b + c + d}$$

Jaccard (JA)

$$JA = \frac{a}{a + b + c}$$

Figure 6. Method of tabulation and formulae for Simple Matching and Jaccard measures of similarity. -- A, method of tabulation for presence-absence categories in binary similarity co-efficients. B, computational formulas for Simple Matching and Jaccard similarity coefficients.

a = total number of co-occurrences.
b = total number of present-absent mismatches.
c = total number of absent-present mismatches.
d = total number of co-absences or co-joint absences.

behavior, relation to other information theoretical measures used in ecology (e.g., Shannon-Weaver index), and relatively short computational formula. Horn's measure or index (R_o) is given in equation 2

$$R_o = \frac{\Sigma(x_i+y_i)\ln(x_i+y_i) - \Sigma x_i \ln x_i - \Sigma y_i \ln y_i}{(X+Y)\ln(X+Y) - X \ln X - Y \ln Y} \quad (2)$$

where x_i = the number of individuals of species i in collection x, y_i = the number of individuals of species i in collection y, X = the total number of individuals in collection x, and Y = the total number of individuals in collection y. This measure varies from zero when no species are held in common between two collections to one when the species identities and abundance proportions in the two collections are identical.

Dissimilarity between all paired combinations of the 12 (3 segments x 4 times) community estimates (CEs) in the visual transect along the Punta Doble peninsula was calculated by the Mean Character Difference coefficient (M.C.D.). The M.C.D. coefficient (Cain and Harrison 1958; Clifford and Stephenson 1975) varies from 0, when the species identity and coded frequencies are identical, to 1.0, when all the species coded frequencies are maximally different for any pair of CEs and is given in equation (3).

$$M.C.D. = \frac{1}{N_a} \sum_{i=1}^{N} \frac{|X_{ai} - X_{bi}|}{X_{max}} \quad (3)$$

N_a is the total number of species comparisons in which at least one of the coded frequencies was non-zero, X_{ai} is the coded frequency of species i in CE a, X_{bi} is the coded frequency of species i in CE b, and X_{max} is the highest coded frequency value (X_{max} = 4 in this study).

Using each of these similarity measures a $\binom{50}{2}$ or 1225 element similarity matrix was calculated for all possible pair-wise collection comparisons. Computer programs were written in Fortran IV by the author.

Numerical Cluster Analysis Methods

Several numerical methods were used to sort the similarity matrices and graphically display the resulting associations among entities (collections or visual community estimates). These methods involve agglomerative, heierarchical, polythetic clustering methods (Anderberg 1973) applied to the set of similarities between entities (similarity matrix) that were calculated from the vectors of variables associated with each entity. In this case the vectors of variables were species presence-absence and numerical abundance information. In this study the similarity matrix produced using each similarity measure was reduced sequentially using the clustering or sorting algorithm to produce a dendrograph (McCammon and Weninger 1970) which graphically displays the degree of association or correlation among the original entities. The clustering algorithm used involves evaluating potential mergers of clusters or entities (collections) by calculating the average arithmetic similarity for links between the two clusters or entities that are candidates for admission to extant clusters. This algorithm is variously known as the 'unweighted pair-group' method (Sneath and Sokal 1973), 'average linkage between merged groups' method (Anderberg 1973), or 'group average method' (Clifford and Stephenson 1975). A dendrograph (McCammon and Weninger 1970) expresses the average within-group correlation along the entity axis and average between-group correlation along the index axis (Fig. 7; see also Fig. 9, p. 37 and Fig. 11, p. 40).

All numerical analyses were performed on the University of Arizona Computer Center CDC Cyber 175. All statistics were done using SPSS version 7.0 programs (Nie et al. 1975) on the same computer system.

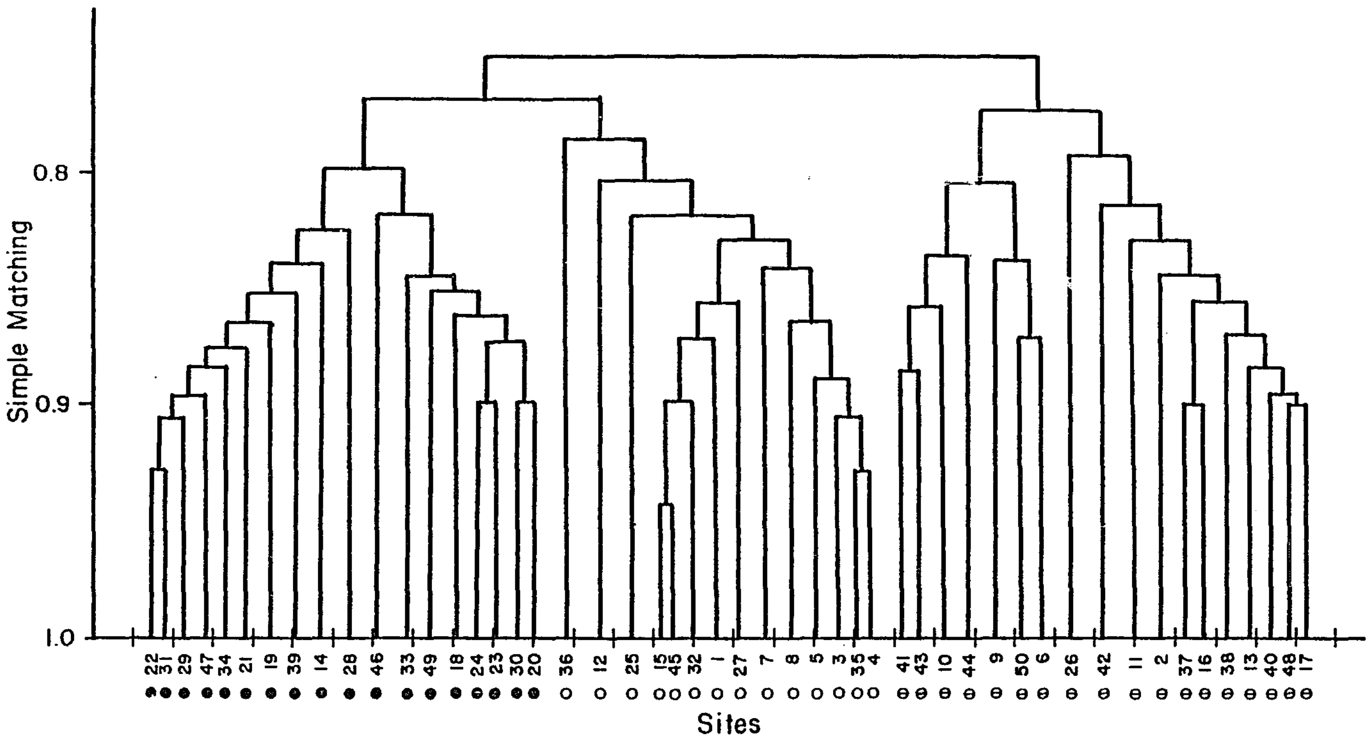

Figure 7. Dendrograph of sites (collections) in the Gulf of California using the Simple Matching Coefficient. -- Collection numbers refer to Figure 1 and Appendix A. See text for explanation of symbols.

CHAPTER 3

RESULTS

The 28 island and 22 mainland sites in the Gulf of California (Fig. 1) together with physical and community diversity data for each collection are given in Appendix A. Island and mainland physical data are given in Tables 1 and 2, respectively. Although Isla Venado (site no. 15 (Fig. 1 and Appendix A) is geographically an island, it is treated in this study as a mainland locality due to the questionable separation of its rocky reef habitats from the mainland rocky coastline.

A total of 68 species from 13 families from the 50 quantitative samples of the rocky-shoreline fish community were used in the analyses (Appendix B). Numerical abundance of each species at each site is given in Appendix C and a summary of species abundances, biomass, collecting frequency and body size in Appendix D. These species form an ecologically homogeneous group with regard to general habitat requirements. From Table 4 it can be seen that 84% have demersal eggs or are viviparous (i.e., they are primary residents), and 75% are benthic predators. They can additionally be defined by their relatively low adult mobility and inability to avoid an ichthyocide. Endemism in this group is high with 34% of the species having geographic distributions entirely or primarily within the Gulf of

Table 4. Characteristics of the 68 rocky-shore Gulf fishes analyzed in this study with respect to: residency; biogeographic affinity; egg type; food habits. -- Compiled from Appendix B.

Category	Percent of Fauna
<u>Residency</u>	
Primary (1°)	84
Secondary (2°)	16
<u>Biogeographic Affinity</u>	
Panamic	54
Gulf endemic	34
Mexican endemic	8
San Diegan	3
Indo-west Pacific	1
<u>Reproductive Products</u>	
Demersal eggs	82
Pelagic eggs	16
Viviparous	2
<u>Food Habits</u>	
Benthic invertebrate predators	75
Planktivorous	16
Herbivorous	6
Piscivorous	3
Other	4

California. If only the 17 most abundant species in the 50 samples are considered the level of endemism jumps to 62%. These 17 species (listed in order of abundance in Appendix D) account for 90% of all individuals collected.

<u>Test of Sampling Effectiveness</u>

A standard collection (see Methods) was made near Punta Candelero, Baja California Sur on 25 July 1976 (no. 42, Fig. 1, Appendix A). To evaluate sampling effectiveness, i.e., determine how many fishes were missed with standard collecting effort even though they had been killed by the ichthyocide, dead fishes were censused in the site the following day using SCUBA. The census of dead fish represents individuals that were undetected or had become dislodged from crevices subsequent to the initial collection, excluding, of course, fishes removed by scavengers or currents or those still hidden in crevices. Nineteen individuals of ten species were found out of a sample collection that originally yielded 431 individuals of 31 species. This was, incidentally, the richest of the 50 collections made in the entire study. This uncollected portion represents 4.2% of all individuals that were either collected or observed or a 95.8% individual collecting effectiveness, assuming that there were no losses. All ten of the species in the census were present in the original collection and therefore the species collecting effectiveness was 100%, assuming no losses. These ten census species represented 61.5% of the total number of individuals in the original collection and were therefore primarily the most common species. Individuals censused were not used in any further data analyses.

From these results I conclude that while it is unlikely that all individuals killed will be collected, the likelihood of not collecting a species that is present or of underestimating the abundance of any species is quite small. These samples, therefore, accurately reflect the species composition and the distribution of individuals in this habitat.

Collection Variables

The number of species in a collection varied from 8 to 31 and the number of individuals varied from 41 to 1138. Most of this variance in species number and abundance can be accounted for by the marked latitudinal gradients of physical environmental variables within the Gulf.

The major trends among the physical variables for each collection site may be summarized by the correlation coefficients in Table 5. Lower mean monthly minimum sea surface temperature (MIN), greater tidal range (TID), and decreasing volume of ocean within 20 km of a site (VOL) are all positively correlated with latitude. Although sea temperature at the collection site (WT) was not correlated with latitude there does appear to be a positive relationship between water transparency (SD) and sea temperature at the site (WT). Increasing water volume within 20 km of sites may reflect both a greater maximum depth and a larger area of ocean impinging upon a coastline site (i.e., greater exposure). Both of these factors may moderate sea temperature near shore and expose the coastline sites to open ocean currents which will influence dispersal and colonization by planktonic

Table 5. Pearson's correlation coefficient between 12 collection variables for 50 collections of fishes in the Gulf of California. -- * = $p < .05$; ** = $p < .005$.

SD - secchi depth
WT - water temp.
MIN - mean monthly min. sea temp.
MAX - mean monthly max. sea temp.
TID - tide range
VOL - volume of water within 20 km
LAT - latitude
S - number of species
N - number of individuals
B - total biomass
H'_n - numerical species diversity
H'_b - biomass species diversity

	SD	WT	MIN	MAX	TID	VOL	LAT	S	N	B	H'_n	H'_b
SD												
WT	.293*											
MIN	.007	-.007										
MAX	.084	.194	.197									
TID	-.297*	.081	-.496**	-.080								
VOL	.178	-.074	.254*	-.519**	-.349**							
LAT	-.155	.022	-.900**	-.100	.771**	-.406**						
S	.488**	.263*	.308*	.282	-.512*	.178	-.446**					
N	.438**	.385*	.124	.191	-.256*	.115	-.221	.673**				
B	.034	.070	.029	.149	-.068	-.001	-.049	.478**	.448**			
H'_n	.435**	.028	.230*	.319*	-.575**	.152	-.391**	.783**	.295*	.427**		
H'_b	.525**	.345*	.006	.244*	-.326	.215	-.150	.637**	.528**	.070	.564	

propagules. Higher mean monthly sea surface temperature in the lower Gulf suggests a buffering of temperature extremes by large volumes of Pacific water at the mouth of the Gulf.

Species diversity (H_n and H_b) is positively correlated with water clarity (SD) and mean monthly maximum sea temperature (MAX) and negatively correlated with tidal range (TID). Number of species is positively correlated with water clarity (SD), all the sea temperature variables (WT, MIN, MAX). This correlation analysis essentially reflects the strong latitudinal gradient of sea temperature (MIN) with latitude ($r = -.900$, $p < .005$) and the latitudinal diversity gradient. Although density of individuals (N) was correlated with neither (MIN) nor (LAT), since number of species (S) was correlated with density (N) greater richness may be, at least in part, an artifact of greater sample size.

Biogeographic Cluster Analysis of Collections

Geographic trends in the composition of this rocky-shore fish community were analyzed by identifying areas homogeneous with respect to composition based on several measures of association discussed in the Methods (Chap. 2). Each collection is treated as a site-entity described by a vector of presence-absence or abundance information. Numerical cluster analysis procedures sort these inter-entity association measures into graphical form.

Using the Simple Matching Coefficient (SMC) it can be seen from the dendrograph (Fig. 7) and corresponding map (Fig. 8) that three main groups or clusters of sites are identified, the most

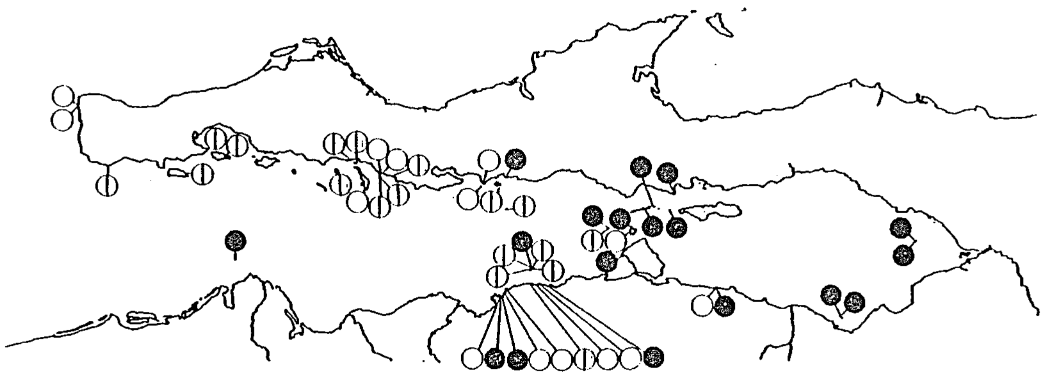

Figure 8. Map representation of site groups or clusters from the dendrograph produced using the Simple Matching Coefficient. -- See Figure 7 and text for explanation of symbols.

distinct being an upper-central group (solid circles, Fig. 8). There is considerable geographic overlap in the remaining faunal groupings (open and half circles). Part of the reason for this large overlap may be due to the real overlap in species geographic distribution as a result of dispersal vagaries. Since this measure (SMC) is insensitive to proportional abundances of species, this is to be expected. The simple matching coefficient approaches unity not only as the number of species in common to each collection increases in relation to mismatches, but also as the number of species absent from both collections increases. This means that two sites with relatively short species lists will be quite similar (high index value) on the basis of the large number of species that they both lack rather than the actual species identity similarity. This property may result in clustering that runs contrary to the biogeographer's intuition of areas and boundaries. Ecologically however, these clusters could represent species-poor communities that may be the result of similar sorts of diversity regulating mechanisms. For example, this may account for the clustering or fusion of Isla Farallon (no. 46, Fig. 1) with sites in the upper Gulf. One interesting observation from the dendrograph produced using the SMC measure (Fig. 7) is that the three highest similarities (earliest fusions) are between sites that are close to one another geographically (nos. 15 and 45, 4 and 35, 22 and 31 in Fig. 1). The three sites that fuse late and independently (outliers) show no real affinity or correlation (nos. 12, 25, and 36) with any group and consequently should not be designated as belonging to any group.

The Jaccard index (JA) neglects species co-absence information entirely. The dendrograph produced using this measure is given in Figure 9 and the site clusters identified on the map in Figure 10. This measure defines fairly well the upper Gulf community (solid circles). Notice that the most southerly of these sites are not well clustered (i.e., earlier fusions) suggesting subtle distinctions in this area. Within the other major branch of the dendrograph representing the rest of the Gulf collections one sub-group is rather well defined (half-circles) and identifies a very strong central Gulf pattern of species composition. The better latitudinal segregation of sites and consequent biogeographic areas produced using this measure (JA) reflects the real similarities in the species lists and perhaps is more appropriate than the SMC measure in empirical definition of multi-species biogeographic groups.

It can be shown that Horn's index of similarity (R_o), although it is sensitive to abundances, uses only information about proportional abundances in the co-occurrence category (see Fig. 5a and 5b). Consequently, two sites with relatively dissimilar species lists will yield a high similarity value if the few most abundant species in each collection are identical. Conversely, two collections with relatively similar species lists will yield a low value if the species present in both collections are widely disparate in their respective abundance proportions. The use of similarity measures that are sufficiently sensitive to differences in proportional abundance may be very important where sample sizes differ and should provide better resolution of biogeographic areas in groups such as marine shore fishes that often

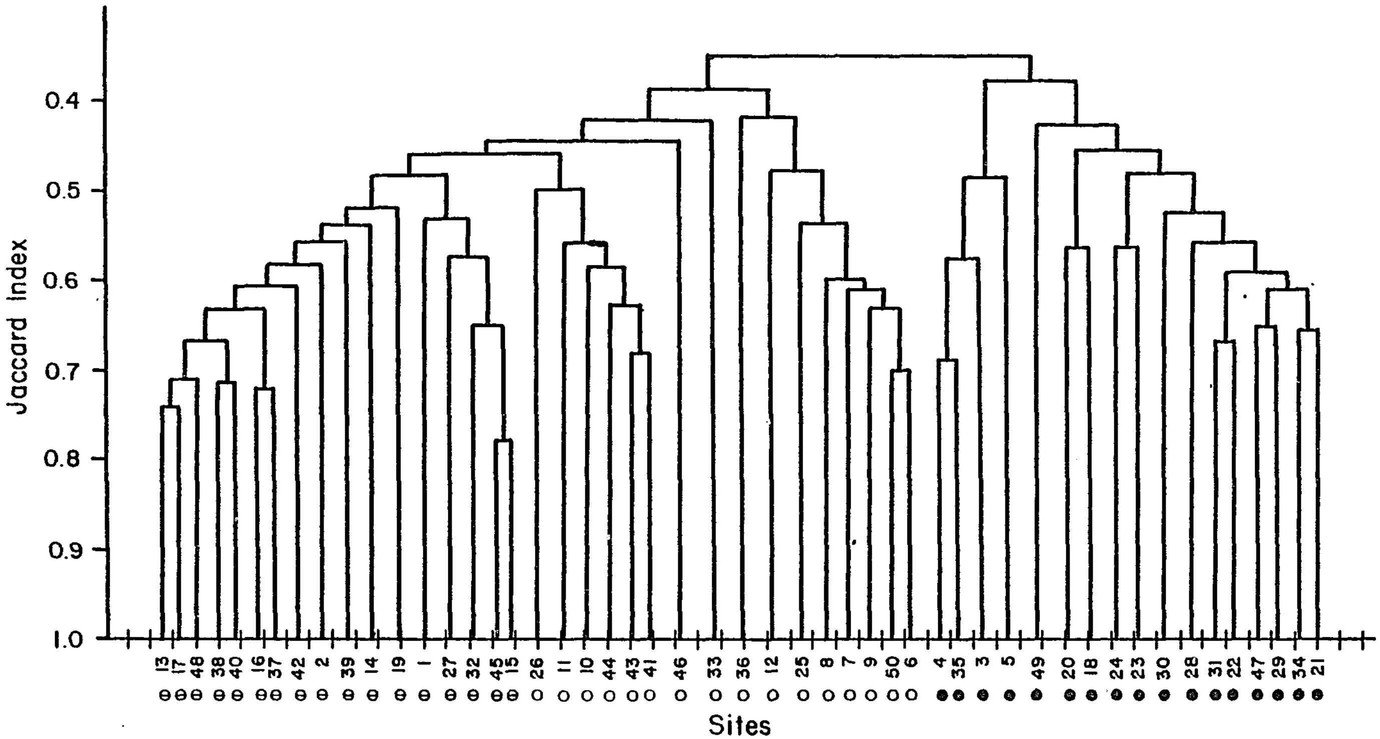

Figure 9. Dendrograph of sites (collections) in the Gulf of California using the Jaccard Coefficient. -- Collection numbers refer to Figure 1 and Appendix A. See text for explanation of symbols.

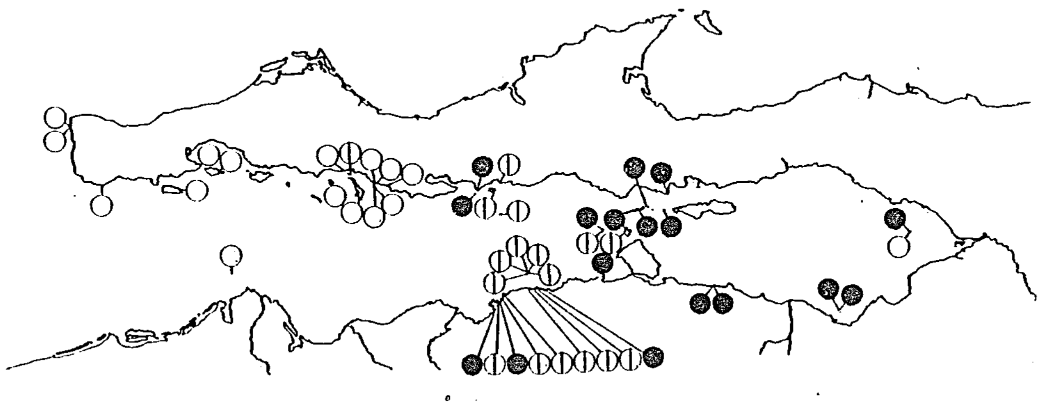

Figure 10. Map representation of site groups or clusters from the dendrograph produced using the Jaccard Coefficient. -- See Figure 9 and text for explanation of symbols.

have, due to the vagaries of larval dispersal, distributional ranges that extend beyond their principal or breeding ranges. Four groups of sites can be identified at the 0.6 phenon line using the R_o coefficient (Figs. 11 and 12). Clearly the lower Gulf or cape area including Isla San Ignacio Farallon forms a rather distinct cluster representing a composition unlike most of the rest of the Gulf. Site number 12 in this geographic area (Fig. 1) shows no great affinity or similarity to any other sites suggesting a continuum of community composition in this group. The sites in the upper Gulf and along the Sonoran coast to Isla Tiburon also show a strong degree of geographical coherence again suggesting that both identity and regularity of species abundances are important in revealing regional biogeographic patterns of community composition. Two broadly overlapping clusters occur within the rest of the Gulf that have been identified as open circles and half circles in Figures 11 and 12. An interesting and obvious geographical relationship between these two groups or community types is among the extensively sampled coastline area north of Guaymas and Isla San Pedro Nolasco. Here all but one of the mainland collections cluster in one group and all but one of the Island collections cluster in the other group indicating a fundamental difference in the composition of the community in the two areas. Another observation is that sites 30 and 39 (Fig. 1), the northernmost Baja collections, were not well separated from the upper Gulf group (Fig. 11). With only slight differences these two sites could easily have been included in the upper Gulf group suggesting a pattern of southward extension of the upper Gulf community on mainlands and a northward extension of the

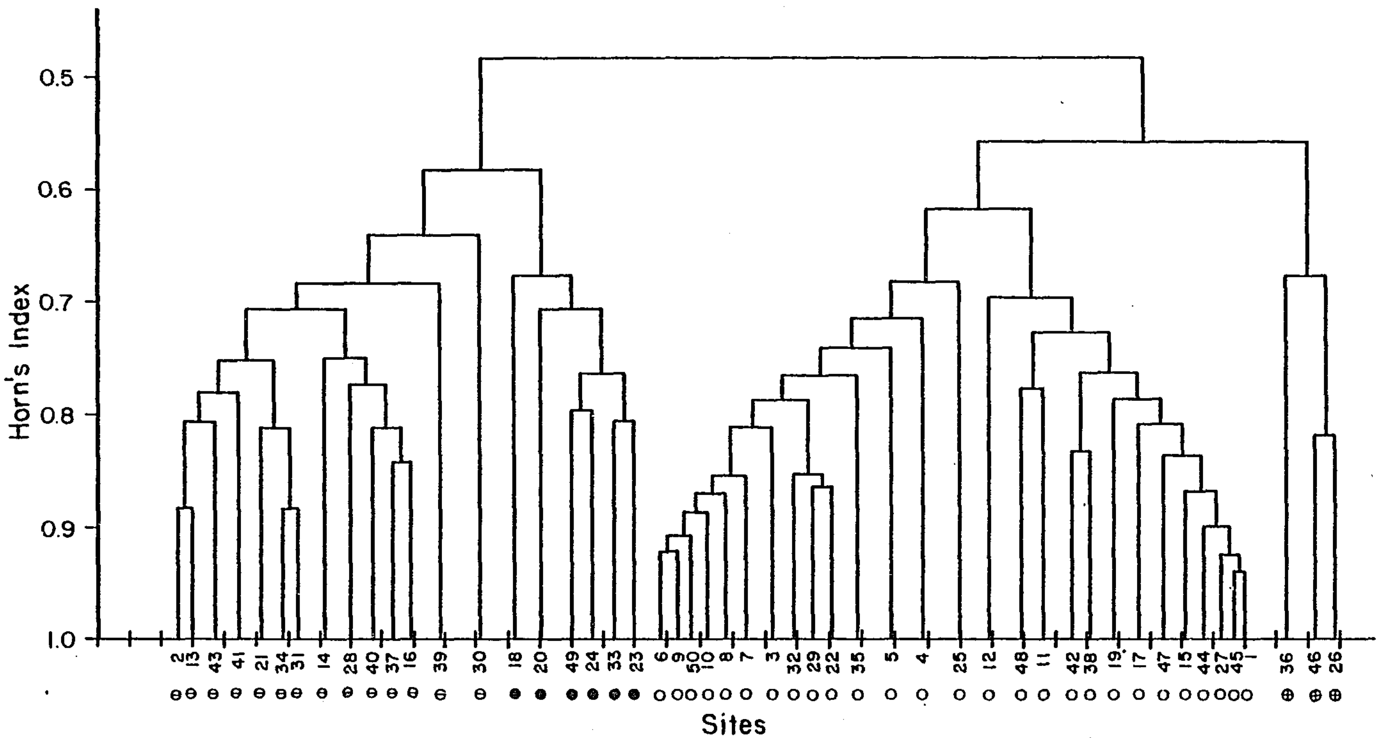

Figure 11. Dendrograph of sites (collections) in the Gulf of California using Horn's index. -- Collection numbers refer to Figure 1 and Appendix A. See text for explanation of symbols.

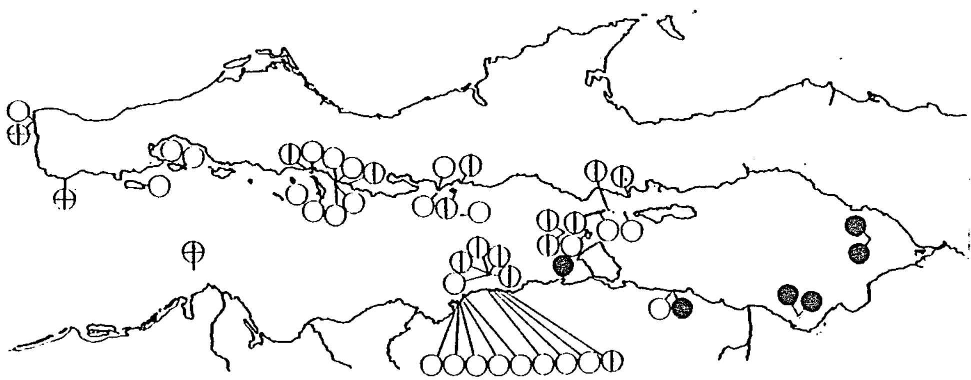

Figure 12. Map representation of site groups or clusters from the dendrograph produced using Horn's index. -- See Figure 11 and text for explanation of symbols.

central Gulf community on islands (Fig. 12). Based on this analysis of rocky shoreline resident fishes, Walker's (1960) biogeographic scheme could be amended such that the central Gulf would include more of the midriff area and Baja coastline to the north and more of the western Gulf and Baja coastline south of La Paz. Even so, this scheme agrees remarkably well with Walker's regions and those based on other marine taxa (Glassell 1934; Dawson 1960; Garth 1960; Soule 1960; Yensen 1973).

The relative strengths of the diversity and physical differences between these major biogeographic areas, the upper Gulf (north of Isla Tiburon along the Sonoran coast), central Gulf, and lower Gulf (Isla Farallon and the La Paz area south), were analyzed on the basis of key physical, environmental and diversity measures. Table 6 indicates that although the upper and lower Gulf sites were most different physically, the diversity measures show stronger divergence between upper and central areas. Physical and diversity differences between central and lower Gulf areas are not as great as either of the former comparisons. The boundary zone between the upper and central Gulf is characterized by an abrupt change in tidal range and tidal currents. This is a region of upwelling and has a more pronounced barrier (the large midriff islands) than does the central-lower Gulf transition zone.

In this section I have presented results obtained by using numerical methods to partition the variability of sampled communities into geographical and physical patterns within the Gulf of California.

Table 6. Significant differences in sample variables between the 7 upper (U), 36 central (C) and 7 lower (L) Gulf collection sites. -- * = $p < .05$; ** = $p < .005$; NS = not significant.

	U	L	t	U	C	t	L	C	t
S	11.9	18.6	-3.70**	11.9	19.1	-5.21**			NS
N			NS	183.6	391.1	-3.55**			NS
H'_n	1.595	2.027	-2.48*	1.595	2.120	-3.10*			NS
H'_b			NS	1.393	1.798	-5.57**			NS
SD			NS	5.1	8.7	-2.82*			NS
VOL	6.4	65.1	-4.75	6.4	37.4	-7.54**	65.1	37.4	2.67*
TID	3.9	1.0	6.30**	3.9	1.5	5.30**	1.0	1.5	-8.02**
MIN	15.5	19.3	-8.67**	15.9	16.2	-2.75*	19.3	16.2	7.13**

S = number of species; N = number of individuals; H'_n = numerical diversity; H'_b = biomass diversity; SD = secchi disc depth (m); VOL = volume of ocean within 20-km radius from site (km^3); TID = tide range (m); MIN = mean monthly minimum sea surface temperature (°C).

Each pattern is valid depending upon decisions about the propriety and usefulness if the similarity measures are chosen.

Island-Mainland Analyses

Together, island and mainland collections showed significant negative correlations of number of species with latitude (Fig. 13). Islands, however, had stronger correlation ($r = -.614$, $p < .001$) than mainlands ($r = -.386$, $p < .05$) which is attributed, in part, to the lack of comparable mainland samples in the northernmost Gulf, an area of generally low diversity. The gently sloping rocky shores of the upper Gulf mainland along with the great spring tide ranges prohibited sampling sites comparable to the steeper rock surfaces of the two northern Gulf islands.

The northernmost islands (Roca Consag and Isla San Jorge) physically resemble rocky shorelines in the central Gulf. To compare island and mainland sites in this region, data from fish collections analyzed by Thomson and Lehner (1976) at Puerto Peñasco were used which approximate the kind of collections made in this study. Four collections from one mainland tide pool from 1967 to 1973 were compared to two collections each from the northern Gulf islands. Island and mainland diversities are similar (Table 7), however the tidepool samples are considerably larger. The major difference between these island and mainland collections is the identity of the species found. Three species were collected on the mainland but were absent from the four island collections (*Bryx arctus*, *Hypsoblennius jenkinsi*, *Gobiosoma* sp.), however, 10 species were collected on the islands (Table 7) that are

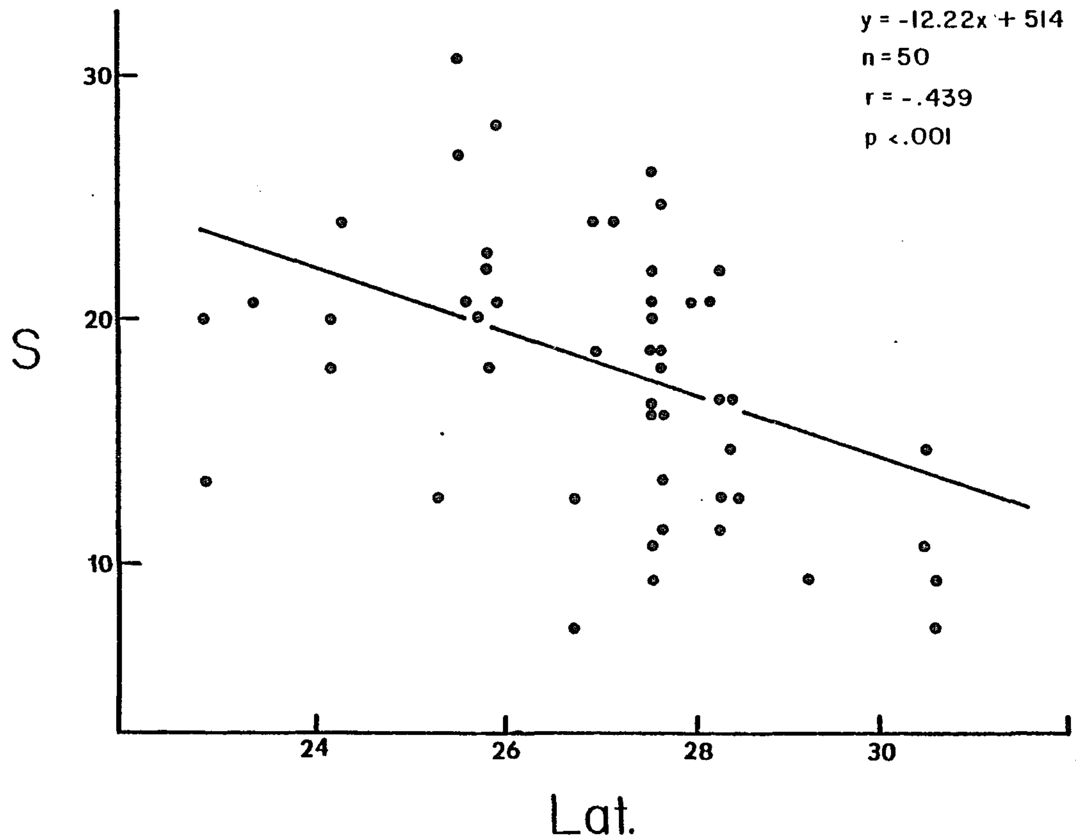

Figure 13. Correlation of number of fish species (S) in Gulf collections with latitude (Lat.) of collecting site.

Table 7. Comparison of four mainland tidepool collections with four island shore collections in the upper Gulf.

	$\bar{x}S$	$\bar{x}N$	$\bar{x}H'_n$	Total S
Puerto Peñasco tidepool collections	11.5	389.2	1.444	16
Islas San Jorge and Roca Consag	11.0	165.2	1.412	20

Tidepool collections from Thomson and Lehner 1976; only primary residents used in analysis.

Species not collected in these four island collections but were collected in mainland tidepool samples: Bryx arctus, Hypsoblennius jenkinsi and Gobiosoma sp. (undescribed sp.). Species collected in these four collections but were absent or rare in all tidepool collections from Puerto Peñasco from 1964 to 1979: Lizard triplefin blenny, Cortez triplefin blenny, Malacoctenus hubbsi, Xehomedea rhodopyga, Starksia spinipenis, Acanthemblemaria crockeri, Coralliozetus micropes, Protemblemaria bicirrus, Chaenopsis alepidota, and Coryphopterus urospilus.

extremely rare or absent from the adjacent mainland (Puerto Peñasco) where over 130 collections from rocky habitats have been made from 1963 to 1978. These island species are all common in collections throughout the rest of the Gulf. Eight other reef species (Haemulon maculicauda, Chromis atrilobata, Epinephelus afer, Serranus fasciatus, Malacoctenus tetranemus, Ioglossus sp., Lythrypnus dalli, Tomicodon boehlkei) occur regularly on these islands but are absent or have been only rarely reported from the adjacent mainland (Puerto Peñasco).

The large central Gulf area (excluding upper Gulf sites 18, 20, 23, 24, 33, 35, 49 and lower Gulf sites 9, 10, 11, 12, 26, 36, 46) where a relatively large number of islands and mainland sites were sampled and where mean island site latitude does not differ from mean mainland site latitude is most characteristic of the Gulf in general. Here the island-mainland comparisons yielded the most surprising and significant results. Table 8 gives the island and mainland means and t-tests for a number of physical parameters and diversity measures. It can be seen that there is a significantly greater number of species, higher density, greater biomass, and higher information diversity (H'_n and H'_b) on islands. These differences parallel significant differences in water clarity (SD) and volume of ocean near island sites (VOL).

Island-mainland comparisons of physical environment and reef-fish diversity in the lower Gulf are made difficult for two reasons. First, only three island collections and four mainland collections were made in the lower Gulf and second, the lower Gulf is, in general, more insular in nature (Walker 1960) -- its faunal affinities reflecting the

Table 8. Means and t-tests of physical and diversity measures for 20 island and 16 mainland sites in the central Gulf of California.

	$\bar{x}$ Island	$\bar{x}$ Mainland	df	t	p
SD	9.9	5.8	25	2.34	$<.05$
VOL	50.0	21.7	34	4.41	$<.001$
S	20.6	17.1	34	2.02	$<.05$
N	507.9	245.2	34	3.53	$<.001$
B	594.1	361.4	34	2.27	$<.05$
H'_n	2.228	1.984	34	2.02	$<.05$
H'_b	1.967	1.586	34	5.02	$<.001$

The symbols are the same as those used in Tables 1 and 2.

proximity to larger ocean currents and dispersal from more distant regions (e.g., offshore eastern Pacific islands). Nevertheless, several points are made about the community composition differences between these island and mainland collections in the following section.

Community Composition of Islands and Mainlands in the Upper, Central, and Lower Gulf

Appendix F gives the rank and mean abundance for each species on islands and mainlands in the upper, central, and lower Gulf areas. In the upper Gulf the rankings of the 12 most abundant species in islands was compared to the rankings of the 12 most abundant primary resident tidepool fishes from Puerto Penasco during comparable sea temperature periods (Thomson and Lehner 1976). Since comparable rocky shoreline habitats generally do not exist along the gently sloping sandy and silty coastlines of the upper Gulf, these rock, tidepool collections are the closest approximation to sampling in similar habitats. Using Spearman's Rank Correlation Coefficient, it was found that the ranks were quite dissimilar ($r_s = .207$) and in fact independent and uncorrelated ($p > .05$).

The composition of the large central Gulf area (36 of the 50 collections made in the study) is perhaps most characteristic of the Gulf in general. The 13 most abundant species in the central Gulf (see Fig. 17, p. 66) represents 85% of all individuals collected in the study. Additionally, not only are 8 of these 13 species endemic to the Gulf (62%), but these 8 endemics represent 56% of all individuals collected in the Gulf from all sites. A comparison of the abundance ranks of these 13 species from the 20 island and 16 mainland sites in the central Gulf by Spearmann's Rank Correlation Coefficient revealed that the rankings of the species are significantly correlated and thus not independent ($r_s = .607$, $.01 < p < .05$). However, even though the rankings of these most abundant species do not differ significantly there are certain key species whose ranking changes may be taken as an indication of community differences between island and mainland habitats. The 15 most abundant species in central Gulf island and mainland collections are listed in decreasing order of abundance in Table 9. It can be seen from this table that *Acanthemblemaria crockeri*, *Enneanectes* sp. and *Corraliozetus micropes* are species that represent a proportionally larger part of the island community and that *Axoclinus carminalis* and *Xenomedea rhodopyga* are species that represent a proportionally larger part of the mainland community. There were no species collected only on islands or mainlands that had abundances greater than or equal to an individual per collection. Although five species were found only in island samples and three species were found only in mainland samples in the central Gulf (from Appendix D), all were rare in collections and nothing can be inferred from their presence or absence.

A comparison of the rankings of the most abundant species on islands and mainlands in the lower Gulf are given in Table 10. From this table it can be seen that the triplefin blenny *Axoclinus carminalis*, whose range extends well beyond the Gulf to the south, tops the island ranking while its Gulf endemic congener (*Axoclinus* sp.) tops the mainland ranking. Similar to this is the higher ranking of

Table 9. Rank and relative abundance of the 15 most common species in island and mainland collections in the central Gulf of California.

Species (Islands 20)	$\bar{x}$ nos./ coll.	Rank	$\bar{x}$ nos./ coll.	Species (Mainlands 16)
Cortez triplefin (*Axoclinus* sp.)	80	1	39	Cortez triplefin (*Axoclinus* sp.)
Malacoctenus hubbsi	64	2	32	*Axoclinus carminalis*
Acanthemblemaria crockeri	62	3	29	*Malacoctenus hubbsi*
Flag triplefin (*Enneanectes* sp.)	49	4	22	*Xenomedea rhodopyga*
Lizard triplefin (n.gen.& sp.)	40	5	17	*Tomicodon boehlkei*
Tomicodon boehlkei	29	6	14	*Acanthemblemaria crockeri*
Coralliozetus micropes	26	7	14	Lizard triplefin (n.gen.& sp.)
Paraclinus sini	21	8	12	*Paraclinus sini*
Axoclinus carminalis	18	9	10	Flag triplefin (*Enneanectes* sp.)
Xenomedea rhodopyga	18	10	10	*Labrisomus xanti*
Labrisomus xanti	14	11	7	*Coralliozetus micropes*
Ophioblennius steindachneri	12	12	5	*Apogon retrosella*
Scorpaenodes xyris	11	13	4	*Ophioblennius steindachneri*
Apogon retrosella	10	14	4	*Tomicodon humeralis*
Ogilbia sp.	7	15	3	*Malacoctenus tetranemus*

Table 10. Rank and mean abundance of the most abundant reef fish species in island and mainland collections in the lower Gulf of California.

Species (Islands)	$\bar{x}$ nos./ coll.	Rank	$\bar{x}$ nos./ coll.	Species (Mainlands)
Axoclinus carminalis	62	1	44	Cortez triplefin (*Axoclinus* sp.)
Acanthembemaria crockeri	49	2	33	*Ophioblennius steindachneri*
Cortez triplefin (*Axoclinus* sp.)	47	3	32	*Malacoctenus hubbsi*
Ophioblennius steindachneri	22	4	32	*Axoclinus carminalis*
Coralliozetus micropes	18	5	21	*Coralliozetus micropes*
Enneanectes sp.	15	6	19	*Labrisomus xanti*
Malacoctenus hubbsi	14	7	10	*Acanthemblemaria macrospilus*
Tomicodon boehlkei	13	8	9	*Paraclinus mexicanus*
Gobiosoma chiquita	10	9	8	*Tomicodon boehlkei*
Apogon retrosella	8	10	5	*Coralliozetus angelica*

the blenny Malacoctenus hubbsi, a Gulf endemic, on islands (third) and lower ranking on mainlands (seventh). Contradictory to this pattern, the Gulf endemic tube blenny Acanthemblemaria crockeri ranks second on islands but is absent from the top ten altogether on mainlands, apparently replaced by its more southerly distributed congener Acanthemblemaria macrospilus (ranked seventh on mainlands). As noted earlier regarding the samples from the lower Gulf, the small number of collections, higher variance in abundances, and the insular nature of the region in general suggest caution in interpreting these results.

Community composition differences indicated by the abundance rankings of species in collections made at Isla San Pedro Nolasco (5 collections) and the adjacent mainland coastline (9 collections) reflected essentially the same differences that were observed for central Gulf islands and mainlands. The tube blenny Acanthemblemaria crockeri and the triplefin blenny Enneanectes sp. represented a larger part of the island community and the triplefin blenny Axoclinus carminalis represented a larger part of the mainland community, but in addition, the clingfish Tomicodon boehlkei and the tube blenny Coralliozetus micropes were much less abundant on San Pedro (both ranking below ten) than on other central Gulf islands (see Table 9).

Studies and Collections in the San Carlos/Isla San Pedro Nolasco Area

Isla San Pedro Nolasco was the most extensively sampled island and the adjacent Sonoran coastline was the most extensively sampled and studied mainland in the Gulf (Figs. 1 and 14). The island-mainland comparisons and visual census studies here may be taken as the most

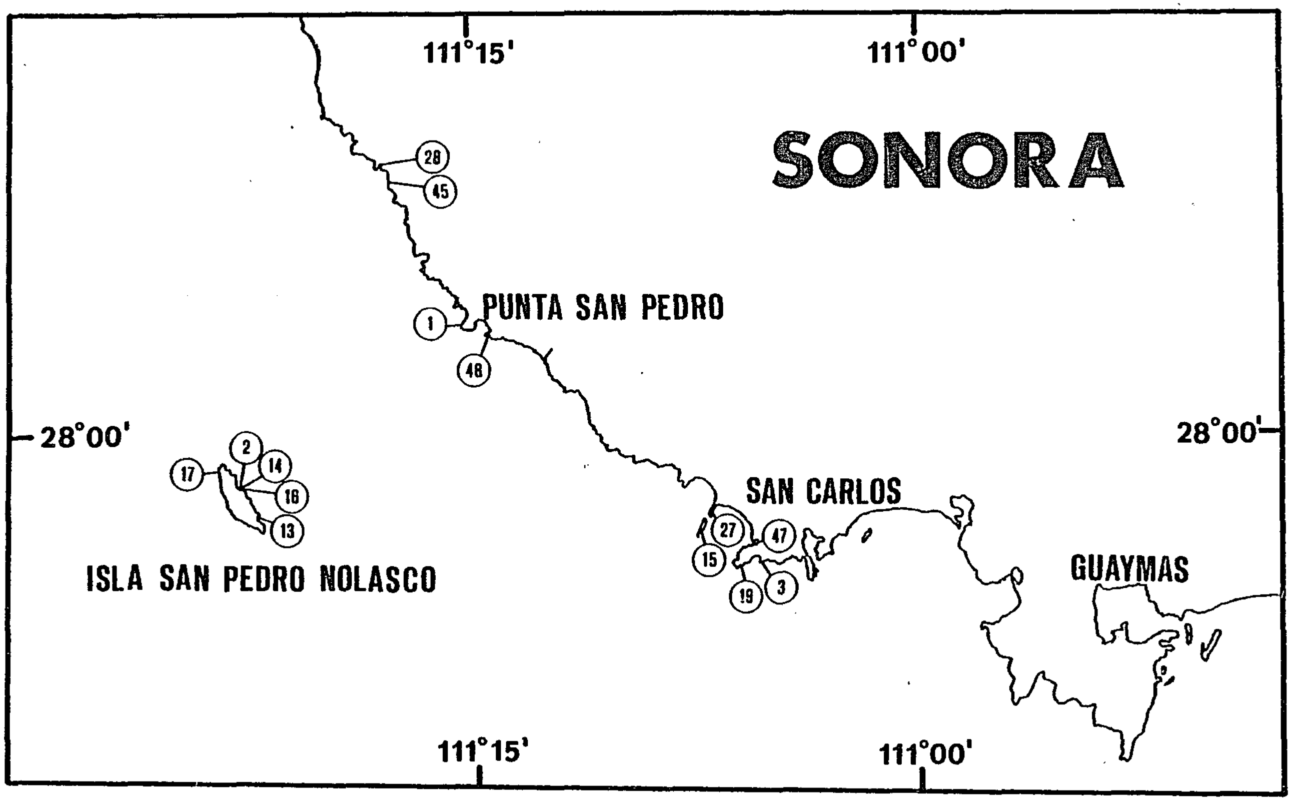

Figure 14. Detail map of site localities where collections were made at Isla San Pedro Nolasco and adjacent Sonoran coastline in the central Gulf of California. -- Collection numbers refer to Appendix A.

characteristic and indicative of the nature of rocky shoreline fish communities in the Gulf.

Differences in physical and community measures between these two areas were even more significant, statistically, than those between islands and mainlands in the central Gulf in general (Table 11). Again, island habitats are characterized by greater water clarity, greater volume of ocean near the shoreline, greater number of species, greater density of individuals, more biomass of fishes, and higher species diversity measures. The variance in all these measures was consistently higher among the mainland samples than among the island samples. Site to site species turnover, another measure of community variance which is discussed in more detail in the following section, was highest among the mainland collections and lowest among the island collections. This low species turnover or high similarity among island collections is reflected in the dendrographs as well (Figs. 7, 9, and 11).

These kinds of island/offshore-mainland/inshore differences in the regularity or predictability of reef fish community composition have been corroborated by visual studies. A small peninsula near San Carlos, Sonora (Fig. 5) which represents a shoreline gradient from inshore/protected to offshore/exposed habitats was censused repeatedly by Gilligan (in press) in order to identify diversity and species turnover patterns in the fishes. In this study, each species' frequency of encounter was recorded within each of three equal segments of the peninsula's west shoreline (Fig. 5a and 5b) over four observation periods. Greater compositional predictability of the community

Table 11. Means and t-tests of physical and diversity measures for collections at Isla San Pedro Nolasco and the adjacent Sonoran coastline in the central Gulf of California. -- See Figure 17. Symbols are the same as those used in Tables 6 and 7.

	n	Island	Mainland		t	p
SD	8	9.02	6.67	6	0.90	<.05
VOL	14	56.62	17.45	12	20.67	<.001
S	14	21.4	16.0	12	2.31	<.05
N	14	455.8	210.2	12	2.37	<.05
B	14	543.7	321.4	12	1.44	<.05
H'_n	14	2.2926	1.9627	12	2.70	<.02
H'_b	14	1.9722	1.5700	12	3.38	<.01

at the point was indicated by lowest mean species turnover within that segment and a more unpredictable bay segment species composition was indicated by the highest mean species turnover within that segment (Table 12).

Species-Area Correlations

A nearly significant log/log correlation between habitat area and species number for all Gulf samples was found ($r = .230$, $p = .054$, $n = 50$). Habitat area was estimated by perimeter for islands and contiguous rocky coastline length for mainlands (Tables 1 and 2). Island perimeter and rocky coastline length are better estimates of habitat area for shore fishes than total island area since suitable habitats of the submerged shelf of rocky islands assume a "ring" configuration for all but the smallest islands and patch reefs. It must be pointed out that these are only rough estimates of supposed contiguous habitat area and that decisions regarding the continuity of some areas was arbitrary. A log/log species-area curve for all island samples was significant ($r = .355$, $p = .032$, $n = 28$), but considering only the 20 central Gulf islands it was not ($r = .135$, $p = .258$).

Two sampling methods, the use of ichthyocides that favor collection of the more sedentary primary residents and visual censuses that favor the more mobile secondary residents, would be required to obtain reasonable estimates of total species number on islands. Combined data from species counts by visual methods on patch reefs (from Molles 1978) and small nearshore islands in the San Carlos area of the central Gulf of California (Fig. 4, Table 3, and Appendix E) has produced remarkably good fit for a log/log species-area curve

Table 12. Mean number of species and mean species turnover within and between the point, middle, and bay segments of the Punta Doble peninsula. -- For N=3 April observation period excluded (from Gilligan in press).

Segment	N	Point	Middle	Bay
Mean species	3	25	33	23
	4	24	33	25
Mean turnover	3	.430	.488	.622
within	4	.432	.457	.592
Mean turnover	3	.509	.505	
between			.641	

(Fig. 15). The z-value (slope constant) in this relation falls within the range predicted by MacArthur and Wilson (1967) for near islands where barriers to dispersal are weak.

Species Turnover Within and Between Island and Mainland Sites

The rate of replacement of species along a gradient and the rate of replacement of species from time to time at a locality due to colonization and extinction have been termed beta-diversity and species turnover, respectively. Although formulation of beta-diversity measures (Pielou 1975) may differ from measures of species turnover (Diamond 1969; Simberloff 1969) both are concerned with the comparison of presence or absence of species in two or more samples. If we view the samples of the resident rocky-shore fish community in the central Gulf as successive samples of one type of habitat at various localities from an island or the mainland, then we may observe indirectly the regularity or patchiness with which species are distributed on islands and mainlands by measuring this site to site compositional change or species turnover within habitats.

A simple measure of species turnover is just the number of absence-presence changes (colonist analogs) and presence-absence changes (extinction analogs) per species in two samples which can be calculated as 1 minus the Jaccard Coefficient of similarity. The Jaccard Coefficient is the number of co-occurrences (presence-presence species) per species in two samples (Clifford and Stephenson 1975). This kind of species turnover is unrelated to species turnover from time to time at a site and is not the same as turnover or rate of

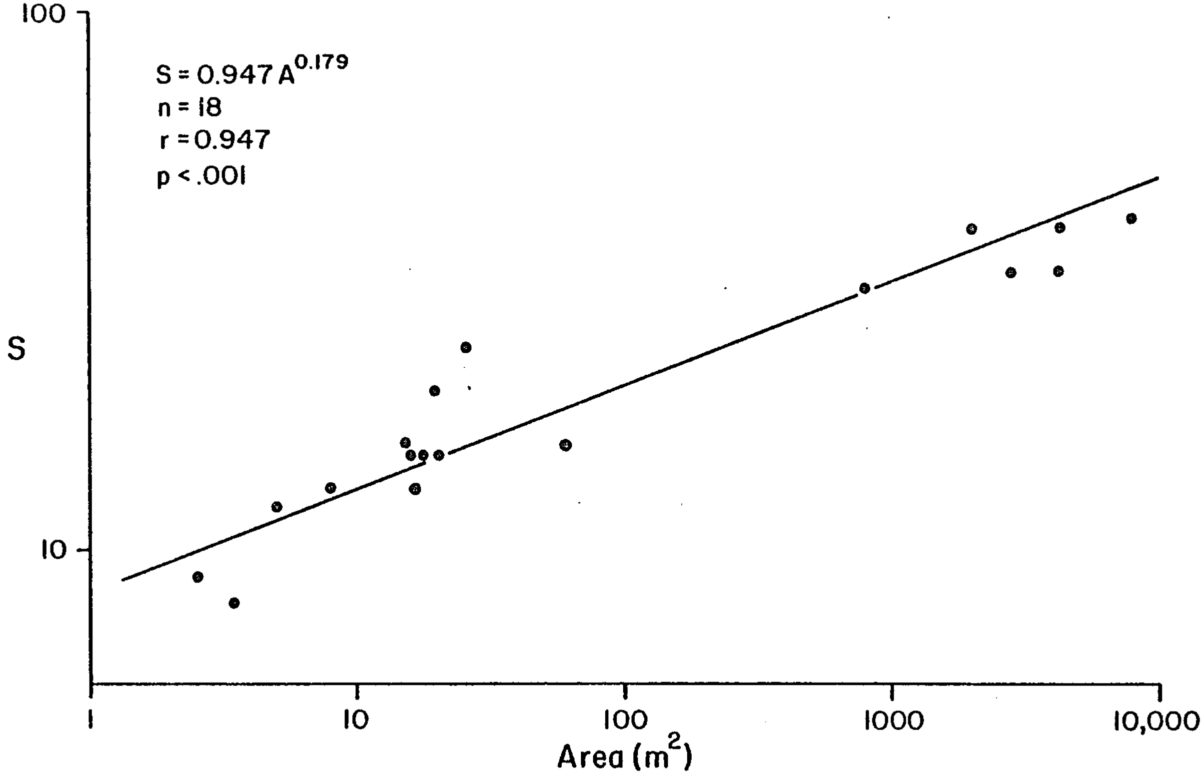

Figure 15. Log/log species-area curve for rocky-shore fish species on small near-shore natural patch reefs (100 m^2, Molles 1976) and small nearshore islands (100 m^2, see Table 9) in the San Carlos area of the central Gulf of California.

replacement of species along a habitat gradient (beta diversity) therefor I will call this site to site within habitat species turnover 'gamma-diversity.' Gamma-diversity measures the predictability of species composition within habitats in different areas, regions, continents, etc. In this case it will compare islands and mainlands in the Gulf of California. Figure 16 shows how the number of within island, within mainland, and between island and mainland comparisons are distributed.

A Kruskal-Wallis one-way analysis of variance of the turnover values in each category using the 20 island and 16 mainland sites in the central Gulf (Table 13) showed that the average species turnovers were not equal ($x^2 = 69.45$, $p < .001$) and that gamma diversity (site to site within habitat species turnover) is lowest within islands and highest within mainland sites. The same qualitative results were obtained comparing the Isla San Pedro Nolasco sites (5 collections) with the corresponding mainland coastline (9 collections, see Fig. 14).

Latitudinal and Island Body-size Trends

Mean weight per individual for each species in each collection was calculated by dividing total weight of all individuals of a species in a collection by the total number of individuals in that collection and was used as an estimate of mean body size. Among the 30 species that were collected at at least 10 sites in the central Gulf 5 (*Gobiesox pinniger*, *Tomicodon boehlkei*, *Hypsoblennius brevipinnis*, *Axoclinus carminalis*, *Gobiosoma chiquita*) had significant positive correlations ($p < .05$) of body size with latitude and only one

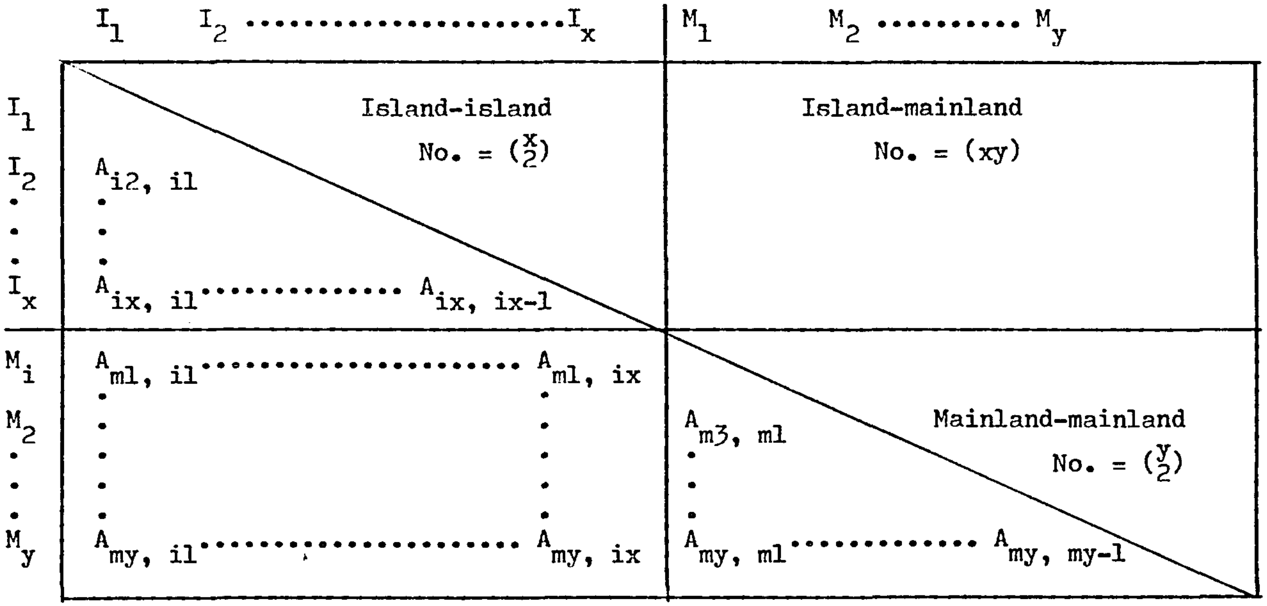

Figure 16. Matrix arrangement and number of within island (island-island), within mainland (mainland-mainland) and between island and mainland species turnover (A) values for x island and y mainland fish collections.

Table 13. Kruskal-Wallis one-way analysis of variance of species turnover within and between 20 island and 16 mainland collections in the central Gulf of California.

	No. of Comparisons	Mean Rank	x^2	p
Island-Island	$\binom{20}{2} = 190$	231.0 (low turnover)	69.45	.001
Island-Mainland	(20)(16) = 320	332.1		
Mainland-Mainland	$\binom{16}{2} = 120$	399.9 (high turnover		

(*Hypsoblennius gentilis*) had a significant negative correlation. At $.05 < p < .19$ another nine species had positive correlations of body size with latitude (*Apogon retrosella*, Lizard triplefin, *Labrisomus striatus*, *L. xanti*, *Malacoctenus hubbsi*, *Xenomedea rhodopyga*, *Acanthemblemaria crockeri*, *Corraliozetus angelica*, *Barbulifer pantherinus*) and none showed a negative correlation. Admittedly this kind of estimate of body size may be somewhat biased by the contribution of juveniles in samples and therefor may not accurately reflect the true adult body size trends. However, there are two lines of evidence that suggest that the trend of increasing body size with latitude is a real one and that it may even be quite prevalent among the smaller resident rocky-shore fish species in the Gulf. First, Flanagan and Gilligan (n.d.) have found that latitudinal size clines do exist in species in the families Clinidae and Tripterygiidae (measuring only the maximum length of individuals in hundreds of collections) in the Gulf of California despite the fact that the trend was undetectable in some of these species in the present study. Second, unusually large individuals of species in the families Clinidae, Chaenopsidae, and Gobiidae have been collected in the midriff island area of the upper-central Gulf. For some of these species this area represents the northern limit of their geographic distribution. Even though the present analysis may be to some extent biased by the contribution of juveniles in some collections, juveniles in general were uncommon in collections; therefore it is likely that this pattern is real.

Among the 13 most frequently collected species (pictured in Fig. 17) there appears to be a trend toward decrease in body size on islands. A rough estimate of body size difference between island and mainland populations in the central Gulf was expressed as a percent increase or decrease of mean body weight on islands. Percent change in body size on islands is given in equation (4)

$$\frac{\bar{x}_i - \bar{x}_m}{\bar{x}_m} \tag{4}$$

where $\bar{x}_i$ is the mean weight per individual of a species on islands and $\bar{x}_m$ is the mean weight per individual of that species on mainlands. The results are graphed in Figure 18 where the species are ranked in decreasing order of overall size (mean weight over all collections) from left to right. The only species that had a statistically significant difference in the mean weight ($p < .05$) between the 20 island and 16 mainland collections was Xenomedea rhodopyga with a 29% decrease on islands. In all, 8 of the 13 species showed trends of decreasing body size on islands with seven of these showing decreases of between 17 and 33 percent. Of the 5 species with trends of body size increase on islands only one was more than 9 percent.

An interesting observation related to island body size differences is the phenomenon that biomass diversity (H'_b) of collections appears to increase at a greater rate with numerical diversity (H'_n) on islands than it does on mainlands (Fig. 19). The two slopes (island and mainland) are not significantly different; however, reflected by the fact that the pooled data result in a better fit (Table 14). In other words, one line through the pooled data is better than two,

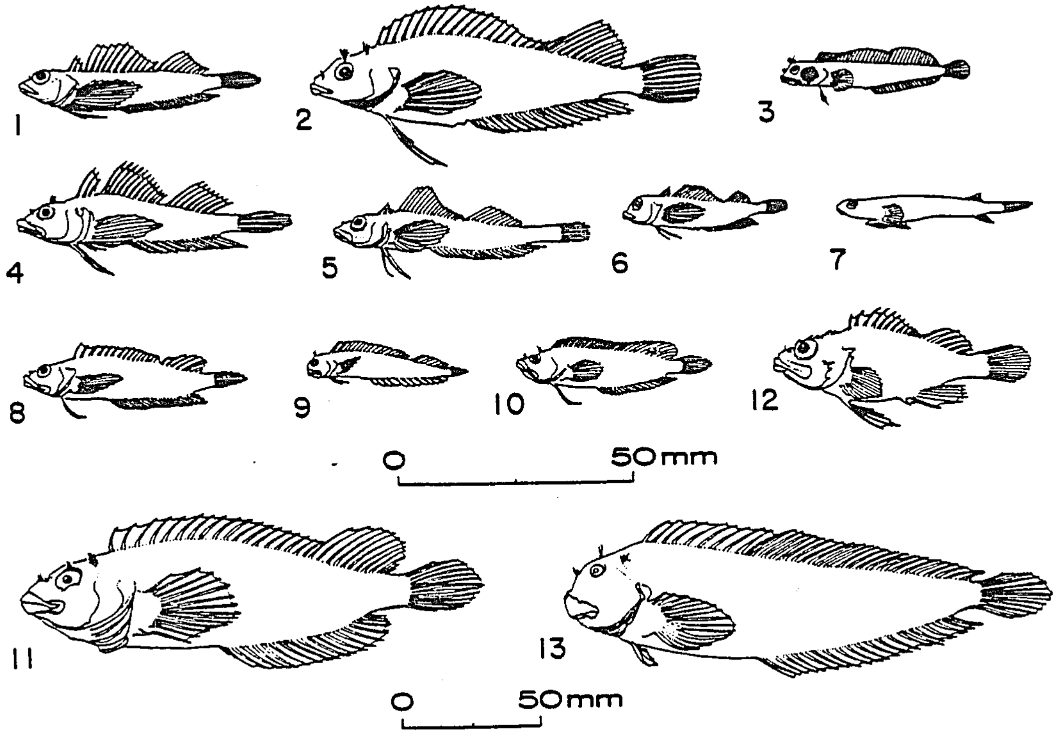

Figure 17. The 13 most abundant rocky-shore fish species collected by ichthyocide methods in the central Gulf of California (36 collections). -- Listed in decreasing order of abundance: 1. Axoclinus sp. (Cortez triplefin), 2. Malacoctenus hubbsi, 3. Acanthemblemaria crockeri, 4. Enneanectes sp. (flag triplefin), 5. Lizard triplefin (new genus and species), 6. Axoclinus carminalis, 7. Tomicodon boehlkei, 8. Xenomedea rhodopyga, 9. Coralliozetus micropes, 10. Paraclinus sini, 11. Labrisomus xanti, 12. Scorpaenodes xyris, 13. Ophioblennius steindachneri.

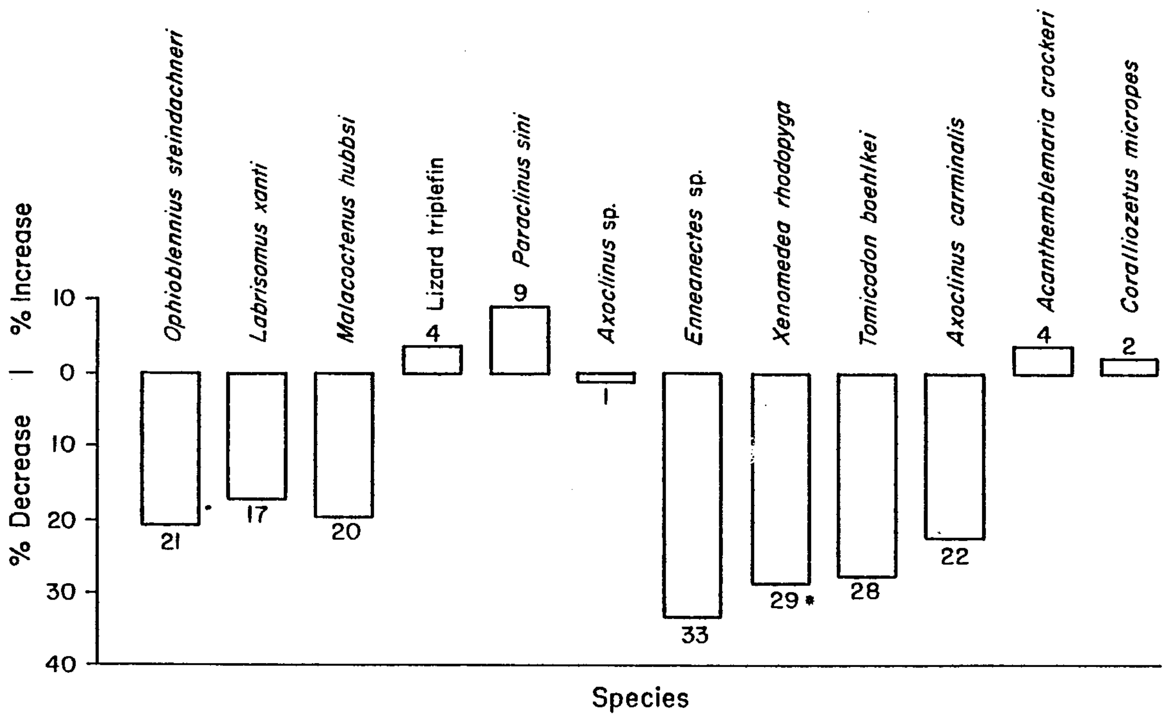

Figure 18. Island body size trends in the most abundant central Gulf rocky-shore fish species in ichthyocide collections. -- Percent change in body size on islands for each species is based on mean weight per individual of species lots from 20 island and 16 mainland collections in the central Gulf of California. Species appear left to right in order of decreasing overall body size.
* = difference in mean body weight was significant at the 0.05 level.

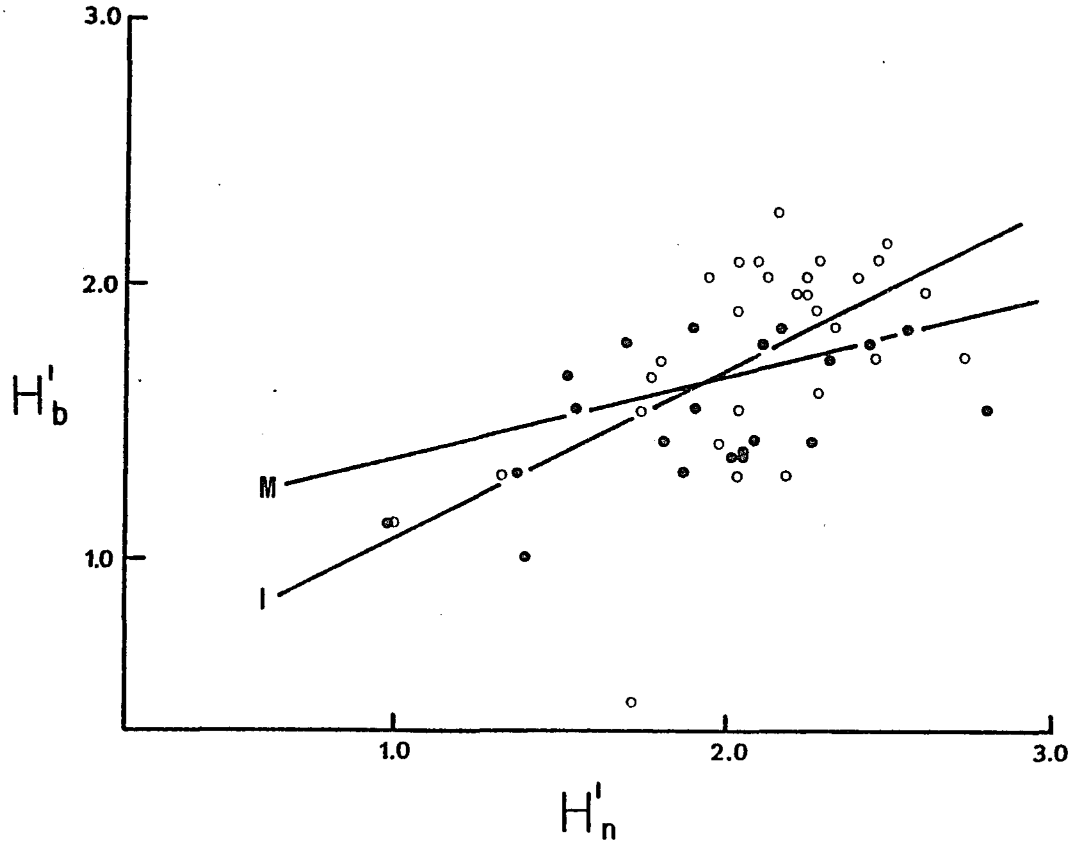

Figure 19. Plot of change in biomass species diversity (H'_b) with numerical species diversity (H'_n) for island (open circles) and mainland (solid circles) collections in the Gulf of California.

Table 14. Regression analysis of biomass diversity change with numerical diversity for 28 island, 22 mainland and all collections.

		df	SS	MS	F	p
Mainland regression	model	1	.3187	.3187	7.2665	.014
	error	20	.8334	.0439		
Island regression	model	1	1.4132	1.4132	13.7072	.001
	error	26	2.7840	.1031		
Pooled regression	model	1	1.9014	1.9014	22.3846	.001
	error	48	4.0771	.0849		

and there is no statistically significant difference in the relationship between islands and mainlands. The pooled data relationship simply reflects the latitudinal diversity gradient and the increasingly equitable biomass contribution in more diverse collections.

CHAPTER 4

DISCUSSION

The biogeographic and ecological nature of islands in marine systems is quite different from that of terrestrial systems. Although open ocean and deep water are barriers to the movement of many marine shore species they are not formidable barriers to the distribution of species with planktonic means of dispersal, which includes most marine biota. Distance over open ocean must be great, such as the Eastern Pacific Barrier (EPB), or environmental conditions very different, due to major ocean currents, to effect major changes in the faunal composition of shore biotas. The EPB which separates the Indo-west Pacific biota from that of the eastern tropical Pacific is about 90% effective from west to east and nearly 100% effective from east to west (Briggs 1961; Rosenblatt 1967; Vermeij 1978), although favorable ocean currents exist for both paths of immigration. Besides distance and ocean current direction, it is clear that ecological factors such as species-specific dispersal potential and competitive competency become important determinants of successful colonization. Of the transpacific shore fishes that have established populations in the eastern Pacific (Rosenblatt, McCosker and Rubinoff 1972), most are secondary resident reef fishes with pelagic eggs and long-lived pelagic larvae. They are also species that tend to be very common throughout their ranges undoubtedly providing an abundant source of propagules. In the eastern tropical Pacific the transpacific immigrants are most commonly found on the far offshore islands (e.g., Islas Revillagigedo, Galapagos) and at the tip of Baja California, a region that may at one time have been an island (Durham and Allison 1960) and which now has an 'insular' shore fish fauna (Walker 1960). It is not clear what an insular fauna is, however. In the eastern Pacific there is clearly no insular biogeographic region since, as Rosenblatt and Walker (1963) have noted, of the seven species listed by Snodgrass and Heller (1905) as "eastern Pacific insular species" (restricted to two or more islands) four have been found to have ranges that extend to the mainland. Yet many shore species have restricted distributions and the fauna of isolated oceanic islands tends to have a high percentage of endemic species (e.g., Hawaiian, Galapagos and Easter islands). The more distinct endemics are usually derived from those taxa that have more limited means of dispersal (e.g., primary resident species with demersal eggs and short-lived pelagic larvae), a correlation between differentiation and vagility noted by Rosenblatt and Walker (1963). Taxonomically there seems to be a trend toward synonomy of island species with their mainland and more widely distributed geminates since, especially for the secondary residents, most are morphologically indistinguishable (Robins, personal communication 1979). The relatively high endemism of tropical rocky-shore fishes along Mexico's Pacific coast (22%) is largely from the primary resident fishes (47 spp.) rather than the secondary residents (5 spp.). It appears that 'insular' faunas at this level are characterized by fugitive species with wide distributions and dispersal capabilities and on very isolated archipelagos by endemics that are generally much more restricted in their dispersal potential. Starck (1968), Robins (1971), and Gilbert (1972) have all noted 'insular' and 'continental' distributional patterns of fishes in the western tropical Atlantic. They suggest that they are related to the nature of continental vs. island habitats with respect to habitat specializations of the species rather than barriers to dispersal per se.

The Gulf of California is almost a microcosm of the significant characteristics of insular and inshore 'continental' habitats that may be important in distinguishing biogeographic processes in the marine environment. Here we find that individual islands accommodate a high proportion of the available fish species pool regardless of island size, in contrast to the rather low proportion of the total available species pool of the terrestrial fauna found on even large islands close to shore. Although this may be primarily due to the much greater effectiveness of open ocean as a barrier to terrestrial species it may also indicate something about the nature of competition, resource utilization and coexistence in terrestrial vs. marine communities. Furthermore, rates of marine immigration and colonization are, in general, high leading to depression of extinction rates or the "rescue effect" as proposed by Brown and Kodric-Brown (1977). Both island and mainland reefs receive propagules primarily from outside sources since a great majority of reproductive products are swept away by currents and become part of the plankton community (meroplankton). The planktonic early life stages settle and transform, either selectively (Marliave 1977) or randomly in response to hard or relatively fixed substrates, in habitats that are often quite different from those of the adults. Considering the differences between marine and terrestrial animals in the characteristics of immigration, colonization, the use of space resources (Sale 1977), and complexity of life histories one might not expect a M-W type equilibrium to be observed for most marine insular habitats. However, in small-scale insular systems Molles (1978) found that patterns of immigration and extinction of Gulf of California reef fishes on experimental model reefs approximated M-W prediction when species turnover was highest. Nevertheless, fish species composition was similar on all of his 12 model reefs, contrasting sharply with results of Sale and Dybdahl (1975) who showed random patterns of fish species composition on experimental coral heads in the Great Barrier Reef. This difference can mainly be attributed to the larger species pool and smaller size of reefs in Sale and Dybdahl's experiments. It seems likely that colonization will always appear stochastic or random if the scale of habitat or sample area is too small to contain some reasonable proportion of the species pool.

In the present study I have examined the island-mainland distribution of resident rocky-shore fishes concentrating on primary residents by sampling representative patches within similar shoreline habitats with rotenone ichthyocide. A discussion of the physical and biological nature of these kinds of environments and habitats is presented in the following two sections with detailed discussions of the results following these. A discussion of the visual census study and a synthesis of the studies conclude this chapter.

Physical Environments of Islands and Mainlands

The physical environments of oceanic islands and continental coasts differ markedly and may be associated with major differences in marine coastal faunas (Starck 1968; Robins 1971; Gilbert 1972). The key to understanding these differences is the nature of the ecotone between their respective shoreline zones and the surrounding ocean. Offshore island shore faunas form a rather sharp gradient with the pelagic oceanic province whereas mainland coasts form broader ecotones with the pelagic neritic province and the benthic sublittoral zone of the inner and outer continental shelf. Thus offshore islands surrounded by depths greater than 200 m tend to be influenced strongly by the open ocean and its characteristic biota. Gulf of California islands range from offshore (e.g., San Pedro Martir and Tortuga) to inshore (e.g., Carmen and Espiritu Santo). The marine environment of Gulf island and mainland coasts essentially reflects the differing physical regimes of the surrounding water masses. One can expect a moderation of sea surface temperature extremes (due to ambient air temperatures and solar radiation) with distance offshore from shelf areas. Although data on sea temperature near islands in the Gulf are unavailable, offshore isotherm profiles produced by several hydrographic cruises indicate that the water around islands gets neither as cold in the winter nor warm in the summer as inshore mainland areas. This phenomenon alone may be important in preventing winterkills of inshore fishes on islands. Winterkills due to low sea temperature occur periodically in the upper Gulf (Thomson and Lehner 1976) and Gulf islands may act as refugia for populations of warm water and tropical species which are most severely affected during these periods of density independent environmental stress. Island-mainland salinity differences, in contrast to temperatures, are slight and unlikely to be of any significance to the rocky-shore community.

The Gulf as a whole is protected from the large waves and swells of the Pacific. Calm seas and absence of heavy surge in rocky areas are normal conditions throughout the Gulf during fair weather. Nevertheless, the heaviest locally generated wave action may be expected on islands and mainland points near deep water. On the mainland coastline the shallower sea floor absorbs some of the wave energy, stirring up sediments and creating a heavier sediment load in longshore currents. Robins (1957) noted that silting and sediment loads in Florida inshore waters caused by storms can cause mortality in adult fishes by erosion of gill filaments. It is conceivable that reduced breeding success and mortalities of developing eggs, larvae and juveniles by more subtle stresses associated with silting may have even more severe effects on reef fish populations than adult mortality. In addition to this, the silting over of reefs caused by the deposition of these fine sediments along the coast could cause mortalities of reef invertebrates and algae. Islands have a greater extent of unprotected or exposed shorelines than mainlands, and it is interesting to note that Jones and Chase (1975) found considerably more species of coral reef fishes on the unprotected outside reef and channel walls of a lagoon in Guam than on patch reefs and reef flats within the protected lagoon.

Although current measurements are generally unavailable for Gulf shoreline areas, observation shows that currents are strongest around islands and exposed mainland points. This greater water circulation by more oceanic sediment-free water prevents silting of rocky substrates and efficiently carries away the pelagic eggs and larvae of reef fishes and invertebrates, although eddy formation may serve to retain some of these (Boden 1953; Emery 1972).

Tides show less effect on shoreline communities of islands in the Gulf due to the steeper slopes, exposing less reef area at low tide and requiring less vertical migration by resident fishes. The gentle slopes and great tides of the upper Gulf mainland platform reefs severely restricts the use of the reef area by resident fishes at low tides. Consequently, the intertidal fish community is regulated by the availability of tide pools.

The greater water clarity around islands in contrast to continental shores is a function of lower plankton densities as well as smaller quantities of suspended sediments. Storms cause greater disturbances to mainland than island communities due to the greater prevalence of unconsolidated sediments (boulders, cobbles, sand) which may scour or completely cover portions of the reef when wave action is heavy (Yensen, personal communication 1979) and alter special aspects of rocky reef habitats.

Biological Environments of Islands and Mainlands

Since little hard data are available regarding the biological nature of island versus mainland habitats the following discussion represents primarily a general impression based upon qualitative observations of numerous islands and mainlands in the Gulf of California. Therefore most of the conclusions must be considered hypotheses to be tested. One would expect the nature of plankton communities to have a very strong influence on the reef community both as a food resource for planktivores and by their propagule content. The ecological efficiencies of productivity in the open ocean (10%), coastal zones (15%) and upwelling areas (20%) and the character of planktonic food chains (Ryther 1969) have implications for island and mainland reef communities. The offshore islands in the Gulf would be expected to have a more oceanic type plankton community characterized by a greater proportion of holoplanktonic species (entire life as plankton) than meroplanktonic forms (larvae of benthic invertebrates and fishes): whereas, the neritic plankton community of the continental shelf and inshore areas would be expected to have a greater proportion of meroplankton. Preliminary analysis of numerous zooplankton samples from the Gulf indicates that this is the case (Siegel-Causey, personal communication 1979). The longer food chains of oceanic plankton communities would provide a greater diversity of food particle size for planktivores which, if resource partitioning according to food particle size is important, could allow higher diversity of filter feeders and other selective planktivores. This is especially true for the relatively non-mobile planktivorous primary resident fishes (e.g., tube blennies). If this reasoning is correct, then even though the density of plankton per unit volume oceanic or offshore water is less than inshore, because currents are usually greater near offshore rocky areas, the actual biomass of plankton available for consumers may be equivalent or even higher in offshore rocky habitats.

There does appear to be more profuse growth (greater percent cover) of stony corals (branching types and sea fans) and hydroids on island reefs. The only extensive growths of coral in the eastern Pacific are along islands (Isla Jaltemba, Clipperton Island) and 'insular' mainland shores (Bahias Pulmo and Los Frailes in the Cape region of Baja California). This is consistent with Robins' (1971) conclusions about coral reefs around islands in the tropical western Atlantic.

Other trends in the non-fish biota are the dominance of encrusting red algae (Rhodopyta) on islands and large browns (Phaeophyta) in sheltered bays along the mainland rocky coasts of the Gulf. Asteroidean echinoderms (sea stars) are more diverse on islands in the Gulf and holothuroidean echinoderms (sea cucumbers) more diverse on mainland coasts (Maluf, personal communication 1979), the latter due perhaps to the greater abundance of sediments and suspended material along the mainland. The fact that islands appear to have a lower profile with respect to algae and encrusting invertebrates suggests lower productivity, but because fish densities and diversities are high suggests that either the standing crop is low and productivity high or that local productivity is unimportant in parts of the fish community. Productivity must be partitioned into local primary productivity (benthic algae) and allochthonous input in the form of phyto- and zooplankton.

Regional Biogeography of the Gulf

Biogeographic separation of the Gulf into upper, central and lower areas by other authors was justified and empirically supported by numerical analyses of quantitative collections throughout the Gulf of California. Most classical biogeography based regional separation upon distributional information; however, often much of the distinction was left to the specialist's experience and intuition which sometimes appears rather unsystematic. The analyses presented here provide several alternatives to this classical approach and provide a basis for standardizing biogeographic classification. These quantitative numerical approaches can be used in a variety of ways (e.g., different similarity indices) to display the pattern most appropriate or useful to the investigator. Perhaps the most important point to be made regarding biogeographic patterns is that they are among the most important aspects of community structure (i.e., the patterns of spatial and temporal abundance of species and the patterns of resource allocation (Cody and Diamond 1975).

Species-Area Considerations

When one considers isolated rocky shoreline habitats and species-area relationships it is necessary to keep in mind the kinds of fish species that one is considering and the diversity of microhabitats. Quite naturally there is an increase in the variety of microhabitats with both increasing island area and increasing length of continuous rocky coastline (e.g., more sandy areas, coves, points). According to MacArthur and Wilson (1967) species number should increase for larger islands due to the inclusion of new habitats and greater topographic complexity. Therefore, considering all fish species one would expect inclusion of some sand or rock-sand associated species. But even considering only reef species this appears to be the case as was shown for small natural patch reef and small nearshore islands in the Gulf (Fig. 18). The use, interpretation and statistics of the species-area relationship have recently been reviewed by Connor and McCoy (1979). They find three alternative hypotheses for explaining this widely observed correlation: (1) passive sampling; (2) habitat diversity; and (3) area per se. The first requires no biological explanation and is simply a sampling phenomenon, the second requires habitat specialization, and the third a balancing of species immigration and extinction. For small samples such as ichthyocide samples, we would expect the numbers of species to increase with overall habitat area (e.g., island perimeter or contiguous rocky coastline) due to transient species and the transient hypothesis (Connor and McCoy 1979). Preston (1962) and MacArthur and Wilson (1967) argue that many transient species will be encountered in non-isolated areas and that species numbers in small areas (quadrats) will therefore be inflated, increasing with overall area. In this study, all transient and non-resident fishes were excluded from analysis of fish collections from comparable small reef areas and only those species that reside directly within these sampled areas were considered yet still species numbers in samples appeared to increase with overall habitat area (see Results). The relationship, although far from clear, suggests that this and perhaps most species-area correlations require a multiplicity of explanations each tailored to the individual case and circumstances and that detailed analyses are generally required to discriminate between alternative explanations and hypotheses (e.g., habitat diversity, area *per se*, etc.).

Island and Mainland Differences

Island collections consistently contained greater numbers of individuals and greater biomass of resident reef fishes than mainland collections even though sampling effort and physical substrate types were comparable. One explanation might be that islands have greater productivity or greater food resources available such that a higher carrying capacity is realized. This appears to be contradicted by the fact that macroscopic attached algae is less abundant on islands and by the fact that offshore oceanic water has less nutrients and plankton densities are typically lower than inshore mainland areas. As mentioned earlier this apparent contradiction can be resolved if: (1) the low algae profile (low standing crop) is due to high grazing by herbivores and productivity is indeed high on islands; and (2) even though plankton densities per unit volume are low, greater currents near islands make the quantity and diversity of plankton actually available as food for planktivorous primary resident reef fishes high and thus increase the food resource base of this community.

Island collections had higher alpha-diversity as measured by both number of species and species diversity indices (H_n and H_b), however greater richness (number of species) may be partially due to higher densities of individuals (larger sample sizes) in island collections. Nevertheless, there appears to be a real trend toward greater diversity of rocky-shore fishes on Gulf islands although the difference is not great in these collections. Explanations for this trend toward higher diversity, a phenomenon that apparently runs contrary to predictions of the M-W model of island biogeography, will be considered here and in the following sections. Recruitment rates of marine fishes, especially in reef areas (Sale 1978) are largely independent of existing population sizes (Cushing 1973). From this one would, if constructing a simple model, assume that immigration rates for reef habitats are uniform regardless of island size or distance from propagule sources. Mortality subsequent to larval settlement would thus be a major factor affecting species diversity. Although competitive processes have recently been shown to be important in the local distribution of some reef fish species (G. B. Smith 1979; Hixon 1978; Larson 1978), many kinds of disturbances exist that may maintain diversity in non-equilibrial reef communities (Sale 1978; Connell 1978).

Another factor that strongly influences reef fish diversity, and that has been generally overlooked, is the vertical relief and complexity of the substrate. Molles (1978) found good correlations of species diversity of central Gulf fishes with height of patch reefs but found no significant differences in species diversity when he varied the interspace size diversity of his model patch reefs. Contrary to this, Risk (1972) found good correlations of reef fish diversity with substrate topographic complexity in the Virgin Islands and Luckhurst and Luckhurst (1978) found that species richness of fishes on coral reefs was highly correlated with substrate rugosity in the Lesser Antilles. The rocky shorelines and narrow surrounding

Gulf islands are typically steeper than the more gently sloping shelves of the mainlands. As a result there is often a greater vertical profile heterogeneity of nearshore rocky habitats around islands. Whether this kind of difference can translate into higher diversity in island collections is questionable since these shorelines are comparable in vertical relief and substrate rugosity.

Trends in Body Size

The trend of increasing body size in primary residents with latitude in the Gulf was suggested from cursory analysis of the collection data. Although this phenomenon will be discussed in more detail elsewhere (Flanagan and Gilligan n.d.), the pattern seems to evoke three alternative explanations. First, and most likely, larger body size at higher latitudes may reflect slower and more extended growth in cooler temperatures. This may be true in the Gulf because even though summer sea temperatures are fairly uniform throughout the Gulf (Maluf n.d.), not all breeding and early development occurs during the warmest season. Especially since many of these species only live one or two years it seems likely that temperatures could severely affect their maximum size. It is expected that cooler temperatures will result in slowed but extended periods of growth delaying sexual maturity and, resources being equal, promoting greater maximum size and longevity. At higher temperatures (lower latitudes) more rapid growth initially and earlier sexual maturity may contribute to earlier decline in growth rates and result in smaller maximum size. Second, since densities of individuals and diversities of primary resident rocky-shore fishes is greater at lower latitudes, one might expect that more competitive conditions would exist in these reef habitats such that social and competitive growth limitation (Smith 1978) may result. Third, selection for smaller body size as a result of the advantages conferred by earlier, precocious metamorphosis from larvae to juveniles may be stronger at lower latitudes. Among those species with limited dispersal ability (i.e., primary residents) one would expect a greater loss of larvae in the plankton near areas of open ocean, therefore advantages would accrue to those individuals whose larvae minimized their period of larval existence becoming reef-fit earlier and at a smaller size. The latter hypothesis is perhaps the least likely since dispersal rates are in general high enough to prevent gene flow restriction between areas of the Gulf.

The same kinds of explanation for decreased body size at lower latitudes may be used to explain decreased body size on islands in the Gulf. Islands in the Gulf, like mainlands at lower latitudes, have more moderate temperatures (higher winter temperatures), have more species and higher densities of individuals on comparable areas and are under the influence of more oceanic currents and larger volumes of water than corresponding mainlands.

Species Turnover between Sites and Species Composition on Islands and Mainlands

Within habitat species turnover between sites (gamma diversity) was highest for mainlands and lowest for islands. In one sense this kind of turnover measures the way that species number accumulates with area on islands and mainlands. Greater predictability of species composition (low turnover) on islands means that one would have to make more mainland collections in order to realize the same number of species from any given sample area of the mainland since islands in general tend to have more species than mainland areas. Two different kinds of explanations can be offered for this kind of within habitat distribution of species. First, if microhabitats are more evenly distributed on mainlands, that is, a mainland sample area contains some smaller number microhabitats than a comparable island area, then turnover would be lower from site to site on mainlands if the species show a certain amount of microhabitat specialization. Second, if extinction rates are higher on mainlands as a result of greater disturbance (e.g., low temperatures, silting), then species turnover within sites and consequently between sites will be higher. On islands lower disturbance and lower within site species turnover would allow more species to accumulate within each site as long as competitive abilities are nearly equal and there is a certain amount of habitat specialization.

The species composition and relative abundance ranks of the 15 most common fishes in collections in the central Gulf was similar on islands and mainlands. The dominant guild, triplefin blennies (tripterygiids: 41% island; 43% mainland) consisted of four species of active fishes that live on the surfaces of boulders and ledges along the shoreline. Two species of tube blennies (Chaenopsidae), small fishes that live in tubular dwellings vacated by various invertebrates (polychaetes, gastropods, barnacles) were relatively more numerous on islands (19% vs. 9%), whereas five species of clinid blennies (Clinidae) were relatively more numerous on mainlands

(34% vs. 25%). The most abundant species in both island and mainland collections was the small, boulder surface active Cortez triplefin, an undescribed species of *Axoclinus* endemic to the Gulf of California. There was remarkable similarity in the identity and abundance of the 15 most abundant central Gulf species (over 90% of all individuals collected) on islands and mainlands in contrast to the upper Gulf where the dissimilarity was pronounced. The few significant changes in central Gulf ranking (e.g., *Axoclinus carminalis*, *Enneanectes* sp., *Acanthemblemaria crockeri*) were not dramatic and not a single species could be considered primarily 'insular' or 'continental' in its Gulf distribution. The great similarity in species composition of the central Gulf collections both between islands and mainlands and in general (see biogeographic cluster analysis) is in concordance with Molles (1978) results of visual censuses of model and natural patch reefs in the Guaymas-San Carlos area of the central Gulf and with Thomson and Lehner's (1976) repetitive defaunation of tide pools in the upper Gulf. These results suggest a rather deterministic system regulating the composition of Gulf fish communities and lend no support to Sale's (1978) lottery hypothesis or chaos view of community structure.

While the composition of island and mainland collections in the central Gulf were very similar, upper Gulf island and mainland collections were markedly dissimilar. Many species that are rare or absent on the mainland coast were present in the northernmost island collections. These northern range extensions on islands may be attributed to the more benign environment around islands and the severe effects of the physical environment associated with the broad intertidal and shallow mainland coasts of the upper Gulf.

Competition and Predation

The roles of competition and predation are too complex to evaluate on a community level due to the confounding effects of age- and size-specific habitat shifts and flexible growth rates that allow a great deal of accommodation to occur. However, it is assumed that competition is more intense in island communities simply due to increased population density. Piscivorous predation is different in the two environments. Pelagic predators such as yellowtails, black skipjacks, and sharks may be more common near islands whereas needlefishes, barracudas, and sierra mackerel might be more frequent along mainland shores. It is difficult to assess the effects of this kind of predation on the reef community since these predators do not prefer to feed on resident reef fishes. They may, however, actually maintain part of the resource base of shoreline reef communities by forcing smaller schooling fishes within the range of reef predators such as *Mycteroperca rosacea*, the leopard cabrilla. Mainland rocky shores are often adjacent to shallow sandy areas where jacks, corvinas, snappers, flounders, small sharks and stingrays may prey on juvenile reef fishes. Because of the presence of such rock-sand interface predators, predation pressure on the community in general may be more intense on mainland shores. This may also account for the lower density of fishes in mainland collections.

The MacArthur-Wilson Model

The results of the distribution patterns of rocky-shore fishes was not in agreement with the sorts of predictions made by the MacArthur-Wilson equilibrium model of island biogeography. The high degree of uniformity in the species composition and relative abundance ranks in island collections and island vs. mainland collections in the central Gulf indicate a low degree of stochasticity and high degree of predictability of community composition. Gamma-diversity was not high enough to suspect that random events play a major role in species composition; however, predictability was less in mainland shores. G. Smith (1979) concluded that after natural defaunation "eastern Gulf of Mexico reef fish communities develop according to predictable rather than chance processes implicit in the M-W model." He found that colonization of patch reefs after natural defaunation by a red tide seemed to follow a successional sequence leading to a climax community which consisted of a fairly constant assemblage of species that resisted further colonization by other species. Thomson and Lehner (1976) showed that repeated defaunation of tidepool communities with rotenone ichthyocide and a natural winterkill did not change the community composition of intertidal fishes subsequent to recolonization and immigration. Much of the recolonization in the former case was probably by juveniles and adults rather than larvae, however. The reason that marine systems behave differently than terrestrial systems may be that marine colonization processes do not necessarily fit a diffusion model as is assumed in the M-W theory, i.e., uniform decrease in the density of propagules in all directions from a colonizing source. In marine environments predictable current patterns will produce dispersal patterns that favor dispersal in some directions over others. Assuming closer proximity to major currents and consequently higher shoreline rates of water transport on islands, points, and the tips of peninsulas, it is likely that these offshore areas will receive propagules from farther distances than inshore protected areas. This factor may contribute significantly to the insular biogeographic nature of the Cape region with its distant Indo-west Pacific faunal affinities. In this view rocky reef and shoreline areas in protected embayments become isolates in the M-W sense analogous to terrestrial islands. Faunal similarity of islands is much greater than would be expected by geographical distance suggesting higher dispersal rates offshore. In fact, the Gulf islands may maintain the species pool and be a major source of propagules whereas mainland rocky shores may be the relatively depauperate island analogs.

Although the dynamics of propagule dispersal is poorly understood it is clear that enormous losses must be suffered during passive transport in the plankton. That marine species in general exhibit an almost absolute predominance of reproductive strategies characterized by large numbers of pelagic eggs and larvae serves as a clue to the nature of reef habitats in the marine environment. This predominance suggests that: (1) habitats for juveniles and settling larvae are quite different from those of adults; or (2) that suitable habitats are so small and patchily distributed as to preclude the coexistence of parents with cohorts of their offspring; or (3) that competition and predation is so intense on adult habitats that only in other (perhaps marginal) habitats do settling larvae have a reasonable chance of success (Johannes 1978; Balon 1978). The argument that only larvae below some threshold size are at a disadvantage when attempting to establish themselves in an adult habitat does not seem to be an adequate explanation since if this were the case, then we might expect to see a higher frequency of mouth brooding and parental care as is the case with many African cichlids that occupy rocky habitats. However, mouth-brooding is rare and parental care of young almost non-existent in tropical oceans. Clearly it is the transitional nature of and major changes in the resource requirements of reef fishes throughout life, and the high levels of reef predation that have been major selective forces acting on the reproductive fitness components in this community. Given the limited ability of adults of reef species to traverse soft bottoms and open water, and the presumed selective disadvantage of reproductive investment in large eggs and parental care in this kind of environment, it would seem that high dispersal is the central mechanism ensuring that offspring will be provided with the appropriate spectrum of age- and size-dependent resources as well as being exposed to fewer predators.

Low extinction rates on reefs and rocky shorelines, even with high predation rates, may be facilitated by biological accommodations such as size and age-dependent niche shifts, including ontogenetic and developmental changes in predator avoidance and social behavior (Helfman 1978) and flexible growth rates (C. L. Smith 1978).

The Lottery Hypothesis

Sale's (1977) lottery hypothesis of community structure predicts high variability in local community composition due to stochastic colonization by larvae, which essentially coincides with M-W predictions. The hypothesis also maintains that space is the only resource ever in short supply and that colonization success is decided by whoever gets there first rather than by competitive differences between species. Sale also suggests that reef-fish communities are unstable and will not tend to recover (return to similar species composition) following removal or addition of fish. There are few data supporting this hypothesis, and to the contrary, considerable data refuting such predictions.

According to Sale (1977) areas of greater exposure would be the areas of highest diversity of fishes due to higher rates of disturbance that would create new living spaces. Given uniformly high dispersal rates among reef fishes, a minimum of habitat selection and maximum resource overlap among species, which Sale implies, it seems that the only way higher rates of disturbance could result in higher diversity is if the average size of territorial residents is reduced by higher species turnover rates resulting in greater numbers of individuals per unit area and consequent increase in species number due to passive sampling phenomena. This would appear to be the case in the Gulf since it was found that island sites support higher densities and more species of generally smaller body size but it has not been shown that there is greater disturbance (density independent mortality) in exposed (island) areas nor has it been shown that greater mortality results in greater diversity. Since it appears that, to the contrary, mainland inshore areas have the potential to be the more severely disturbed to the point of diversity decrease, the 'intermediate disturbance' hypothesis (Connell 1978) might explain higher island diversity. Results in accord with the lottery hypothesis may be the result of these incorrect assumptions or, in other words, the right answer for the wrong reason.

Intermediate Disturbance, Refuges, Rescue and Interference Effects

Several hypotheses have been advanced regarding present day diversity maintenance besides the lottery hypothesis that have bearing upon reef fish communities and the inshore (mainland) and offshore (island) distribution of species.

The 'intermediate disturbance' hypothesis holds that for some communities, mostly high diversity tropical sessile organisms, disturbance intermediate in scales of frequency and intensity will permit local existence of competitively inferior species with competitively superior ones and that communities are thus non-equilibrium. Disturbance here usually denotes density independent physical environmental factors (e.g., storms, floods, lethal temperatures, silting) that will remove individuals (intermediate) rather than species *in toto* (extreme) from a habitat. Sale (1977) views exposed areas (points, islands) as the areas where disturbance is most likely to have some effect on the supply of living space for reef fishes. However, it is not clear that inshore reef areas are less 'disturbed' since in these areas of shallower nearshore depth lower winter sea temperatures, silting, reduced current and nutrient circulation may severely affect reef communities. In the Gulf of California islands and points may be the least disturbed environments but since there are strong seasonal temperature changes throughout the Gulf (Maluf n.d.) then islands may be intermediate in the frequency and severity of this disturbance when compared to inshore (mainland) areas. This could partially explain the higher observed diversity of fishes on islands in the Gulf.

Refuge hypotheses encompass a wide variety of mechanisms of escape from competitive exclusion in time and space. It has been shown several times (Skellman 1951; F. E. Smith 1972; Horn and MacArthur 1972; Levins and Culver 1971; Slatkin 1974; Levin 1974, 1976a, 1976b) that, even with competitive superiority, diversity may be maintained in heterogeneous environments where dispersal between patches occurs. Recently Dale (1978) has extended this concept to reef fishes and proposed, using a financial analogy, a model to explain coexistence in reef fishes in a manner similar to Sale's (1977) lottery hypothesis.

In the rescue-effect (Brown and Kodric-Brown 1977) high immigration rates have the effect of reducing extinction rates on isolates and results in opposite predictions from the M-W model regarding the effect of isolation on equilibrium turnover rates. High immigration will, according to Brown and Kodric-Brown (1977), reduce species turnover and prevent extinctions of species that are favored by suitable habitats, competitive superiority or absence of predators. This results in a more deterministic system than the M-W model or the lottery hypothesis even though nearly the same assumptions were made for the lottery hypothesis (high dispersal rates). The difference is apparently in how much habitat selection and competitive superiority is allowed subsequent to immigration and colonization.

Recently introduced is another modification of the M-W model called the 'interference effect' (Bohnsack 1979). This was shown for reef fishes on islands very close to the colonizing source or species pool where, as a result of competition and predation by transient fish species from the source area, the carrying capacity and consequently the number of species is drastically reduced on these very near islands. This essentially results in higher extinction rates on very near islands and presumably high turnover since immigration rates would be high as well. It appears that there are two basic effects that need to be considered here. First, temporary transient predators on small near islands can reduce population sizes of resident species (prey) and second, temporary transient predators can act as competitors with the resident species reducing resource levels (macroinvertebrates). Also transient herbivores may reduce the standing crop of primary production thus undercutting the resource base of resident herbivores. In any case, these transient reef associated species may be important in the population dynamics of patch reefs and small isolates.

Propagule Dispersal to and Colonization of Islands and Mainlands

As suggested earlier, islands and offshore localities in the Gulf might be surrounded by water containing a high diversity, albeit low density, of plankton due to more oceanic forms but due to higher current rates densities actually available to reef planktivores may be comparable. Considering the meroplankton, especially resident reef fish larvae, the same kind of phenomenon may be occurring with respect to colonization. In offshore rocky habitats near deep water and major currents it seems likely that of the propagules dispersed from these habitats most will be lost or transported away, local colonization reflecting the diversity of propagules in the incoming water masses. There is a good probability that these incoming water masses, due to mixing and transport from more distant areas contain, if suitable reef areas exist upcurrent, some higher diversity of propagules than could have been locally produced. In inshore mainland areas, on the other hand, since currents are generally less strong and one would expect more eddy formation due to embayments and coastline rugosity, one might expect to find a higher percentage of locally produced propagules in the plankton. Here, colonization by new species from greater distances would be less likely resulting in lower diversity.

Before the M-W theory of island biogeography can be quantitatively applied to fishes that inhabit rocky coastlines it needs to be shown that decreased colonization rates due to small target size of habitat isolates totally outweighs any increase in colonization rates for islands due to more rapid movement of propagule-bearing water past their shores. It appears that currents are stronger near points and on islands because here bottom and shoreline topography will be closest to major currents. Turbulence is caused where coastlines impinge upon currents and reduce current flow such that in very protected inshore areas calm reduced current conditions exist. Because flow of sufficiently high Reynolds Number cannot be decelerated to rest (by coastlines) in a steady fashion vorticity, laminar instability and stochastic flow patterns result which are not easily described (Liepmann 1979). Nonetheless, it does seem intuitively reasonable to expect that, given equal rates of dispersal, propagules released from a protected inshore mainland coast are likely to end up settling on reefs and coastlines closer to their origin than propagules released from exposed offshore island coasts. Similarly, we would expect a higher proportion of immigrants and colonists of inshore areas to be locally derived, whereas those of islands to have arrived from greater distances. Depending on the nature of inshore and offshore turbulence, mixing may result in lower propagule concentrations offshore but because currents are often higher a difference in immigration rates may not be perceived.

With a dirth of data on reproduction and dispersal and at the heart an empirical insufficiency regarding the population dynamics of reef species, a model of island biogeography based on colonization-extinction processes as described by MacArthur and Wilson (1967) seems inappropriate for an understanding of the biogeography and evolution of reef fish communities. Species-specific rates of colonization should presumably differ based on their modes of reproduction and reproductive fitness components (type of eggs and larvae) in reef fishes. Ultimately these kinds of differences might be used to predict the number and identity of species on islands.

If the biogeography of rocky shore fishes in the Gulf were to be forced into a M-W framework, it seems clear that mainland rocky shores represent the insular habitats due to high extinction rates caused by unpredictable physical disturbances which tend to increase species turnover and lower diversity (Thomson and Gilligan n.d.). Conversely, islands become 'biogeographic mainlands' and may represent the chief source of propagules for recruitment.

Species turnover within segments of an exposed-protected rocky shoreline habitat gradient in the central Gulf (Gilligan in press) supports the same pattern shown for islands and mainlands in the Gulf. Among the visually censused reef fish species in this study, highest mean species turnover occurred in the bay segment and lowest species turnover occurred in the point segment (see Table 12). In addition, it was shown that a higher proportion of the 'point' segment species had pelagic eggs whereas a higher proportion of the 'bay' segment species had demersal eggs. Gilligan (in press) suggested that reef fish diversity in protected areas is limited by higher environmental variability (e.g., lower winter temperatures, silting, storms) and resource unpredictability and that diversity limitation at exposed points is related to lesser structural habitat complexity and the dominance of vertical rock surfaces. He also provided evidence that the regular patterns of species segregation along this gradient may be be related to the physical characteristics of dispersal and the quality of the environment between protected and exposed habitats.

Several points are made in this habitat gradient study that are significant in relation to the present island-mainland study. First, compositional segregation along this small (1400 m) peninsula, in which a high proportion of the taxa typical of coral reefs (e.g., parrotfishes, surgeonfishes, butterflyfishes, wrasses) were dominant at the point, parallels the insular biogeographic nature of the cape region of the Baja California peninsula with its Indo-Pacific affinities (Walker 1960; Thomson et al. 1979; Thomson and Gilligan n.d.). It is at least suggestive that patterns such as these that span scales of magnitude would have a general causal structure. Second, mean species turnover was lowest at the point and highest in the bay segment. This is precisely analogous to the higher rate of replacement of species from site to site on mainlands and lower rate on islands that was found in the present study. Clearly the same kinds of community patterns seem to hold for both quantitatively sampled and visually assessed communities over a wide spectrum of inshore to offshore rocky shoreline habitats.

The characteristics of protected and exposed rocky shoreline habitats may regulate species diversity by physical constraints and habitat selection in ecological time and may be important determinants of strategies of dispersal and colonization in evolutionary time.

I feel that the characteristics of early development in reef fishes (e.g., adaptations to planktonic existence) co-evolve with breeding systems and reproductive fitness components, that the nature of protection and exposure of reef habitats are centrally important factors in this regard, and that the patterns of distribution that we observe are a direct result of this kind of community evolution. Without an adequate understanding of the ecology of larval life and dispersal the resolution of current controversies of reef fish community structure and biogeography will be impossible. Larval reef fish ecology is a key to understanding the critical periods in the culture of marine organisms and is a key to understanding the dynamics of natural populations of reef species.

APPENDIX A

FISH COLLECTION LOCALITY DATA

Table A-1. List of data for island and mainland fish collection stations in the Gulf of California. --

UA no. = University of Arizona Fish Collection catalogue number.
Lat°N = Latitude given in decimal degrees.
Sea temp. = Surface sea temperature taken during collection (°C).
S.D. = Secchi disc reading in meters.
S = Total species in collection (including only those species listed in Appendix B).
N = Total number of individuals in collection.
Biomass = Wet preserved weight in grams of total collection.
H'_n = Shannon-Weiner species diversity index using numbers of individuals.
H'_b = Shannon-Weiner species diversity index using weight in grams per lot.

Sta. No.	Locality	Date	UA No.	Lat. (°N)	Sea Temp.	S.D.	S	N	Biomass	H'_n	H'_b
1	Punta San Pedro	7/05/75	75-91	28.05	29.0	-	12	115	137.5	1.997	1.405
2	I. San Pedro Nolasco	7/23/74	74-28	27.95	27.2	8	19	276	512.5	2.271	1.678
3	San Carlos	7/24/74	74-29	27.97	-	-	10	159	231.6	1.505	1.690
4	I. Santa Inez	7/28/74	74-32	27.05	29.0	4.6	13	247	349.5	2.123	2.070
5	Punta Chivato	7/28/74	74-33	27.10	26.1	2.0	8	83	355.9	1.391	1.053
6	I. Coronado	7/31/74	74-34	26.13	28.1	6.4	28	770	845.1	2.260	2.072
7	I. Carmen	8/01/74	74-35	26.02	28.8	7.0	22	408	388.6	2.391	2.040
8	Loreto	8/01/74	74-36	26.12	30.5	-	18	412	221.8	1.880	1.874
9	I. Espirito Santo	8/05/74	74-37	24.42	28.3	-	24	489	315.0	2.253	1.998
10	La Paz	8/06/74	74-38	24.35	28.3	-	18	392	798.2	2.076	1.469
11	I. Cerralvo	8/08/74	74-40	24.32	28.5	10.0	20	248	114.8	1.950	2.048

Table A-1--continued. List of data for island and mainland fish collection stations in the Gulf of California.

Sta. No.	Locality	Date	UA No.	Lat. (°N)	Sea Temp.	S.D.	S	N	Biomass	H'_n	H'_b
12	Cabo San Lucas	8/9/74	74-41	22.87	26.7	5.0	20	363	768.9	2.237	1.485
13	I. San Pedro Nolasco	10/19/74	74-57	27.95	26.0	6.1	26	847	1039.6	2.275	2.149
14	I. San Pedro Nolasco	3/27/75	75-32	27.95	18.0	7.0	19	134	201.5	2.462	1.780
15	I. Venado	3/28/75	75-33	27.98	18.0	-	16	151	221.6	2.052	1.577
16	I. San Pedro Nolasco	7/04/75	75-38	27.95	27.0	12.0	22	508	218.0	2.169	2.315
17	I. San Pedro Nolasco	7/01/75	75-37	27.95	27.0	12.0	21	514	747.1	2.290	1.939
18	I. Tiburon	6/27/75	75-35	28.78	29.0	4.0	15	125	529.9	2.193	1.322
19	Punta San Antonio	3/26/75	75-31	27.95	16.0	5.0	11	46	68.2	2.053	1.433
20	South of Libertad	6/22/75	75-34	29.70	25.0	10.0	10	114	114.4	1.805	1.452
21	I. San Lorenzo	7/28/75	75-74	28.67	26.0	10.0	22	428	1225.5	2.463	2.110
22	I. San Lorenzo	7/28/75	75-75	28.67	27.0	8.5	13	370	432.7	1.813	1.790
23	Roca Consag	10/10/75	75-64	31.12	28.0	4.8	10	226	377.4	1.331	1.369
24	I. San Jorge	10/11/75	75-66	31.03	28.8	6.0	15	225	1088.5	1.977	1.460
25	Loreto	6/16/73	73-73	26.00	21.0	5.1	20	172	433.3	2.322	1.757
26	Cabo Pulmo	6/23/73	73-80	23.45	26.7	5.0	21	234	287.4	2.092	1.817
27	I. Venado	10/13/73	73-100	27.95	22.2	-	20	318	489.2	2.032	1.374
28	Punta San Pedro Area	6/30/75	75-36	28.05	28.0	12.0	25	309	802.5	2.420	1.829
29	I. Partida Norte	7/29/75	75-76	28.87	25.0	5.5	17	300	485.4	2.102	2.132
30	Punta Qué Malo	7/30/75	75-77	28.95	29.0	5.5	13	419	153.9	0.963	1.180

Table A-1--continued. List of data for island and mainland fish collection stations in the Gulf of California.

Sta. No.	Locality	Date	UA No.	Lat. (°N)	Sea Temp.	S.D.	S	N	Biomass	H'_n	H'_b
31	I. San Esteban	7/31/75	75-78	28.67	27.0	9.0	12	259	229.1	1.740	1.600
32	I. San Esteban	7/31/75	75-79	28.67	27.0	-	17	485	508.8	1.777	1.702
33	Roca Consag	7/09/73	73-89	31.12	25.6	1.8	8	69	54.3	1.004	1.156
34	I. San Pedro Martir	7/27/75	75-73	28.37	29.0	6.1	21	565	354.4	2.026	1.929
35	Punta San Pedro Area	6/22/75	75-51	28.08	25.0	4.0	14	385	1081.3	1.516	1.618
36	Cabo San Lucas	6/28/73	73-83	22.87	21.0	-	14	43	53.5	1.866	1.349
37	I. San Pedro Martir	6/30/76	76-13	28.37	28.5	20.0	21	257	344.7	2.489	2.196
38	I. Tortuga	7/01/76	76-14	27.45	29.0	15.0	24	338	584.7	2.616	2.015
39	Santa Rosalia	7/02/76	76-15	27.33	25.0	8.0	19	152	435.2	2.562	1.879
40	I. San Marcos	7/20/76	76-16	27.33	26.0	5.0	24	541	1510.5	2.722	1.778
41	Loreto Area	7/20/76	76-24	26.20	29.0	-	21	362	304.2	2.160	1.878
42	Loreto Area	7/25/76	76-26	25.73	29.5	6.0	31	431	985.3	2.796	1.612
43	I. Danzante	7/27/76	76-31	25.80	29.7	15.0	21	755	461.9	2.036	2.132
44	I. Monserrate	7/28/76	76-32	25.70	29.3	5.5	27	1138	650.5	2.333	1.916
45	Punta San Pedro	7/02/75	75-121	28.08	29.0	-	16	193	434.9	2.043	1.410
46	I. Farallon	3/15/76	76-02	25.50	18.0	6.3	13	195	1117.0	1.713	0.522
47	San Carlos	7/15/76	76-22	27.95	30.0	-	16	162	196.3	1.879	1.581
48	Bahia San Pedro	10/19/74	74-58	28.03	26.0	3.0	18	439	311.3	1.684	1.852
49	I. San Jorge	10/11/75	75-65	31.05	27.8	4.8	11	141	133.2	1.337	1.377
50	I. Coronado	7/22/76	76-25	26.12	28.5	15.0	23	1017	790.9	2.209	2.039

APPENDIX B

ROCKY-SHORE FISHES

Table B-1. List of rocky-shore fishes used in the analyses, including their residency status, biogeographic affinity, type of egg and food habits. --

Residency: 1°, primary resident; 2°, secondary resident

Affinity:
- G, Gulf of California endemic
- M, restricted to Mexican waters
- N, northern (San Diegan) affinities
- P, Panamic, range extends to Panama and sometimes further south
- I, Indo-west Pacific immigrant

Eggs: p, pelagic; d, demersal; v, viviparous

Food Habits:
- h, herbivorous, grazes on benthic algae
- b, benthic predator, feeds on small benthic invertebrates such as crustaceans, mollusks, worms, etc.
- f, piscivorous, feeds on fishes
- z, planktivorous, feeds on zooplankton
- o, other (feeds on ectoparasites or mucus of other fishes)

Family	Genus Species	Residency	Affinity	Egg Type	Food Habits
Muraenidae (morays)	Gymnothorax castaneus (Jordan and Gilbert 1882)	2°	P	P	b,f
	G. panamensis (Steindachner 1876)	2°	P	P	b
	Muraena lentiginosa Jenyns 1843	2°	P	P	b
	Uropterygius necturus (Jordan and Gilbert 1882)	2°	P	P	b
	U. sp. (undescribed species)	2°	?	P	b
Ophidiidae (brotulas)	Ogilbia sp. (undescribed species)	1°	-	V	b
	Oligopus diagrammus (Heller & Snodgrass 1903)	1°	P	?	b

Table B-1--continued. List of rocky-shore fishes used in the analyses.

Family	Genus Species	Residency	Affinity	Egg Type	Food Habits
Scorpaenidae (scorpionfishes)	*Scorpaena mystes* Jordan and Starks 1895	2°	P	P	b,f
	Scorpaenodes xyris (Jordan and Gilbert 1882)	2°	P	P	b
Grammistidae (soapfishes	*Rypticus bicolor* (Valenciennes 1846)	2°	P	P	b
Apogonidae (cardinalfishes)	*Apogon retrosella* (Gill 1863)	1°	M	d	z,b
Sciaenidae (drums)	*Pareques viola* (Gilbert 1898)	2°	P	P	b
Cirrhitidae (hawkfishes)	*Cirrhitichthys oxycephalus* (Bleeker 1855)	2°	I	P	b
	Cirrhitus rivulatus Valenciennes 1855	2°	P	P	b
Blenniidae (comb tooth blennies)	*Entomacrodus chiostictus* (Jordan and Gilbert 1883)	1°	P	d	h
	Hypsoblennius brevipinnis (Gunther 1861)	1°	P	d	h
	H. gentilis (Girard 1854)	1°	N	d	h
	Ophioblennius steindachneri Jordan & Evermann 1898	1°	P	d	h
	Plagiotremus azaleus Jordan and Bollman 1890	1°	P	d	O
Tripterygiidae (triplefin blennies)	Lizard triplefin (undescribed genus and species)	1°	G	d	b
	Axoclinus carminalis (Jordan and Gilbert 1882)	1°	G	d	b
	Cortez triplefin (undescribed *Axoclinus* sp.)	1°	G	d	b
	Enneanectes sexmaculatus (Fowler 1944)	1°	P	d	b
	Flag triplefin (undescribed *Enneanectes* sp.)	1°	G	d	b

Table B-1--continued. List of rocky-shore fishes used in the analyses.

Family	Genus Species	Residency	Affinity	Egg Type	Food Habits
Clinidae (clinid blennies)	Exerpes asper (Jenkins & Evermann 1889)	1°	G	d	z
	Labrisomus striatus Hubbs 1953	1°	P	d	b
	L. xanti Gill 1860	1°	M	d	b
	Malacoctenus gigas Springer 1959	1°	G	d	b
	M. hubbsi Springer 1959	1°	P	d	b
	M. margaritae (Fowler 1944)	1°	P	d	b
	M. tetranemus (Cope 1877)	1°	P	d	b
	Paraclinus beebei Hubbs 1952	1°	P	d	b
	P. mexicanus (Gilbert 1904)	1°	P	d	b
	P. sini Hubbs 1952	1°	M	d	b
	Stathmonotus sinuscalifornici (Chaubanaud 1942)	1°	G	d	b
	Starksia spinipenis (Al-Uthman 1960)	1°	P	d	b
	Xenomedea rhodopyga Rosenblatt & Taylor 1971	1°	G	d	b
Chaenopsidae (tube blennies)	Acanthemblemaria balanorum Brock 1940	1°	P	d	z
	A. crockeri Beebe and Tee-Van 1938	1°	G	d	z
	A. macrospilus Brock 1940	1°	P	d	z
	Chaenopsis alepidota (Gilbert 1890)	1°	M	d	z
	Coralliozetus angelica (Bohlke and Mead 1957)	1°	P	d	z
	Coralliozetus micropes (Beebe and Tee-Van 1938)	1°	G	d	z
	C. rosenblatti Stephens 1963	1°	G	d	z
	Ekemblemaria myersi Stephens 1963	1°	P	d	z

Table B-1--continued. List of rocky-shore fishes used in the analyses.

Family	Genus Species	Residency	Affinity	Egg Type	Food Habits
Chaenopsidae (cont.)	Protemblemaria bicirris (Hildebrand 1946)	1°	P	d	z
Gobiidae (gobies)	Aruma histrio (Jordan 1884)	1°	G	d	b
	Bathygobius ramosus Ginsburg 1947	1°	P	d	b
	Barbulifer pantherinus (Pellegrin 1901)	1°	G	d	b
	B. sp. (undescribed species)	1°	?	d	b
	Chriolepis zebra Ginsburg 1938	1°	G	d	b
	Coryphopterus urospilus Ginsburg 1938	1°	P	d	b
	Elacatinus diqueti (Pellegrin 1901)	1°	P	d	o
	E. sp. (undescribed species)	1°	P	d	o
	E. punticulatus (Ginsburg 1938)	1°	P	d	b
	Gobiosoma chiquita (Jenkins & Evermann 1889)	1°	G	d	b
	Gobulus hancocki Ginsburg 1938	1°	P	d	b
	Gymneleotris seminudus (Gunther 1864)	1°	P	d	b
	Lythrypnus dalli (Gilbert 1890)	1°	N	d	b
	Lythrypnus pulchellus Ginsburg 1938	1°	G	d	b
	Pyconomma semisquamatum Rutter 1904	1°	G	d	b
Gobiescocidae (clingfishes)	Arcos erythrops (Jordan and Gilbert 1882)	1°	M	d	b
	Gobiesox adustus Jordan and Gilbert 1882	1°	P	d	b
	G. pinniger Gilbert 1890	1°	G	d	b
	Pherallodiscus funebris Gilbert 1890	1°	G	d	b

Table B-1--continued. List of rocky-shore fishes used in the analyses.

Family	Genus Species	Resi-dency	Affin-ity	Egg Type	Food Habits
Gobiescocidae (cont.)	*Tomicodon boehlkei* Briggs 1955	1°	G	d	b
	T. eos (Jordan and Gilbert 1882)	1°	G	d	b
	T. humeralis (Gilbert 1890)	1°	G	d	b

APPENDIX C

FISH COLLECTION RAW ABUNDANCE DATA

Table C-1. Species abundances in each of the 50 Gulf of California collections. -- Collection numbers refer to Appendix A and Tables 1 and 2.

	20	23	24	33	49	18	35	17	2	13	14	16	4	6	7
Gymnothorax castaneus	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
G. panamensis	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-
Muraena lentiginosa	-	-	-	-	-	-	-	-	-	4	-	-	-	-	1
Uropterygius necturus	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-
U. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13
Arcos erythrops	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-
Gobiesox pinniger	-	10	2	-	-	-	2	-	-	-	-	-	41	3	12
G. adustus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pherallodiscus funebris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tomicodon humeralis	-	-	-	-	-	-	6	-	-	-	-	-	-	11	2
T. boehlkei	-	-	-	-	-	-	1	18	-	3	1	4	5	25	4
T. eos	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ogilbia spp.	-	2	-	3	-	2	1	3	3	9	-	8	2	11	2
Oligopus diagrammus	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
Scorpaena mystes	-	-	-	-	-	1	-	-	-	1	-	-	1	1	-
Scorpaenodes xyris	-	-	-	-	-	14	-	33	-	-	10	26	-	2	-
Rypticus bicolor	-	-	-	-	-	-	-	-	2	4	-	1	-	-	-
Apogon retrosella	-	2	4	1	2	3	-	-	8	143	13	2	-	1	3
Parecues viola	1	-	4	-	-	18	-	-	-	1	-	-	-	3	-
Cirrhitichthys oxycephalus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cirrhitus rivulatus	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Entomacrodus chiostictus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hypsoblennius brevipinnis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
H. gentilis	11	3	11	2	-	13	16	-	-	-	-	-	16	-	-
Ophioblennius steindachneri	-	-	-	-	-	-	-	9	12	18	3	1	-	8	1
Plagiotremus azaleus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

6	7	21	22	29	31	32	34	37	38	40	43	44	50	15	19	27	45	47	48	28	1	3	5
-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	-	-	1	-	4	-	-	3	-	-	-	-	-	-	-	-	-	-
-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	-	-	-	-	-	-	-	-	1	1	-	-	3	-	-	-	-	-	-	-	-	-	-
-	13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	12	-	-	13	-	3	-	-	-	-	-	-	-	-	-	2	-	-	-	1	-	-	2
-	-	-	-	-	-	-	-	-	-	-	-	3	-	1	-	2	1	-	-	-	-	-	-
-	-	-	-	-	-	7	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
11	2	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-
25	4	34	34	74	-	168	3	5	17	6	9	100	67	4	-	69	32	8	16	9	14	31	3
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	2	16	1	3	-	8	5	5	7	12	5	5	31	2	-	-	1	1	2	13	-	-	-
-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1	-	1	-	1	-	-	-	-	-	-	-	4	-	-	-	3	-	1	-	-	-	-	-
2	-	10	4	1	5	-	46	43	8	31	3	2	2	-	2	-	-	6	-	8	-	-	-
-	-	-	-	-	-	-	-	-	5	6	2	-	-	-	-	-	-	-	-	1	-	-	-
1	3	10	-	1	-	-	-	1	5	6	2	-	-	-	8	7	-	-	13	8	1	-	-
3	-	3	-	-	10	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	4
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	1	17	1	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	1	6	-	-	-	-	-	-	-	-	-	-	-
-	-	5	-	2	1	-	2	-	-	-	-	-	-	1	-	-	-	2	-	1	-	18	-
8	1	1	-	-	-	2	5	5	26	53	7	51	32	-	-	2	1	-	3	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

.9	27	45	47	48	28	1	3	5	8	25	30	39	41	42	9	10	11	12	26	36	46
-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	3	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	1	2	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	1	-	-	7	-	2	-
-	2	-	-	-	1	-	-	2	13	4	-	-	-	-	-	-	-	-	-	-	-
-	2	1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	4	-	-	-
-	1	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	11	48	-	-	-	-	10	-	-	-	-	2	-
-	69	32	8	16	9	14	31	3	15	17	-	-	3	43	38	20	-	12	-	1	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-
-	-	1	1	2	13	-	-	-	-	9	-	-	1	12	1	-	1	17	1	2	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	3	-	1	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	1
2	-	-	6	-	8	-	-	-	-	-	-	19	3	5	-	1	3	-	1	-	-
-	-	-	-	-	1	-	-	-	-	3	-	-	1	1	-	-	-	-	1	2	-
8	7	-	-	13	8	1	-	-	-	23	-	10	2	-	4	2	5	-	8	-	14
-	-	-	-	-	1	-	-	4	-	-	1	9	-	1	-	-	-	-	2	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-
-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-
-	-	-	-	-	-	-	-	-	-	5	-	-	2	4	-	-	-	5	10	5	2
-	-	-	-	-	-	-	-	-	-	-	-	3	3	6	2	3	1	0	7	-	3
-	-	-	2	-	1	-	18	-	-	2	4	-	-	1	-	-	-	-	-	-	-
-	2	1	-	3	-	-	-	-	3	-	-	20	20	12	8	31	15	78	24	-	44
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	1	-

Table C-1--continued. Species abundances.

	20	23	24	33	49	18	35	17	2	13	14	16	4	6	7	21
Axoclinus carminalis	-	-	-	-	-	-	-	15	9	35	4	3	-	13	7	-
A. sp. (Cortez triplefin)	-	24	1	-	-	-	199	25	7	37	16	102	28	243	93	77
gen. sp. (Lizard triplefin	3	134	96	52	87	39	-	7	32	127	10	138	-	4	1	70
Enneanectes sexmaculatus	-	-	-	-	-	-	-	2	1	2	-	-	-	-	-	-
E. sp. (Flag triplefin)	-	-	-	-	-	-	-	54	39	126	3	2	-	36	15	59
Exerpes asper	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Labrisomus striatus	-	-	-	-	-	-	-	-	-	-	-	-	-	5	2	-
L. xanti	-	10	32	-	1	-	7	3	-	1	-	-	41	44	20	9
Malacoctenus gigas	-	-	26	-	5	-	39	-	5	-	-	-	-	-	-	-
M. hubbsi	18	1	4	-	-	11	56	186	28	73	18	81	20	70	16	41
M. margaritae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
M. tetranemus	-	-	-	-	-	1	-	6	0	8	1	-	-	-	-	-
Paraclinus beebei	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. mexicanus	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-
P. sini	29	-	11	-	20	2	11	38	8	26	3	28	47	23	9	1
Starksia spinipenis	-	-	-	2	-	-	-	11	7	6	-	1	-	3	2	-
Xenomedea rhodopyga	1	38	6	3	15	4	-	48	4	5	4	40	-	3	-	29
Stathmonotus sinuscalifornici	-	-	-	-	-	-	-	19	1	1	-	4	-	1	3	10
Acanthemblemaria crockeri	7	-	6	-	2	3	-	12	91	195	18	41	-	114	59	37
A. balanorum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
A. macrospilus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Coralliozetus angelica	-	-	-	-	-	-	-	20	2	5	-	3	-	-	-	-
Coralliozetus micropes	-	-	12	-	-	-	4	1	-	5	-	-	7	123	62	6
C. rosenblatti	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ekemblemaria myersi	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Protemblemaria bicirris	2	2	8	-	5	2	-	-	-	-	-	-	-	-	-	-

	6	7	21	22	29	31	32	34	37	38	40	43	44	50	15	19	27	45	47	48	28	1	3	5
	13	7	-	-	-	-	-	-	-	53	7	7	199	11	42	5	55	19	-	234	11	20	5	-
	243	93	77	137	91	1	160	9	39	15	61	84	106	257	21	11	43	53	37	12	37	29	83	18
	4	1	70	17	29	56	-	201	15	-	25	70	3	-	-	1	2	-	1	21	81	-	-	-
	-	-	-	-	-	-	-	-	-	-	1	-	-	6	-	-	-	-	-	4	-	-	-	
-	36	15	59	23	23	53	12	69	10	67	41	164	7	169	2	2	3	1	3	3	-	-	-	
-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	
-	5	2	-	-	-	-	-	-	-	2	1	-	-	9	-	-	-	-	-	-	1	-	-	
1	44	20	9	3	6	1	8	7	2	16	20	4	28	72	2	-	10	11	1	1	6	4	1	1
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
0	70	16	41	15	14	81	49	81	52	23	46	13	346	28	28	9	87	43	51	76	4	26	9	3
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	14	-	1	-	
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
7	23	9	1	5	0	8	13	14	16	31	87	5	46	4	24	5	21	14	37	16	14	7	-	
-	3	2	-	-	-	-	1	-	2	4	-	-	2	-	-	-	-	-	-	-	-	-	-	
-	3	-	29	5	8	2	1	25	20	1	41	110	-	7	1	1	1	5	-	9	29	4	-	
-	1	3	10	16	4	1	10	2	6	8	19	-	-	-	15	1	-	2	-	1	-	-	-	
-	114	59	37	9	11	40	4	78	5	29	39	219	62	170	4	-	6	2	8	9	49	6	-	
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
-	-	-	-	-	-	-	-	-	-	-	-	-	15	-	-	-	-	-	-	-	-	-	-	
-	-	-	-	-	-	-	1	-	2	4	-	-	60	-	-	-	1	-	-	-	-	1	-	
7	123	62	6	85	16	-	36	1	-	3	11	38	4	128	-	-	1	4	1	4	1	2	3	
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	

	19	27	45	47	48	28	1	3	5	8	25	30	39	41	42	9	10	11	12	26	36	46
:	5	55	19	-	234	11	20	5	-	10	1	-	-	27	77	1	14	102	3	93	17	83
.	11	43	53	37	12	37	29	83	18	200	21	1	6	28	19	137	137	4	40	-	-	-
.	1	2	-	1	21	81	-	-	-	-	-	88	10	12	1	-	-	18	-	-	-	1
-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	5	-	-	-	-	1	-	-
2	2	3	1	3	3	-	-	-	-	10	6	1	10	84	35	18	6	11	-	1	-	17
-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	26	-	-	-	-	-	-	-
-	-	-	-	-	-	1	-	-	-	1	2	-	-	-	2	9	1	-	3	-	1	-
2	-	10	11	1	1	6	4	1	13	16	10	-	10	65	6	12	37	4	39	1	-	-
-	-	-	-	-	-	-	-	-	5	-	-	2	-	-	-	-	-	-	-	-	-	-
8	9	87	43	51	76	4	26	9	37	24	2	-	1	20	50	29	39	12	87	2	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	1	0	0
-	-	-	-	3	14	-	1	-	-	-	-	-	28	-	9	-	2	5	-	13	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	35	-	-	-
24	5	21	14	37	16	14	7	-	1	13	2	2	3	1	26	12	11	2	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	2	-	3	2	4
1	1	1	5	-	9	29	4	-	-	-	-	294	8	-	4	-	-	-	-	-	-	-
15	1	-	2	-	1	-	-	-	-	-	-	-	1	-	4	3	-	-	-	-	-	-
4	-	6	2	8	9	49	6	-	-	5	-	3	7	81	40	105	18	42	-	-	-	1
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14	-	-	12	2	34	3	4
-	-	1	-	-	-	-	1	-	-	-	-	-	4	1	-	-	-	-	-	21	-	20
-	-	1	4	1	4	1	2	3	-	69	-	8	-	3	8	53	66	-	19	-	-	-
-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	2	-	-	-	-	-	-	-

Table C-1--continued. Species abundances.

	20	23	24	33	49	18	35	17	2	13	14	16	4	6	7
Chaenopsis alepidota	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Aruma histrio	6	-	2	-	-	0	10	-	-	-	-	1	2	4	40
Bathygobius ramosus	-	-	-	-	-	-	-	-	11	-	-	-	-	-	-
Barbulifer pantherinus	-	-	-	-	-	-	-	1	-	4	4	9	-	-	-
B. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chriolepis zebra	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
Coryphopterus urospilus	-	-	-	5	2	-	-	-	-	-	-	-	-	-	-
Elacatinus digueti	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-
E. punticulatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
E. sp.	-	-	-	-	-	-	-	3	-	7	8	-	-	-	-
Gobiosoma chiquita	-	-	-	-	-	6	32	-	-	-	-	-	36	7	41
Gobulus hancocki	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gymneleotris seminudus	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
Lythrypnus dalli	3	-	-	-	-	6	-	-	-	-	19	2	-	-	-
L. pulchellus	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Pycnomma semisquamatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

4	6	7	21	22	29	31	32	34	37	38	40	43	44	50	15	19	27	45	47	48	28	1	3
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	4	40	-	-	3	-	2	1	-	4	4	6	3	6	1	-	-	2	1	-	1	-	2
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
-	-	-	-	-	-	-	-	10	14	6	9	2	1	-	2	-	-	2	-	-	11	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	3	-	-	-	-	-	9	-	-	-	-	-	-	-	-	-	-	-	4	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	2	-	-	-	-	-	-	-	-	-	12	-	-	-	-	-	-	-	5	-	-
-	-	-	-	-	-	-	-	-	2	6	10	-	2	-	-	-	-	-	-	-	-	-	-
36	7	41	-	-	-	-	-	-	-	-	-	-	4	4	1	-	1	-	-	-	-	-	4
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-
-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	3	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-

15	19	27	45	47	48	28	1	3	5	8	25	30	39	41	42	9	10	11	12	26	36	46
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1	-	-	2	1	-	1	-	2	1	13	5	13	-	1	10	8	-	-	-	-	-	-
-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	2	-	-	-
2	-	-	2	-	-	11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-
-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-
-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	1	1	1	3	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-
1	-	1	-	-	-	-	-	4	1	1	2	-	-	-	-	29	2	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
-	-	-	-	-	-	5	-	-	-	-	1	-	-	-	-	1	1	-	-	-	1	-
-	1	-	-	-	-	3	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

APPENDIX D

SPECIES SUMMARY

Table D-1. Summary of species abundance, biomass, collecting frequency and mean body-size in all Gulf collections.

Species	N	P	W	P	C	P	wt/md
Gymnothorax castaneus	7	.0004	2.9	.0001	3	.0588	.4143
G. panamensis	16	.0009	12.1	.0005	6	.1176	.7563
Muraena lentiginosa	12	.0007	170.3	.0069	6	.1176	14.1917
Uropterygius necturus	12	.0007	325.7	.0132	5	.0980	24.1417
U. sp.	13	.0007	145.2	.0059	1	.0196	11.1692
Arcos erythrops	33	.0019	35.3	.0014	7	.1373	1.0697
Gobiesox pinniger	108	.0062	162.1	.0066	13	.2549	1.5009
G. adustus	13	.0007	16.0	.0007	6	.1176	1.2308
Pherallodiscus funebris	10	.0006	4.5	.0002	3	.0588	.4500
Tomicodon humeralis	95	.0054	37.6	.0015	8	.1569	.3958
T. boehlkei	913	.0527	276.2	.0112	3	.7200	.3025
T. eos	3	.0002	.4	.0000	2	.0392	.1333
Ogilbia spp.	207	.0119	175.1	.0071	35	.6863	.8459
Oligopus diagrammus	4	.0002	4.2	.0002	3	.0588	1.0500
Scorpaena mystes	17	.0010	194.7	.0079	12	.2353	11.4529
Scorpaenodes xyris	288	.0165	409.2	.0165	25	.4902	1.4208
Rypticus bicolor	16	.0009	467.0	.0189	9	.1765	29.1875
Apogon retrosella	312	.0180	1,302.8	.0529	3	.6000	4.1756
Pareques viola	60	.0034	923.3	.0373	15	.2941	15.3883
Cirrhitichthys oxycephalus	3	.0002	21.8	.0009	1	.0196	7.2667

Table D-1--continued. Summary of species abundance, biomass, collecting frequency and mean body-size in all Gulf collections.

Species							
Cirrhitus rivulatus	5	.0030	23.4	.0010	3	.0588	4.6800
Entomacrodus chiostictus	52	.0030	64.6	.0026	10	.1961	1.2423
Hypsoblennius brevipinnis	36	.0021	13.2	.0005	11	.2157	.3667
H. gentilis	111	.0064	209.0	.0084	18	.3529	1.8829
Ophioblennius steindachneri	495	.0284	5589.5	.2259	29	.5686	11.2919
Plagiotremus azaleus	6	.0003	4.4	.0002	2	.0392	.7333
Axoclinus carminalis	1,182	.0682	329.7	.0134	31	.6200	.2789
A. sp. (Cortez triplefin)	2,765	.1596	1536.3	.0624	44	.8600	.55
gen. sp. (Lizard triplefin)	1,485	.0851	1090.5	.0441	33	.6471	.7343
Enneanectes sexmaculatus	22	.0013	5.2	.0002	8	.1569	.2364
E. sp. (Flag triplefin	1,185	.0679	602.1	.0243	36	.7059	.5081
Exerpes asper	32	.0018	11.5	.0005	5	.0980	.3594
Labrisomus striatus	39	.0022	234.0	.0095	13	.2549	6.0000
L. xanti	584	.0337	5250.5	.2134	4	.8000	8.9906
Malacoctenus gigas	82	.0047	300.3	.0122	6	.1200	3.6622
M. hubbsi	2,007	.1150	3054.4	.1234	45	.8824	1.5219
M. margaritae	1	.0001	.7	.0000	1	.0196	.7000
M. tetranemus	137	.0079	164.3	.0067	15	.3000	1.1993
Paraclinus beebei	3	.0002	.4	.0000	1	.0196	.1333
P. mexicanus	38	.0022	19.7	.0008	2	.0392	.5184

Table D-1--continued. Summary of species abundance, biomass, collecting frequency and mean body-size in all Gulf collections.

Species							
P. sini	696	.0402	407.9	.0165	42	.8400	.5848
Starksia spinipenis	53	.0030	24.1	.0010	16	.3137	.4547
Xenomedea rhodopyga	776	.0448	265.5	.0108	33	.6600	.3421
Stathmonotus sinuscalifornici	132	.0076	30.6	.0012	22	.4314	.2318
Acanthemblemaria crockeri	1,637	.0945	388.5	.0158	39	.7800	.2374
A. balanorum	1	.0001	.8	.0000	1	.0196	.8000
A. macrospilus	84	.0048	18.3	.0007	7	.1373	.2179
Coralliozetus angelica	145	.0084	28.9	.0012	14	.2800	.1993
Coralliozetus micropes	784	.0452	81.3	.0033	31	.6200	.1037
C. rosenblatti	1	.0001	.1	.0000	1	.0196	.1000
Ekemblemaria myersi	2	.0001	.2	.0000	2	.0393	.1000
Protemblemaria bicirris	22	.0013	4.2	.0002	7	.1373	.1909
Chaenopsis alepidota	1	.0001	.6	.0000	1	.0916	.6000
Aruma histrio	150	.0086	28.3	.0011	25	.4902	.1887
Bathygobius ramosus	16	.0009	17.9	.0007	3	.0588	1.1188
Barbulifer pantherinus	78	.0045	17.8	.0007	14	.2745	.2282
B. sp.	3	.0002	.4	.0000	1	.0196	.1333
Chriolepis zebra	21	.0012	4.2	.0002	5	.0980	.2000
Coryphopterus urospilus	14	.0008	9.3	.0004	5	.0980	.6643
Elacatinus digueti	6	.0003	.9	.0000	1	.0196	.1500

Table D-1--continued. Summary of species abundance, biomass, collecting frequency and mean body-size in all Gulf collections.

Species							
E. punticulatus	24	.0014	3.9	.0002	6	.1176	.1625
E. sp.	43	.0025	5.7	.0002	9	.1765	.1326
Gobiosoma chiquita	168	.0096	69.7	.0028	13	.2549	.4149
Gobulus hancocki	2	.0001	.2	.0000	1	.0196	.1000
Gymneleotris seminudus	15	.0009	2.3	.0001	7	.1373	.1533
Lythrypnus dalli	38	.0022	4.9	.0002	10	.1961	.1289
L. pulchellus	2	.0001	.2	.0000	2	.0392	.1000
Pycnomma semisquamatum	3	.0002	3.0	.0001	1	.0196	1.0000
Totals	17,326	24,609.0					

APPENDIX E

VISUAL CENSUS DATA

Table E-1. Visual census data for nearshore islands (Fig. , Table) in the Guaymas-San Carlos area of Sonora, Mexico in the Gulf of California. -- See Table for explanation of letters (x = present, blank = absent).

Species	A	B	C	D	E	F
Abudefduf troschelii	x	x	x	x	x	x
Anisotremus interruptus	x	x	x			x
Acanthemblemaria crockeri	x		x	x	x	x
Apogon retrosella	x	x	x	x	x	
Lizard triplefin	x	x	x	x	x	x
Axoclinus carminalis	x	x	x	x	x	x
Axoclinus sp.		x				
Balistes polylepis	x	x	x	x	x	x
Bodianus diplotaenia	x	x	x	x	x	x
Calamus brachysomus	x	x	x	x	x	x
Chaetodon humeralis			x		x	x
Chromis atrilobata	x	x	x	x	x	x
Cirrhitichthys oxycephalus	x				x	
Cirrhitus rivulatus	x	x	x	x	x	
Coralliozetus angelica		x		x	x	
Coralliozetus micropes			x			x
Coryphopterus urospilus	x	x	x	x	x	
Diodon holocanthus					x	x
Elacatinus punticulatus	x	x	x	x	x	x
Epinephelus labriformis		x			x	
Epinephelus afer			x		x	x
Eucinostomus currani ms		x				
Eupomacentrus rectifraenum		x	x		x	x

Table E-1--continued. Visual census data for nearshore islands.

Species	A	B	C	D	E	F
Eupomacentrus flavilatus	x	x	x	x	x	x
Fistularia commersonii		x			x	
Girella simplicidens		x	x	x	x	x
Haemulon sexfasciatum	x		x	x	x	x
Halichoeres dispilus	x	x	x	x	x	x
Heniochus nigrirostris	x	x	x		x	x
Hermosilla azurea	x	x			x	
Holocanthus passer	x	x	x	x	x	x
Adioryx suborbitalis			x			x
Hoplopagrus guentheri		x				
Hypsoblennius brevipinnis	x	x	x	x	x	
Kyphosus elegans		x		x	x	x
Labrisomus xanti	x		x	x		
Lutjanus argentiventris	x	x	x		x	x
Lutjanus novemfasciatus						x
Malacoctenus hubbsi	x	x	x	x	x	x
Malacoctenus tetranemus		x	x	x		
Microlepidotus inornatus	x		x	x	x	
Microspathodon dorsalis	x	x				x
Mugil cephalus		x				
Muraena lentiginosa		x			x	
Mycteroperca rosacea	x	x	x	x	x	x
Myripristis leiognathos	x	x	x		x	
Ophioblennius steindachneri	x	x	x	x	x	x
Pareques viola		x	x		x	
Epinephelus panamensis		x	x		x	x
Pomacanthus zonipectus	x		x	x		x
Prionurus punctatus	x		x	x		
Scarus perrico			x	x	x	x
Scorpaena mystes		x	x			
Scorpaenodes xyris				x		

Table E-1--*continued*. Visual census data for nearshore islands.

Species	A	B	C	D	E	F
Thalassoma lucasanum	x	x	x	x	x	x
Tomicodon boehlkei	x	x				x
Xenistius californiensis		x				

APPENDIX F

RANK AND MEAN ABUNDANCE SUMMARY

Table F-1. Rank and mean abundance per collection of species from islands and mainlands in the upper, central, and lower Gulf of California. -- Average rank position assigned to tied values with the next value given the same rank as if there were no ties (Goldstein 1964); species listed in order of abundance for all 50 collections.

	Upper Gulf				Central Gulf				Lower Gulf			
	Island (5)		Mainland (2)		Island (20)		Mainland (16)		Island (3)		Mainland (4)	
SPP	Rank	$\bar{x}N$	Rank	$\bar{x}N$	Rank	$\bar{x}N$	Rank	$\bar{x}N$	Rank	$\bar{x}N$	Rank	$\bar{x}N$
Axoclinus sp. (Cortez tripletin)	7	5	1	100	1	80	1	39	3	47	1	44
Malacoctenus hubbsi	10	3	2	37	2	64	3	29	7	14	3	32
Acanthemblemaria crockeri	15	2	9.5	4	3	62	6.5	14	2	49	13	5
Lizard triplefin (n. gen. & sp.)	1	82	5	18	5	40	6.5	14	12	6	-	-
Axoclinus carminalis	-	-	-	-	9.6	18	2	32	1	62	4	32
Enneanectes sp. (Flag triplefin)	-	-	-	-	4	49	9.5	10	6	15	19	2
Tomicodon boehlkei	-	-	17	<1	6	29	5	17	8	13	9	8
Coralliozetus micropes	13	2	12	2	7	26	11	7	5	18	5	21
Xenomedea rhodopyga	2	13	17	<1	9.5	18	4	22	-	-	-	-
Paraclinus sini	4	7	3	20	8	21	8	12	15	5	15	3
Labrisomus xanti	3	9	9.5	4	11	14	9.5	10	13.5	5	6	19
Ophioblenninnius steindachneri	-	-	-	-	12	12	12	4	4	22	2	33
Apogon retrosella	13	2	-	-	14	10	13	5	10	8	16.5	3
Scorpaenodes xyris	11	3	-	-	13	11	17	3	25.5	1	32.5	<1

Table F-1--continued. Rank and mean abundance per collection of species.

	Upper Gulf				Central Gulf				Lower Gulf			
	Island (5)		Mainland (2)		Island (20)		Mainland (16)		Island (3)		Mainland (4)	
SPP	Rank	$\bar{x}N$	Rank	$\bar{x}N$	Rank	$\bar{x}N$	Rank	$\bar{x}N$	Rank	$\bar{x}N$	Rank	$\bar{x}N$
Ogilbia sp.	16.5	1	17	<1	15	7	18	3	28	<1	11.5	5
Gobiosoma chiquita	18.5	1	6	16	18	5	28.5	<1	9	10	32.5	1
Aruma histrio	20.5	<1	8	8	19	4	16	3	18	3	-	-
Coralliozetus angelica	-	-	-	-	17	5	28.5	<1	11	7	10	5
Malacoctenus tetranemus	24	<1	-	-	22	3	15	3	21	2	14	4
Stathmonotus sinuscalifornici	-	-	-	-	16	5	21	2	25.5	1	-	-
Hypsoblennius gentilis	6	6	7	14	25	1	19	2	-	-	-	-
Malacoctenus gigas	5	6	4	20	47	<1	28.5	<1	-	-	-	-
Gobiesox pinniger	13	3	14.5	1	20	4	22	1	-	-	-	-
Tomicodon humeralis	-	-	11	3	30.5	<1	14	4	16	3	32.5	<1
Acanthemblemaria macrospilus	-	-	-	-	32	<1	25	<1	13.5	5	7	10
Barbulifer pantherinus	-	-	-	-	21	3	24	<1	-	-	-	-
Pareques viola	8	4	17	<1	28	<1	23	1	-	-	32.5	<1
Starksia spinipenis	20.5	<1	-	-	23	2	52	<1	19.5	2	21.5	1
Entomacrodus chiostictus	-	-	-	-	28	1	28.5	<1	28	<1	11.5	5
Elacatinus sp.	-	-	-	-	24	2	52	<1	22.5	1	-	-
Labrisomus striatus	-	-	-	-	28	1	33.5	<1	17	3	21.5	1
Lythrypnus dalli	18.5	1	13	-	26	1	33.5	1	-	-	-	-

Table F-1--continued. Rank and mean abundance per collection of species.

SPP	Upper Gulf				Central Gulf				Lower Gulf			
	Island (5)		Mainland (2)		Island (20)		Mainland (16)		Island (3)		Mainland (4)	
	Rank	$\overline{x}N$	Rank	$\overline{x}N$	Rank	$\overline{x}N$	Rank	$\overline{x}N$	Rank	$\overline{x}N$	Rank	$\overline{x}N$
Paraclinus mexicanus	-	-	-	-	49.5	<1	-	-	-	-	8	9
Hypsoblennius brevipinnis	24	<1	-	-	42	<1	26	<1	19.5	2	16.5	3
Arcos erythrops	-	-	-	-	30.5	<1	38	<1	34	<1	18	2
Exerpes asper	24	<1	-	-	49.5	<1	20	2	31.5	<1	-	-
Elacatinus punticulatus	-	-	-	-	33.5	<1	38	-	22.5	1	38	<1
Protemblemaria bicirris	9	3	14.5	1	-	-	45	<1	-	-	-	-
Enneanectes sexmaculatus	-	-	-	-	35	<1	33.5	<1	-	-	38	<1
Chriolepis zebra	-	-	-	-	33.5	<1	41.5	<1	25.5	1	-	-
Scorpaena mystes	24	<1	-	-	38	<1	33.5	<1	31.5	<1	-	-
Rypticus bicolor	-	-	-	-	42	<1	33.5	<1	-	-	26.5	<1
Gymnothorax panamensis	-	-	-	-	37	<1	45	<1	25.5	1	-	<1
Bathygobius ramosus	-	-	-	-	36	<1	45	<1	-	-	32.5	<1
Gymneleotris seminudus	-	-	-	-	42	<1	38	<1	31.5	<1	32.5	-
Coryphopterus urospilus	16.5	1	-	-	-	-	38	<1	28	<1	-	-
Uropterygius sp.	-	-	-	-	34	<1	-	-	-	-	-	-
Gobiesox adustus	-	-	-	-	49.5	<1	33.5	<1	-	-	23	1
Muraena lentiginosa	-	-	-	-	45.5	<1	45	<1	31.5	<1	32.5	<1
Uropterygius necturus	-	-	-	-	39	<1	41.5	<1	-	-	-	-
Pherallodiscus funebris	-	-	-	-	42	<1	45	<1	-	-	-	-

Table F-1--continued. Rank and mean abundance per collection of species.

	Upper Gulf				Central Gulf				Lower Gulf			
	Island (5)		Mainland (2)		Island (20)		Mainland (16)		Island (3)		Mainland (4)	
SPP	Rank	$\overline{x}N$	Rank	$\overline{x}N$	Rank	$\overline{x}N$	Rank	$\overline{x}N$	Rank	$\overline{x}N$	Rank	$\overline{x}N$
<u>Gymnothorax castaneus</u>	-	-	-	-	52	<1	38	<1	-	-	-	-
<u>Plagiotremus azaleus</u>	-	-	-	-	-	-	-	-	-	-	20	2
<u>Elacatinus digueti</u>	-	-	-	-	45.5	<1	-	-	-	-	-	-
<u>Cirrhitus rivulatus</u>	-	-	-	-	53.5	<1	52	<1	-	-	26.5	<1
<u>Oligopus diagrammus</u>	-	-	-	-	42	<1	-	-	-	-	-	-

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