PATTERNS OF REEF FISH DISTRIBUTION AND ABUNDANCE AMONG SELECTED LOCATIONS IN THE GULF OF CALIFORNIA

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ABSTRACT

Stationary underwater video surveys were conducted on rocky habitats near Loreto and coral habitat at Cabo Pulmo in the Gulf of California to obtain non-cryptic reef fish distribution and abundance data. Measurements of habitat variables were also recorded to investigate the influence of habitat on fish distribution and abundance. Differences in fish assemblages were greatest between Loreto and Cabo Pulmo and also detected among the three islands sampled at Loreto. At Isla Carmen, fishes were associated with habitat variables of relief, rugosity, boulder diversity, and percent cover but not habitat type, indicating an influence of habitat morphology on reef fish assemblage structure. Results were similar to other studies conducted in the central Gulf of California indicating stability of reef fish assemblages in the region, although factors other than habitat probably play a greater role in structuring reef fish assemblages there.

INTRODUCTION

Tropical and temperate reef systems support rich and diverse fish assemblages worldwide (Sale 1991; Ebeling and Hixon 1991). The foundation of these systems, coral or rock structures, serve as habitat for fishes by: 1) providing refuge from predators, 2) attracting prey and providing attachment sites for algae and sessile animals which are food for some species, and 3) providing sites for reproduction (Choat and Bellwood 1991). As habitat, reefs can influence processes such as recruitment, predation, and competition, all of which can affect fish assemblage composition by influencing which species are present and in what abundance.

Most habitat studies involving reef fishes have taken place on coral reefs in tropical regions, particularly on the Great Barrier Reef, Australia and in the Caribbean (Sale 1991). Because of this emphasis on the tropics, several authors have expressed a need for more studies in temperate and sub-tropical regions (Gilligan 1980; Ebeling and Hixon 1991), or in regions other than the Caribbean or Australia, and on different types of reef habitat, to better understand the relationship between fish assemblage structure and habitat (Ohman et al. 1997; Ohman and Rajasuriya 1998).

The subtropical Gulf of California (Gulf) is an area in which little ecological research on reef fishes has occurred. Early work describing the fish fauna and biogeography of the Gulf of California by Walker (1960) and Thompson and Gilligan

(1983) divided the Gulf into biogeographic zones of upper (northern), middle (central), and lower (southern) (Figure 1) based on small cryptic reef fishes such as blenniids and gobiids. Gulf fishes are mainly Panamic in origin, with Californian and Indo-Pacific species represented (Walker 1960; Thompson et al. 2000). Many species belonging to families widely accepted as representative of tropical fishes (Choat and Bellwood 1991) are present, the most common being labrids, scarids, pomacentrids, acanthurids, zanclids, chaetodontids, and pomacanthids.

Most recent published works on the fishes of the Gulf have been conducted in or near Bahía de La Paz and are either species lists (Abitia-Cárdenas et al. 1994) or reports on reef fish distribution and seasonality. Pérez-España et al. (1996) reported on the spatial and temporal variation of fishes at four sites near La Paz. Aburto-Oropeza and Balart (2001) investigated the distribution of fishes among habitats at Isla Los Islotes, just north of Bahía de La Paz, and Arreola-Robles and Elorduy-Garay (2002) studied large scale spatial and temporal patterns of reef fish diversity among the islands throughout Bahía de La Paz. I have found no published work on the patterns of fish distribution and abundance near Loreto in the western-central Gulf of California.

The areas of interest for this study were located off Loreto and Cabo Pulmo, along the eastern coast of Baja California Sur, México. All sampling was conducted within the Parque Nacional Bahía de Loreto in the central Gulf of California and within the Parque Marino Nacional de Cabo Pulmo in the southern Gulf (Figure 2). The Parque Nacional Bahía de Loreto (PNBL) was created in 1996 and encompasses an area of 2,065 km^2. Within this area are five islands: Isla Carmen, Isla Coronados, Isla Danzante, Isla Montserrate, and Isla Catalán. Parque Marino Nacional de Cabo Pulmo (PMNCP) was created in 1995 to protect Cabo Pulmo reef, the northernmost coral reef in the eastern Pacific (Brusca and Thomson 1975). The Mexican government set aside 71.11 km^2 for protection, of which 0.45 km^2 is coral reef (Reyes-Bonilla 1997). Both parks restrict commercial fishing activities whereas all fishing activities are prohibited at PMNCP.

Oceanographic conditions in the Gulf create what can be described as typical of an inland mediterranean sea (Maluf 1983). Deep basins, small tidal amplitudes, and wide seasonal surface water temperature fluctuations characterize the central bioregion of the Gulf, which includes Loreto and ends at La Paz. Surface currents move predominantly southeast in the winter and northwest in the summer as a response to prevailing winds. Upwelling occurs on the leeward sides of islands. Oceanographic conditions at Cabo Pulmo in the lower Gulf are more oceanic as it is nearer the mouth of the Gulf. Water temperatures there are moderated by the Pacific Ocean, tidal amplitudes are small, and precipitation is higher.

The geology of PNBL's islands is characterized by the Comandu formation (23 – 17 million years old [Ma]) horneblend andesite lava flows and volcanic breccias, with younger lava flows (15 – 6 Ma) above it (Anderson 1950; Zanchi 1994). Isla Coronados is a single andesite volcanic cone approximately 125,000 years old (Minch et al. 1998). Rocky habitats at Isla Carmen and Isla Coronados consist of lava flows, vertical walls, ledges, caves, and crevices with cobble, boulder, sand, and mixed sediments present. Isla Danzante has similar habitats, and is also characterized by a steeply sloping bottom around most of the island. Hermatypic corals occur near Loreto, though only as isolated coral heads (Brusca and Thomson 1975).

Cabo Pulmo reef is composed of northern, central, and southern sections (Reyes-Bonilla and Calderon-Aguilera 1999). The northern section has sandy bottoms, a low percentage of coral cover, and a seasonal influx of freshwater. The central section is composed of granite blocks, sandstone, and conglomerate that support a high coral cover. At the northern-central portion of the reef, the granite blocks form steps, parallel to shore and with a several meter drop-off on the offshore side. The southern section, protected by the point of Los Frailes, has calm waters and is low in coral cover. Ten species of coral are found at Cabo Pulmo, with *Pocillopora verrucosa* and *P. meandrina* being the most abundant (Reyes-Bonilla and Calderon-Aguilera 1999).

The work presented here provides a baseline study of the distribution and abundance of non-cryptic reef fishes near Loreto. This work was conducted to add to the knowledge of reef fishes in the Gulf of California and to investigate how habitat may influence the distribution and abundance of reef fishes in a seldom studied subtropical region. In addition, reef fishes and coral habitat at Cabo Pulmo in the southern Gulf were examined using identical techniques to provide comparative information between the central and the southern Gulf bioregions and between rock and coral reef habitats.

METHODS

Sampling off Loreto took place during September – October 2000 and 2001 around PNBL's three nearshore islands of Isla Carmen (coastline ≈ 79 km), Isla Coronados (coastline ≈ 13 km), and Isla Danzante (coastline ≈ 12 km). At Cabo Pulmo, PMNCP was intended to be sampled during October 2001 but this was prevented by Hurricane Juliette. During this storm I observed large waves at Cabo Pulmo reef, a drop in sea surface temperature, and the addition of large amounts of fresh water to the surrounding waters. I also observed hundreds of fishes dead on the beach in front of the reef immediately following the storm. The coral reef itself appeared to have suffered minor damage, indicated by only moderate amounts of coral rubble, although the extent of coral rubble present before the storm is unknown. Cabo Pulmo Reef was then sampled in August 2002, one year following the storm.

Video Validation

The presence and abundance estimates of fish species were obtained using underwater stationary video surveys (Bohnsack and Bannerot 1986; Bortone et al. 1991). The stationary video survey was chosen to avoid potential biases that exist with other methods, particularly strip transects. Visual strip transects have known biases, which include the diver's presence influencing fish behavior, and observer error (Russell et al.1978; Davis and Anderson 1989). Some fish tend to move toward a diver whereas others will move away, and the use of a slate, the standard method for recording survey data (Helfman 1983), requires the observer to look down to write, causing some fish to be missed and not counted. Transects have been found to undercount or completely miss sedentary Lutjanids and roving Serranids, although it has been determined that both methods tend to underestimate fish abundances (Samoilys and Carlos 2000).

To validate the use of stationary video surveys with Gulf reef fishes, I compared direct visual observations with video data collection using the following methods near Loreto during June 2000. Using SCUBA, two divers descended to the bottom and swam toward the 10 m isobath. One diver secured a 10 m transect tape to the bottom and extended the tape 5.6 m to demarcate the radius of a survey circle (area = 100 m^2). A three minute waiting period lapsed to allow fish to acclimate to the presence of the divers. During the survey, one diver recorded all non-cryptic fish species and their abundances that were within the survey circle onto a blank slate. The other diver simultaneously recorded fishes using a Sony TRV900 mini-DV digital video camera inside a Light & Motion™ Top Dawg underwater housing. Camera auto-focus was disabled and an orange CY filter was used to restore natural colors at depth. Recording by both divers proceeded in a counter-clockwise direction for five minutes, each quarter of the circle being recorded for approximately 1.25 minutes. An attempt was made to record all fishes entering the circle, from the bottom toward the surface, regardless of which quadrant was being recorded. Fifteen survey replicates were conducted on four habitats, lava (n = 4), large boulder (n = 4), small boulder (n = 3), and mixed habitats (n = 4).

Video was retained in digital format and later reviewed on a high-resolution monitor to maintain picture clarity and colors. Each non-cryptic fish within the 5.6 m radius circle (using the extended tape-measure as a guide) was counted and identified to the lowest taxonomic level possible. If one fish of a school entered the circle, all fish in that school were counted (Brock 1954). The damselfishes Cortez gregory, *Stegastes rectifraenum*, and beaubrummel gregory, *Stegastes flavilatus*, were difficult to differentiate, so these species were recorded as *Stegastes* spp. I performed species identification for both survey methods to ensure consistency.

The two methods were compared using species richness, the Shannon-Weiner diversity index (Shannon and Weaver 1949), expressed as:

$$H' = -\sum_{i=1}^{s} p_i \ln p_i$$

where p_i is the proportion of individuals found in the ith species and ln is the natural logarithm, and abundance were calculated for each method. Data for both methods were tested for normality and equality of variances and compared using paired t-tests, Pearson’s correlaton coefficient (Zar 1983; SPSS 2001), and percentage similarity indices.

Data Collection

Neither high resolution bathymetry nor habitat maps existed for these areas, therefore sample sites at each location could not be pre-selected and had to be chosen by reconnaissance snorkeling immediately prior to sampling. Four habitat types were sampled at Loreto: lava flow, large boulders ($\geq$ 1 m diameter), small boulders ($<$ 1 m diameter), and mixed (approximately 50 m x 10 m area containing any combination of the above habitat types). Coral habitat was sampled only at Cabo Pulmo. An attempt was made to choose continuous habitat areas that were at least 50 m x 10 m in size and contained a minimum of approximately 75% of one habitat type, especially for coral at Cabo Pulmo where coral is growing on granitic blocks and can be patchy. Site coordinates were recorded with a hand-held geographical positioning system (GPS) unit at the surface just before sampling commenced.

All sampling was done at the 10 m isobath (± 3 m) to avoid the influence of depth on fish assemblage structure (García-Charton and Pérez-Ruzafa 1998; Arreola-Robles and Elorduy-Garay 2002), and between the hours of 10:00 and 14:00 to avoid crepuscular activity (Hobson 1968; Ogden & Quinn 1984). Using SCUBA, divers descended to the bottom and swam toward the 10 m isobath. A diver secured a 50 m transect tape to the bottom and extended the tape 5.6 m to demarcate the radius of the first survey circle (area = 100 m^2). The tape was extended along the isobath toward the direction most likely to contain 50 m x 10 m of the desired habitat. Stationary video surveys were conducted using the same methods previously described. Three stationary video surveys were conducted per site; each centered 25 meters apart along the 10 m isobath (Figure 3).

Habitat variables were measured immediately following the three fish surveys. Along the main 50 m transect, three points were chosen randomly from six possible points (e.g., 0 m, 10 m … 50 m). At these points, a 10 m sub-transect was placed across the 50 m tape, perpendicular to it, with 5 m on either side. Habitat variables of relief, rugosity, boulder diversity, and percent cover of encrusting organisms, either algae or invertebrate, were recorded. Relief and rugosity comprised the vertical component of habitat (complexity) while boulder diversity and percent cover comprised the horizontal component of habitat (heterogeneity) (García-Charton and Perez-Ruzafa 1998). At Cabo Pulmo, coral heads were recorded in the same manner as boulders, as it was assumed that they contributed to habitat heterogeneity in a similar way to boulders and at the same scale.

Rugosity was determined using the chain method of Luckhurst and Luckhurst (1978) modified by using tape measures instead of chain. A third tape was placed along the 10 m sub-transect following the bottom contour, into holes, cracks, and crevices, and over rock and/or coral. The ratio of the straight-line distance to linear distance, measured to the nearest decimeter (0.10 m), was used as an index of substratum rugosity. A crude measure of bottom relief (slope) was determined by using a submersible depth gauge to measure bottom depth (± 0.30 m relative to the surface) at both ends of the sub-transect. By dividing the larger value by the smaller value, an index of bottom relief was obtained (Núñez-Lara and Arias-González 1998). To obtain boulder diversity data, all boulders or coral heads directly below the sub-transect tape were counted and categorized by size. Percent cover of encrusting organisms was measured using a modified point-contact method (Schmitt and Holbrook 1986). The presence or absence of encrusting organisms was recorded at every meter along the 10 m sub-transect. All data were recorded on pre-printed Never-tear© sheets. Video was analyzed for fish species and abundance using methods identical to those used to validate stationary video surveys.

Simplifying a complex system by grouping its smaller parts and studying the interactions among these groups can aid in understanding the whole (May 1984). To simplify the fish assemblages encountered, each fish species was assigned to trophic and mobility guilds (Friedlander and Parrish 1998). Fishes were placed into trophic guilds based on their predatory behavior and gut analyses as reported in the literature (Hobson 1968; Thomson et al. 2001) (Table 1). For this study trophic guilds were defined as piscivores, planktivores, herbivores, invertivores, piscivore/invertivore, planktivore/invertivore, and herbivore/invertivore. Here planktivores refers to species that prey on zooplankton by picking them out of the water column. Categorization of fishes by mobility was determined from 65+ hours of personal observation while conducting this study. Fishes were placed into mobility guilds defined by Friedlander and Parrish (1998) as residents, semi-vagile I, and semi-vagile II (Table 1). Resident fishes are those that display high site fidelity, are sedentary, or are territorial. Semi-vagile I fishes move about the reef but usually remain within 10 – 20 meters of one area. Semi-vagile II species are semi-transient fishes that roam, moving several hundreds of meters and from reef to reef during any given time. All fishes that could be identified to species were assigned to a guild.

Data Analysis

Each 50 m transect, and data collected within it, was considered a replicate sample. Fish assemblage composition was described using the descriptors of species richness, abundance, and the Shannon-Weiner diversity index. Species richness and abundance from each transect's three video surveys were pooled to obtain cumulative species richness and mean species abundance. Abundance data were averaged for the three video surveys due to the likelihood that highly mobile individuals would be counted more than once within the same transect, causing an overestimation of species abundance for that transect. Shannon – Weiner diversity was calculated from pooled transect species richness and species abundance data and represented the diversity value for the entire transect. Percentage Similarity Index (PSI), a pair-wise comparison of species presence and abundance between two units of interest, and Dominance, an indication of assemblage unevenness, were calculated for all locations.

For habitat variables, each transect was represented by the mean of the three sub-transects, resulting in one value per variable per transect. Boulder diversity was calculated using the Shannon–Wiener diversity index (Shannon and Weaver 1949;

Ohman and Rajasuriya 1998); each transect's diversity value being the mean boulder diversity of the three sub-transects.

In the resulting data table each transect contained all species encountered and their abundances (zero abundance if not encountered in that transect), and one value each for species richness, species diversity, species abundance, rugosity, relief, boulder diversity, and percent cover of encrusting organisms. These transect values were used for all subsequent analyses.

Cumulative species curves were used to confirm sampling sufficiency at each location. Matlab (Mathworks 2000) was used to randomly sample (1,000 iterations) from the pool of species at each location and produce cumulative curves with corresponding standard errors (J. Adams, Moss Landing Marine Laboratories, pers. comm.).

All data were tested for univariate and multivariate normality and homoscedacity using SPSS and S+ statistical packages (Math Soft Inc. 1995; Legendre and Legendre 1998; SPSS 2001). Individual species abundance data were root-root transformed and guild abundances square root transformed to achieve normality and to minimize the influence of highly abundant fishes. When equality of variances could not be achieved, the Kruskal Wallis H-test was used to compare means and Tamhane's multiple comparison test used to determine differences among locations.

All habitat variable data were standardized using z-scores to account for differing units of measure (Legandre and Legandre 1998). The use of z-scores in charts is also a convenient way to graphically compare values within groups. Fish assemblage descriptor means and guild abundances were compared using Analysis of Variance (ANOVA), or when necessary its non-parametric equivalent, the Kruskal-Wallace H-test. Univariate statistics were calculated using the SPSS statistical software package (SPSS 2001). A confidence level of 95% was used for all analyses.

Species abundances and habitat data (rugosity, relief, boulder diversity, and percent cover) were analyzed using the ordination techniques of principal component analysis (PCA) and redundancy analysis (RDA), a method similar to PCA but which constrains species data to linear combinations of environmental variables. These ordination methods and their subsequent diagrams are useful for describing patterns of variation and for exploring relationships among data sets by reducing multidimensional data into fewer dimensions, allowing for easier interpretation (Legendre and Legendre 1998). These techniques assume multivariate normal distributed data and variance homogeneity. Data were found not to be multivariate normal and it was not possible to transform them to be so. Although not being multivariate normal prevents the use of these data for hypothesis testing using multivariate statistics, data presented here are for exploration and determining patterns of distribution only.

Ordination results were obtained using the software package CANOCO 4.0 (ter Braak 1995) and plotted using the included program CANODRAW 3.0 (Smilaur 1991). Species abundance data were checked for unimodality by calculating segment lengths for each component using Detrended Correspondence Analysis (DCA), available in CANOCO 4.0. Segment lengths less than four standard deviations (SD) indicate linearity, whereas segment lengths greater than 4 SD indicate unimodality (ter Braak and Verdonschot 1995). Species abundance data were found to be linear and were analyzed accordingly. The correlation matrix was used for all ordination analyses. Mardia et al. (1979) suggested using the arbitrary value of 0.7 multiplied by the greatest absolute species score (the measure of the species variation explained by PCA or RDA) to determine which species had sufficient variation explained by the ordination output. Sample (transect) PCA and RDA scores were plotted as the mean and 95% confidence interval of all samples for a given grouping, such as location or habitat.

Certain rules or principles that pertain to biplots and triplots (types of ordination diagrams) are helpful in exposing patterns made evident by ordination (ter Braak & Verdonschot 1995). In a biplot or triplot, the centroid principle explains the relation of species (points) to sites (symbols). It states that sites tend to scatter around the center of a species' niche, in other words, where it is most abundant. The biplot rule helps explain the relation between species and habitat variables (arrows). Arrows point in the direction of the greatest change in that variable. The length of the arrow indicates the strength of that change. How strongly a species is associated with an environmental variable is determined by where the species point lay in relation to the arrow. The closer to the arrow the species point lies, the stronger the correlation between that environmental variable and the abundance of the species. The magnitude of the correlation is determined by how far the species point is from the origin (the mean of the habitat variable). In a pRDA triplot, fish species are placed according to the relationship between their abundances and the linear combination of measured habitat variables (the axes) (ter Braak and Verdonschot 1995). Species are also plotted closest to those sites that had the greatest abundance for that species. Sites are placed based on where their values for habitat variables fit along the axes. Habitat variables are plotted according to their correlations with the axes; the closer to the axis the stronger the correlation and the greater the contribution that variable has to the axis.

Habitat variables were checked for collinearity by plotting their PCA scores (Legandre and Legandre 1998). When two variables were strongly correlated (determined by the vector angles on the PCA biplot), the least significant variable (determined by length of the vector) was discarded.

Isla Carmen

Isla Carmen was chosen as a location to explore a finer scale analysis of the patterns of distribution and abundance of fishes at Loreto. Isla Carmen was analyzed separately using the same methods described previously for locations. Isla Carmen was chosen because it was sampled two years (September 2000 and October 2001), had the most samples of any location (22), and had samples among all four rocky habitat types.

RESULTS

Video Validation

Stationary video surveys produced results that were comparable to stationary visual surveys (Table 2). The percentage similarity index indicated a high similarity (87.3%) in fish assemblage structure for the two methods. Pearson's correlation coefficients indicated significant correlation between the two methods in species richness ($r = 0.666$, $P = 0.007$), species diversity ($r = 0.533$, $P = 0.041$), and fish abundance ($r = 0.818$, $P = 0.000$).

The difference in species richness recorded between the two methods was not statistically significant ($P = 0.215$). The video survey technique recorded a mean of 9.33 ± 0.63 SE species per survey while the visual survey technique recorded a mean of 8.67 ± 0.58 SE species per survey. In addition, the two survey methods were nearly identical in their ability to quantify the diversity of the local fish assemblage. Species diversity calculated from video data was slightly higher than diversity calculated from visual data, although the two methods did not differ significantly ($P = 0.809$).

The video survey method did record a statistically greater total abundance of fish ($P = 0.012$) when compared to the visual survey method. Video recorded a mean of 75.40 ± 50.74 SE fish per survey and the visual method recorded a mean of 53.27 ± 36.20 SE fish per survey. Schooling or aggregating species such as the scissortailed chromis, *Chromis atrilobata*, the Panamic sergeant-major, *Abudefduf troschelii*, and the Cortez rainbow wrasse, *Thalassoma lucasanum*, contributed to most of the variation in fish abundance, especially for video data, which had greater accuracy in enumerating individuals.

No differences in species richness or species diversity were detected between methods when compared among habitats. The video survey method recorded a statistically greater total abundance of fish on small boulder habitat than the visual survey method (P = 0.010). There were no differences in fish abundance between methods on the other habitat types.

Video recorded significantly higher counts of the damselfishes *Stegastes* spp and the leopard grouper, *Mycteroperca rosacea* (Table 2). Video recorded much higher counts of *A. troschelii*, *C. atrilobata*, and the yellowtailed surgeonfish, *Prionurus punctatus*, although the differences were not significant, likely due to high variation in counts of these schooling species among replicates. Video recorded fewer counts of the spottail grunt, *Haemulon maculicauda*, and the blue-bronze sea chub, *Kyphosus analogus*. The differences were not significant.

Patterns of Distribution and Abundance

To determine patterns of distribution and abundance of reef fishes, forty-five transects, composed of 135 video surveys and habitat sub-transects, were completed among the four locations and five habitat types (Figure 2). Among the four locations, only at Isla Carmen were transects conducted on all four rocky habitat types. Isla Coronados had three habitat types, lava, small boulder, and a mix of lava and small boulder habitat. Isla Danzante had only large boulder and a mix of large boulder and lava habitat. Mixed habitat at Isla Carmen was comprised of large boulder and small boulder, and lava and small boulder habitats. Coral was present in abundance only at Cabo Pulmo.

Habitat variables within habitat types differed within and among locations (Figure 4). Relief on lava and small boulder habitat at Isla Coronados was significantly greater than on lava and small boulder habitat at Isla Carmen ($P = 0.011$ and $P = 0.003$ respectively), and among mixed habitats at Islas Carmen, Coronados, and Danzante ($P = 0.008$).When habitat variables were grouped by location (Figure 5), mean relief at Isla Danzante was significantly greater than mean relief at other locations ($P = 0.000$). Though not statistically significant Cabo Pulmo had lower than the average value for every measured habitat variable, while Isla Danzante had higher than the average value for all habitat variables except for percent cover of encrusting organisms, which was much lower than the other locations for that variable.

The measured habitat variables accounted for 65.5% of variation in habitat among locations (Figure 6). Contributing most to that variability was rugosity, followed by boulder diversity, percent cover, and relief. Transects at each location were characterized by discrete combinations of habitat variables (Figure 7). These combinations of variables formed habitat patches (Wiens 1976; Addicott et al. 1987) that existed independently of habitat type, being present within or across them. Each location was thus characterized by a mosaic of habitat patches with similar habitat variable values. Isla Danzante had the highest habitat complexity (relief and rugosity) and lowest percent cover. Cabo Pulmo had the lowest habitat complexity. Isla Carmen, Isla Coronados, and Cabo Pulmo differed mainly in rugosity and boulder diversity.

Fifty-five fish species representing 18 families and 38 genera were observed and counted (Table 1). The most ubiquitous species encountered were the damselfishes *Stegastes* spp, the king angel, *Holacanthus passer*, *T. lucasanum*, and the Mexican hogfish *Bodianus diplotania*. Each of these species were recorded in more than 90% of all transects (Table 3). *Chromis atrilobata*, *T. lucasanum*, and *Stegastes* spp were the most abundant species, accounting for nearly 50% off all individuals surveyed. At Isla Danzante *A. troschelli*, and *Stegastes* spp accounted for 64.5% of the total fish abundance. In contrast, at Isla Carmen six species accounted for 64.6% of total abundance.

Cumulative species curves for each location approached an asymptotic limit with progressively decreasing standard deviation (Figure 8), indicating that sampling was sufficient for characterizing the fish assemblages at all locations. Isla Carmen was sampled most comprehensively with 22 transects. Isla Danzante and Cabo Pulmo were sampled the least with nine transects each.

Fish assemblage structure differed significantly among locations in two of the three descriptors (Figure 9). Species richness was significantly higher at Isla Coronados than at Cabo Pulmo ($P = 0.011$). Isla Coronados had the most species while Cabo Pulmo had the fewest. Species diversity was greatest at Isla Carmen and significantly greater than at Cabo Pulmo ($P = 0.004$) and at Isla Danzante ($P = 0.025$). Mean fish abundance per transect did not differ significantly among locations; however, Isla Coronados had the most fish per transect and Isla Carmen had the fewest.

Overall, fish assemblages were generally dissimilar among locations in this study (Table 4). Isla Danzante was the least similar to all other locations. The greatest similarity was between Isla Carmen and Isla Coronados (0.687), followed by Isla Coronados and Cabo Pulmo (0.611). These values are above the 60% value that Cailliet and Barry (1979) found to be associated with significant correlation coefficients. Isla Danzante and Cabo Pulmo were the least similar locations (0.217). The mean PSI value calculated using all locations was 49.1%, indicating generally low similarity in species assemblage structure among locations.

Species abundance histograms (Figure 10) show that three to four species, *C. atrilobata*, *Stegastes* spp, *A. troschelii*, and *T. lucasanum*, dominated the four locations in abundance. At Isla Danzante, Limbaugh’s chromis, *Chromis limbaughi*, appeared to replace *C. atrilobata* with greater abundance and *Abudefduf troschelii* was completely absent from Cabo Pulmo. Although a few species dominated each fish assemblage, high species richness at each location reduced the contribution of those species to the assemblage, reducing the dominance indices. Fish assemblages at Isla Danzante and Cabo Pulmo were the most dominated (0.257 and 0.250 respectively). Fish assemblages at Isla Carmen and Isla Coronados were the least dominated (0.093 and 0.120 respectively).

Specific abundance varied greatly among locations (Figure 11), especially those between Loreto and Cabo Pulmo. These differences were due to the abundances of the bluechin parrotfish, *Scarus ghobban*, *M. rosacea*, and the graybar grunt, *Haemulon sexfasciatum*, at Loreto, and three wrasses, *T. lucasanum*, the island wrasse, *T. grammaticum*, and the chameleon wrasse, *Halichoeres chierchiae*, at Cabo Pulmo. Locations at Loreto differed in abundances of the barred serrano, *Serranus psitticinus*, at Isla Carmen and the giant damsel, *Microspathadon dorsalis*, and *P. punctatus*, at Isla Coronados.

The first two axes of the biplot (Figure 11) explain only 25.7% of the variation in species abundance among locations. There are, however, 55 potential axes (one per species) while the biplot only displays the two that explain the greatest sources of variation. Furthermore, the biplot is only an attempt at displaying the true relationships among variables and sites, and can distort actual relationships (ter Braak and Verdonschot 1995). For example, Isla Danzante and Cabo Pulmo appear to have similar site scores along PC2. This is caused by similar abundances of the two species mainly responsible for differences in site scores along PC2, *M. dorsalis* and *S.*

psittacinus, at the two locations. In reality Isla Danzante and Cabo Pulmo have very different fish assemblages (Figs. 9 and 12).

Guilds

Patterns of abundances of fishes in trophic guilds were generally similar among locations (Figure 12). Planktivore/invertivores were the most abundant fishes at all locations except for Isla Carmen, which had a greater number of herbivore/invertivores. Piscivores were the least abundant fishes at all locations. Significant differences in abundance were detected among locations of the guilds invertivores, piscivore/invertivores, piscivores, planktivore/invertivores, and planktivores (P =0.036, P = 0.005, P = 0.000, P = 0.002, and P = 0.013 respectively).

Sites within locations varied greatly in trophic guild composition (Figure 13). The greatest variation among sites was in piscivore abundance (PC1), followed by planktivore and piscivore/invertivore abundances (PC2). Sites that had high abundances of planktivores had low abundances of herbivores, herbivore/invertivores, and piscivores. Sites with high abundances of piscivore/invertivores and invertivores had low abundances of planktivore/invertivores. When grouped by location, sites vary the greatest along PC1, a gradient of planktivore/invertivores to piscivores. The islands of Loreto were more similar to each other than to Cabo Pulmo in their abundances of fishes within trophic guilds.

Semi-vagile I fishes were the most abundant at all locations (Figure 14). Isla Danzante had a significantly greater number of resident fishes than the other locations (P = 0.009) and the fewest semi-vagile II fishes, although this was not significant.

Sites with a high abundance of semi-vagile II fishes had few resident fishes and sites with many resident fishes had few semi-vagile II fishes (Figure 15). There was no relation between semi-vagile I fishes and semi-vagile II and resident fishes as indicated by the vector angles. Islas Carmen and Coronados and Cabo Pulmo differed mostly in their abundances of semi-vagile I fishes. Isla Danzante was differentiated from the other location by its high abundance of resident fishes and low abundance of semi-vagile II fishes.

Isla Carmen

Twenty-two transects were completed among rocky habitats of lava, large boulder, small boulder, and mixed at Isla Carmen (Figure 2). Forty-four fish species representing 17 families were recorded (Table 1). Cumulative species curves constructed for each habitat type at Isla Carmen, using the same methods described previously (Figure 16), showed that all habitats approached an asymptotic limit, an indication that a sufficient number of samples were conducted.

No differences were found among habitats in species richness (P = 0.712), species diversity (P = 0.947), or fish abundance (P = 0.414). Large boulder habitat had the greatest number of species with 20; mixed habitat had the least number of species with 17. Species diversity was highest on small boulder habitat and lowest on mixed habitat. Fish abundance was greatest on large boulders and lowest on lava.

Fish assemblages were generally similar among habitats with PSIs all being higher than 50% (Table 5). Lava and small boulders had the most similar assemblages. Lava and large boulders had the least similar assemblages. The mean PSI value for all habitats was a relatively high and significant 65.6% (Cailliet and Barry 1979), mainly due to the very high similarity between assemblages on lava and small boulders.

Species abundance histograms and dominance indices indicated that fish distributions within assemblages were dominated by a few species (Figure 17). Here too the high species richness of each habitat minimized the contribution of those species to the assemblage, reducing the dominance indices. Of the four most abundant species in each habitat, only *Stegastes* spp were common to all. *Chromis atrilobata* was the most abundant species on large boulders and mixed habitats. *Stegastes* spp were the most abundant species on small boulders, and *Thalassoma lucasanum* the most abundant species on lava.

Differences in species abundances were detected between years at Isla Carmen. Numbers of *S. ghobban* and the bicolor parrotfish, *Scarus rubroviolaceous*, decreased significantly from 2000 to 2001 (P = 0.003, and P = 0.004 respectively) while the spinster wrasse, *Halichoeres nicholsina* and *T. lucasanum* increased significantly in abundance from 2000 to 2001 (P = 0.040 and P = 0.013 respectively).

Partial redundancy analysis (pRDA) was subsequently used to remove variation in fish abundances between years (a covariable) for the multivariate analysis.

Fishes were associated most strongly with relief and rugosity, as indicated by the length of the arrows for those variables in the ordination diagram (Figure 18, Table 6). The first axis was, in order of greatest contribution, a linear combination of relief, rugosity, and boulder diversity. The second axis was a linear combination of rugosity, percent cover, and boulder diversity. Species in the upper right quadrant of the diagram corresponded to sites with above average relief, rugosity, boulder diversity, and percent cover. The species in the upper right quadrant with variation sufficiently explained by the habitat variables were *B. diplotaenia*, *A. troschelii*, *C. atrilobata*, *P. punctatus*, the burrito grunt, *Anisotremus interruptus*, and the Panama graysby, *Epinephelus panamensis*. Species in the lower right quadrant, *M. dorsalis*, and the Pacific dogfish, *Lutjanus novemfasciatus*, corresponded to sites with above average relief and rugosity, but below average rugosity and low percent cover. *Serranus psitticinus*, and the Cortez angel, *Pomacanthus zonipectus*, corresponded to sites with below average values for relief, rugosity, boulder diversity, and percent cover, indicated by their positions in the lower left quadrant. Species in the upper left quadrant, the orangeside triggerfish, *Sufflamen verres*, *M. rosacea*, and the cornetfish, *Fistularia commersonii*, corresponded to sites with above average rugosity and percent cover, but below average relief and boulder diversity.

Individual sites within a habitat type were highly variable in their habitat characteristics, as indicated by large confidence intervals (Figure 18). Habitat types varied most along axis 1; however sites within habitat types varied most along axis 2. Large boulder sites were most notable for their higher relief and boulder diversity. Mixed habitat sites had higher rugosity and percent cover, although these sites varied greatly in these variables. Lava sites and small boulder sites were the most similar in their habitat characteristics.

Guilds

Patterns of trophic guild fish abundances were similar among habitat types (Figure 19). Abundances of piscivores and planktivores were significantly different among habitats (P = 0.036 and P = 0.044 respectively). Numbers of piscivorous species were highest on lava habitat while numbers of planktivores were highest on large boulder and mixed habitats. Although not statistically significant, large boulder habitat had the greatest number of fishes per trophic guild for every guild except invertivores and piscivores, possible due to the greater complexity of large boulder sites (Figure 18).

As detected by RDA, trophic groups were primarily influenced by the combination of relief, rugosity, and boulder diversity, and secondarily by the combination of rugosity, percent cover, and boulder diversity (Figure 20). Herbivores, planktivores, and planktivore/invertivores were more abundant at high rugosity mixed habitat sites with higher boulder diversity and relief. Piscivore/invertivores tended to be more abundant at higher relief large boulder sites with higher boulder diversity and rugosity, but lower percent cover. Piscivores and herbivore/invertivores had greater abundances at high percent cover small boulder and lava sites, with slightly higher rugosity but lower relief and boulder diversity. Invertivores were most abundant at lava, small boulder, and mixed habitat sites with average percent cover and lower than average relief, rugosity, and boulder diversity.

No obvious statistical differences of fish abundance within mobility guilds were detected among habitats (Figure 21). Semi-vagile I species were the most abundant fishes in large boulder, small boulder, and mixed habitats. Lava habitat had the most semi-vagile II fishes, large boulder had the most semi-vagile I fishes, and mixed habitat had the most resident fishes.

Semi-vagile II fishes were more abundant among sites with above average boulder diversity, percent cover, rugosity, and average relief (Figure 22). Semi-vagile I fishes had greater abundances at sites with greater than average rugosity, boulder diversity, and relief, and slightly lower than average percent cover. Resident species were counted in greater numbers at sites with above average percent cover and boulder diversity but lower than average rugosity and relief.

DISCUSSION

This study detected fewer species at Loreto than all other published studies conducted in the central Gulf (Pérez-España et al. 1996; Aburto-Oropeza and Balart 2001; Arreola-Robles and Elorduy-Garay 2002) most likely due to the geographic location and sampling methodology. The other studies were conducted near La Paz, the southern limit of the central Gulf bioregion and a transitional zone (Walker 1960; Thomson and Gilligan 1983). More recently, Sala et al. (2002) have placed La Paz well within a southern zoogeographic region based on canonical correspondence analysis of reef fish assemblages on boulders.

Sampling methodologies in this study differed from the other studies in several ways. The studies cited previously were conducted at multiple depths and have shown that depth is a factor in determining reef fish assemblage structure. The present study was conducted at one depth (10 m). In addition, the other studies sampled seasonally while in this study sampling was conducted only in the fall.

To obtain species presence and abundance data, the other studies used visual survey techniques. Although it has been shown here that the use of video is comparable to visual survey techniques, the method is limited in its ability to identify small or cryptic species. Because of this, certain species that were included in the other studies were not counted in this one. Examples of the families or species that were encountered but not included because they are cryptic are Muraenidae, Holocentridae, Scorpaenidae, Apogonidae, Opistognathidae, Tripterygidae, Blenniidae, Gobiidae, the rock croaker, *Pareques viola*, the sharp nosed puffer, *Canthigaster punctatissima*, and the coral hawkfishes, *Cirrhitichthys oxycephalus* and *Oxycirrhites typus*. In addition, in this study, unlike the others, certain species were not counted due to their transient nature or their lack of utilization of the reef proper. Numerous transients and other pelagic species such as carangids or scombrids, and various elasmobranches were seen but not counted.

Reef fishes encountered among the locations of interest in this study were distributed at geographic (100s of kilometers), local (100s of meters to tens of kilometers), and micro (ones to tens of meters) spatial scales (Munday 2002). At the geographic scale, patterns of fish distributions are best explained by gradients in oceanographic conditions (i.e., temperature) present in the Gulf (Lehner 1979). These gradients are responsible for a latitudinal cline of increasing fish species diversity with decreasing latitude in the Gulf (Sala et al. 2002) and a shift toward more tropical Panamic species (Thomson and Gilligan 1983). Effects of these gradients were not unexpected since Cabo Pulmo is 350 kilometers south of Loreto and in a different bioregion (Walker 1960; Thompson et al. 2000). Tropical species like *T. grammaticum* were more abundant at Cabo Pulmo while *H. chierchiae* was present only at that location. The trigger fishes, *S. verres* and *Pseudobalistes naufragium* (the blunthead triggerfish) were more abundant at Cabo Pulmo where they feed on

Lithophaga living in coral (Cortés 1997). Cold tolerant species were either not present at Cabo Pulmo (*A. troschelii*) or had greater abundances at Loreto (*M. rosacea*), which experiences wide seasonal fluctuations in sea surface temperatures (Maluf 1983).

Results of this study indicate that 2002 was an anomalous year at Cabo Pulmo, which had the lowest species richness and diversity of any location sampled. The low recorded species richness and diversity at Cabo Pulmo was opposite of what was expected and what had been previously reported for the area (Villareal-Cavazos et al. 2000). Numerous species were either absent, such as the blue-and-gold snapper *Lutjanus viridis* or the convict tang *Acanthurus triostegas*, or present in very low numbers, like the parrotfishes *S. ghobban, S. compressus,* and *S. rubroviolaceus*.

It is unknown whether the low species richness and diversity at Cabo Pulmo was an effect of the previous year's Hurricane Juliette in September 2001. Coral at Cabo Pulmo was intact and appeared healthy days after the storm but I found it to be covered with encrusting algae, algal turfs, and some fleshy macro-algae one year later. By my estimation, 90% of existing coral at Cabo Pulmo in August 2002 appeared dead. The decline in living coral is not likely to be the direct cause of a decline in fish species richness or diversity since corallivory does not affect coral abundance at Cabo Pulmo (Reyes-Bonilla and Calderon-Aguilera 1999), there are no obligate corallivores in the Gulf, and the species present there are also found among non-coral habitats.

It is more likely that the low fish species richness and diversity, and the low abundance of herbivorous fishes had an affect on the reef. Feeding by scraping herbivorous fishes controls algal coverage, allowing coral growth (Aronson and Precht 2000), and although an increase in fleshy macro-algae has been shown to cause a decrease in the abundance of herbivorous and invertivorous fishes on Kenyan coral reefs (McClanahan et al. 1999), coralline algae and algal turfs dominated on the reef at Cabo Pulmo. Algal turfs have higher nutrient value and are more often eaten by herbivorous fishes (Choat 1991). Live coral coverage has been shown not to be a factor in fish species richness or abundance (Luckhurst and Luckhurst 1978).

The lack of herbivores and some other fishes could have been a result of recruitment failure at Cabo Pulmo reef. The rapid drop in water temperature that I observed, brought on by Hurricane Juliette, may have caused high juvenile mortality, especially among the more temperature sensitive tropical species. This could explain the high abundance of sub-tropical species such as *C. atrilobata* and *Stegastes* spp, and the low abundance or absence of tropical species like *L. viridis*, *A. triostegas*, or the Moorish idol *Zanclus cornutus*.

Despite inherent differences in structure and composition between rock and coral habitats, certain physical and biological similarities between the two bioregions were detected. The coral reef at Cabo Pulmo, like rock habitats, lacks the local scale zonation typical of coral reefs, which usually have multiple zones, each with corresponding physiographic characteristics (Done 1983; Williams 1991). Cabo Pulmo Reef has the reef flat and outer reef slope zones but lacks the reef crest, lagoon, and back reef zones. In addition, Cabo Pulmo Reef, like most eastern Pacific coral reefs, has a low diversity of branching corals relative to other tropical reefs (Cortés 1997). Cabo Pulmo Reef is dominated by two species, *Pocillopora verrucosa* and *P. meandrina* (Reyes-Bonilla 1997), which have short, thick branches that create fewer and smaller interstitial spaces and lower overall rugosity at the scale measured. Although coral species diversity has been correlated with fish diversity and abundance (Chabanet et al. 1997), it is unlikely that the high fish diversity previously reported for Cabo Pulmo (Thomson et al. 2000; Villareal-Cavazos et al. 2000) is due to the coral reef itself, but rather a result of other factors such as temperature and productivity, or the habitat complexity created by the combination of coral reef and rocky habitats.

As measured, habitat at Cabo Pulmo was most similar in characteristics to that of lava habitat at Isla Carmen. Though not detected by the measured habitat variables, Cabo Pulmo probably had more physical and oceanographic traits in common with lava habitat at Isla Coronados. At the northern-central portion of Cabo Pulmo Reef, sites were sampled on the reef flat, close to, but not including the outer reef slope, a drop-off created by the large granite blocks on which the reef grows. Lava sites at Isla Coronados were analogous to reef slopes, as they were sampled on the top of large ledges and sometimes included a small drop-off, accounting for the higher measured relief. Further offshore these drop-offs increased in height, some tens of meters high. In the Indo-Pacific, zooplanktivores have been associated with outer reef slopes where currents carrying the preferred prey of these species first contact the reef

(Harmelin-Vivien 1989). High abundances of planktivorous *T. lucasanum* and *C. atrilobata*, as well as overall fish assemblage composition and the abundance of semi-vagile I fishes could be explained by the unmeasured physical similarities in habitat between Cabo Pulmo and Isla Coronados.

The presence of habitat patches existing independent of habitat types (Figure 7) has potential ecological impacts. Rather than Gulf reef fishes perceiving their world as many micro scale contiguous heterogeneous habitat patches, it is more likely that they see it as one or more local scale-sized heterogeneous units composed of mosaics of smaller patches that share similar traits, such as high relief (García-Charton and Peréz-Ruzafa 1998). These heterogeneous units give a location its local-scale habitat characterization (Figure 6), influencing the composition of the fish assemblage there. This may explain the differences detected in reef fish assemblages among locations at Loreto.

Perception of habitat patchiness by fishes depends on their mobility. Resident fishes likely see their world as small isolated islands of suitable habitat. For semi-vagile I fishes, their world is slightly less patchy, as they have the ability to move more freely among suitable habitat patches. Semi-vagile II fishes are the most likely to view their world as a heterogeneous unit comprised of smaller habitat patches. Having specific habitat needs in a heterogeneous landscape would require greater mobility. At Loreto and Cabo Pulmo, all semi-vagile II species but one were herbivorous. Certain herbivorous species, like *Kyphosus analogus*, and the Gulf opaleye, *Girella simplicidens*, target larger fleshy macro-algas (Choat 1991) which I observed to be patchy in their distribution.

How habitat patches and their cumulative effect influence local-scale fish assemblage composition is determined by individual species and guild response to micro-scale habitat variables. Although few fishes seemed to respond strongly to habitat variables, those that did were responding to variables that provide them with an ecological resource. High relief, high boulder diversity, and high rugosity habitat (right half of Figure 20) creates numerous crevices, holes, and small caves for fishes such as *A. troschelii* and *C. atrilobata* that seek shelter there. *Lutjanus novemfasciatus*, *Epinephelus panamensis*, and *Anisotremus interruptus* seek both shelter and prey in this habitat (Hobson 1968; Thomson et al. 2000). *Sufflamen verres* seeks prey in the flat sandy areas within the vicinity of the reef and seeks protection in small holes within which it wedges itself (Hobson 1968). Thus it is more abundant in low relief but high rugosity habitat.

Habitat patches may have influenced patterns of distribution and abundance of fishes in trophic guilds similarly to individual species. Trophic guilds such as planktivores were associated with high relief, rugosity, and boulder diversity habitat. The three obligate planktivores in this study, *C. atrilobata*, *C. limbaughi*, and *P. colonus*, seek shelter in the voids created by rugosity and boulder diversity, and prey on zooplankton made accessible by currents interacting with high relief (Harmelin 1989). Herbivore/invertivores were associated with higher levels of cover, a food source, and rugosity, a source of shelter. Piscivores were more abundant near potential prey, herbivore/invertivores. Patterns of mobility guilds were insufficiently clear for drawing any conclusions.

The availability of food and shelter provided by habitat does not appear to be a limited resource in the Gulf; possibly minimizing the influence habitat has on the composition of fish assemblages there. Many of the fishes recorded at Loreto and Cabo Pulmo were omnivorous and so had access to a variety of prey. Those species preying on one food type were mostly semi-vagile I or semi-vagile II and had the ability to move within a reef or from reef to reef in search of food. General competition for space is minimal, as few species are territorial. Shelter, another use of space, is not a limited resource for Gulf fishes because they do not have specific hole size requirements when seeking refuge (Molles 1978).

The consequence of the non-specific needs of Gulf fishes is that they are generally present among most locations and habitats, varying only in their abundances (Table 7). This was true of fishes at Loreto and Cabo Pulmo in this study, and for fishes at various locations near Bahía de La Paz (Pérez-España et al. 1996; Aburto-Oropeza and Balart 2001; Arreola-Robles and Elorduy-Garay 2002). Comparisons made of dominant fishes among locations in this study and the others show that four species, *C. atrilobata*, *Stegastes* spp, *A. troschelii*, and *T. lucasanum* were dominant or at least present at nearly every study location. The ubiquity of these species in spite of varying habitat, depths, seasons, and latitude indicates that these species have few specialized resource requirements. Common, but less dominant species such as *P. colonus*, *H. passer*, or *B. diplotaenia* may have stricter resource requirements, resulting in a more ordered distribution. Differences among locations in reef fish assemblage structure are ultimately caused by uncommon or rare species that have more specialized needs.

The similarity in dominant species at Loreto, La Paz, and Cabo Pulmo infers that a certain amount of predictability in reef fish assemblage structure exists in the Gulf of California. This predictability may persist on any hard bottom habitat, be it rock, coral, or even metal, in the case of the shipwreck Pecio Salvatierra (Arreola-Robles and Elorduy-Garay 2002). However, oceanographic conditions may be a better predictor of reef fish assemblage structure, not only at the more obvious geographic scale but at the local scale as well (Gilligan 1983; Aburto-Oropeza and Balart 2001; Arreola-Robles and Elorduy-Garay 2002). To separate factors that influence the distribution and abundance of reef fishes in this region, more research, preferably experimental and accounting for oceanographic variables, is needed.

REFERENCES CITED

Abitia-Cárdenas, L.A., J. Rodríguez-Romero, F. Galván-Magaña, J. de la Cruz-Aguero, and H. Chávez-Ramos. 1994. Lista sistemática de la ictiofauna de Bahía de La Paz, Baja California Sur, México. Cien. Mar. 20(2):159 – 181.

Aburto-Oropeza, O. and E.F. Balart. 2001. Community structure of reef fish in several habitats of a rocky reef in the Gulf of California. Mar. Ecol. 22(4):283 – 305.

Addicot, J.F., J.M. Aho, M.F. Antolin, D.K. Padilla, J.S. Richardson, and D.A. Soluk. 1987. Ecological neighborhoods:scaling environmental patterns. Oikos. 49:340 – 346.

Anderson, C.A. 1950. Geology of islands and neighboring land areas. In: 1940 E.W. Scripps Cruise to the Gulf of California. Geol. Soc. America Mem. 31:362 p.

Aronson, R.B. and W.F. Precht. 2000. Herbivory and algal dynamics on the coral reef at Discovery Bay, Jamaica. Limnol. Oceanogr. 45(1):251 – 255.

Arreola-Robles, J.L., and J.F. Elorduy-Garay. 2002. Reef fish diversity in the region of La Paz, Baja California Sur, Mexico. Bull. Mar. Sci. 70(1):1 – 18.

Bohnsack, J. A., and S. P. Bannerot. 1986. A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. NOAA Technical Report NMFS. 41:15.

Bortone, S. A., T. Martin, and C. M. Bundrick. 1991. Visual census of reef fish assemblages:a comparison of slate, audio, and video recording devices. Northeast Gulf Sci. 12(1):17 – 23.

Brock, V.E. 1954. A preliminary report on a method of estimating reef fish population. J. Wildl. Management 18(3):297 – 317.

Brusca, R.C. and D.A. Thomson. 1975. Pulmo Reef: The only "coral reef" in the Gulf of California. Cien. Mar. 1(3):37 - 53

Cailliet, G.M. and J.P. Barry. 1979. Comparison of food array overlap measures useful in fish feeding habit analysis. 67 – 69. In: Lipovsky, S.J., Simenstad, C.A. (Eds.), Gutshop' 78, Fish Food Habit Studies; Proceedings of the Second Pacific Northwest Technical Workshop, University of Washington Division of Marine Resources, Washington Sea Grant Report WSG-WO-79-1.

Chabanet, P.H., Ralambondrainy, M. Amanieu, G. Faure, and R. Galzin. 1997. Relationships between coral reef substrata and fish. Coral Reefs. 16:93 – 102.

Choat, J.H. and D.R. Bellwood. 1991. Reef fishes: their history and evolution. In: P.F. Sale (ed.) The Ecology of Fishes on Coral Reefs. Academic Press, San Diego. p 39 – 66.

Choat, J.H. 1991. The biology of herbivorous fishes on coral reefs. In: P.F. Sale (ed.) The Ecology of Fishes on Coral Reefs. Academic Press, San Diego. p 120 – 155.

Cortés, J. 1997. Biology and geology of eastern Pacific coral reefs. Coral Reefs. 16 Supplement S39-S46.

Davis, G.E. and T.W. Anderson. 1989. Population estimates of four kelp forest fishes and an evaluation of three in situ assessment techniques. Bull. Mar. Sci. 44(3):1138 – 1151.

Done, T.J. 1983. Coral zonation: Its nature and significance. In: D.J. Barnes (ed.) Perspectives on Coral Reefs Aust. Inst. Mar. Sci., Townsville, Australia. p 107 – 147 .

Ebeling, A.W. and M.A. Hixon. 1991. Tropical and temperate reef fishes: a comparison of community structures. In: P.F. Sale (ed.) The Ecology of Fishes on Coral Reefs. Academic Press, San Diego. p 509 – 563.

Friedlander, A.M., and J.D. Parrish. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. J. Exper. Mar. Bio. Ecol. 224: 1 – 30.

García-Charton, J.A., and A. Pérez-Ruzafa. 1998. Correlation between habitat structure and a rocky reef fish assemblage in the southwest Mediterranean. Mar. Ecol. 19(2):111 – 128.

Gilligan, M.R. 1980. Beta diversity of a Gulf of California rocky-shore community. Env. Biol, Fish. 5(2):109 – 116.

Harmelin-Vivien, M.L. 1989. Reef fish community structure: an Indo-Pacific comparison. In: M. L. Harmelin-Vivien and F. Bourlie`re (eds). Vertebrates in complex tropical systems. Ecological Studies 69, Springer-Verlag, Berlin, Germany. p 21 – 60.

Helfman, G.S. 1983. Underwater methods. In: Fisheries techniques. American Fisheries Society, Bethesda, Maryland. p 349 – 369.

Hobson, E.S. 1968. Predatory behavior of some shore fishes in the Gulf of California. U.S. Fish. Wildl. Serv. Res. Rep. 73:1 – 92.

Legendre, P. and L. Legendre. 1998. Numerical Ecology. Second English Edition. Elsevier Science. Amsterdam. 853 pp.

Lehner, C.E. 1979. A Latitudinal Gradient Analysis of Rocky-Shore Fishes of the Eastern Pacific. Ph.D. dissertation, Univ. of Arizona. 320 p.

Luckhurst, B.E. and K. Luckhurst. 1978. Analysis of the influence of substrate variables on coral reef fish communities. Mar. Biol. 49:317 - 323.

Maluf, L.V. 1983. Physical Oceanography. In: T. J. Case and M. L. Cody, (eds.). Island Biogeography in the Sea of Cortez. U.C. Press, Berkeley. p 28 – 45.

Mardia, K.V., J.T. Kent, and J.M. Bibby. 1979. Multivariate Analysis. Academic Press, London. 518 pp.

May, R.M. 1984. Exploitation of marine communities. Springer-Verlag, Berlin.

McClanahan, T.R., V. Hendrick, M. J. Rodrigues, and N. V. C. Polunin. 1999. Varying responses of herbivorous and invertebrate-feeding fishes to macroalgal reduction on a coral reef. Coral Reefs. 18:195 – 203.

Minch, J.A., Minch E., and Minch J. 1998. Roadside Geology and Biology of Baja California. John Minch and Associates. Mission Viejo, CA. 188 p.

Molles, M. C. 1978. Fish diversity on model and natural reef patches: experimental insular biogeography. Ecological Monographs 48:289–305.

Munday, P.L. 2002. Does habitat availability determine geographical-scale abundances of coral dwelling fishes? Coral Reefs 21:105 – 116.

Núñez-Lara, E. and E. Arias-González. 1998. The relationship between reef fish community structure and environmental variables in the southern Mexican Caribbean. J. Fish Biol. 53:209 – 221.

Ogden, J. C. and T. P. Quinn. 1984. Migration in coral reef fishes: ecological significance and orientation mechanisms. In: J. D. McCleave, G. P. Arnold, J. J. Dodson and W.H. Neill, (eds). Mechanisms of migration in fishes. Plenum Press, New York. p 293 – 308

Ohman, M. C., A., Rajasuriya and E. Olafsson. 1997. Reef Fish Assemblages in North-Western Sri Lanka: Distribution Patterns and Influences of Fishing Practices. Environ. Biol. Fish. 49:pp. 45–61.

Ohman, M.C., and A. Rajasuriya. 1998. Relationships between habitat structure and fish communities on coral and sandstone reefs. Environ. Biol. Fish. 53:19 – 31.

Pérez-España, H., F. Galván-Magaña, and L.A. Abitia-Cárdenas. 1996. Variaciones temporales y espaciales en la estructura de la comunidad de peces de arrecifes rocosos del suroeste del Golfo de California, México. Ciencias Marinas 22:273-294.

Reyes-Bonilla, H. 1997. Cabo Pulmo Reef: A new marine reserve in the Gulf of California. Conserv. Biol. 11(2):838.

Reyes-Bonilla, H. and L.E. Calderon-Aquilera. 1999. Population density, distribution, and consumption rates of three corallivores at Cabo Pulmo Reef, Gulf of California. Mar. Ecol. 20(3-4):347 – 357.

Russell, B.C., F.H. Talbot, G.R.V. Anderson, and B. Goldman. 1978. Collection and sampling of reef fishes. In: D.R. Stoddart and R.E. Johannes (eds.), Monographs on oceanographic methodology 5. Coral Reefs: Research Methods.UNESCO, Norwich, U.K. p 329 – 345.

Sala, E., O. Aburto-Oropeza, G. Paredes, I. Parra, J.C. Barrera, and P.K. Dayton. 2002. A general model for designing networks of marine reserves. Science. 298:1991 – 1993.

Sale, P.F. 1991. The Ecology of Fishes on Coral Reefs. Academic Press, San Diego. 754 p

Samoilys, M. and G.M. Carlos. 2000. Determining methods of underwater visual census for estimating the abundance of coral reef fishes. Environ. Biol. Fish. 57:289 – 304.

Schmitt, R.J., and S.J. Holbrook. 1986. Seasonally fluctuating resources and temporal variability of interspecific competition. Oecologia. 69:1 –11.

Shannon, C. and W. Weaver. 1949. The mathematical theory of communication. University of Illinois Press, Urbana. 117 pp.

Smilaur, P. 1992. CanoDraw Users Guide v.3.0. Microcomputer Power. Ithaca, New York. 118 p

Thomson, D.A. and M. Gilligan. 1983. The rocky shore fishes. In: T.J. Case & M.L. Cody (eds.). Island biogeography in the Sea of Cortez. University of California, Berkeley. p 98-129.

Thomson, D.A., L.T. Findley, and A.N. Kerstitch. 2000. Reef fishes of the Sea of Cortez. University of Texas Press. Austin. 353 p

ter Braak, C.J.F. and P.F.M. Verdonschot. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquat. Sci. 57(3):255 – 289.

Villarreal-Cavazos, A., H. Reyes-Bonilla, B. Bermudez-Almada, and O. Arizpe-Covarrubias. 2000. Los peces del arrecife de Cabo Pulmo, Golfo de California, México: lista sistemática y aspectos de abundancia y biogeografía. Rev. Biol. Trop .48 (2-3):413-424.

Walker, B.W. 1960. The distribution and affinities of the marine fish fauna of the Gulf of California. Sys. Zool. 9(3):123 – 133.

Wiens, J. 1976. Population response to patchy environment. Ann. Rev. Ecol. Systems. 7:81-129.

Williams, D. McB. 1991. Patterns and processes in the distribution of coral reef fishes. In: P. F. Sale, (Ed.) The Ecology of Fishes on Coral Reefs. Academic Press, San Diego, California, USA. p 437 – 474.

Zanchi, A. 1994. The opening of the Gulf of California near Loreto, Baja California, Mexico: from basin and range extension to transtensional tectonics. J. Struct. Geol. 16(12):1619 – 1639.

Zar, J.H. 1996. Biostatistical Analysis. Prentice Hall. Englewood Cliffs, NJ. 660 p

Table 1. List of species by family and their guild membership. Species names abbreviations used in this paper are the first letter of the genus and the first three letters of the species (non-italicized letters).

Species List

FAMILY	SPECIES	TROPHIC GUILD	MOBILITY GUILD
Acanthuridae	Acanthurus xanthopterus	Herbivore	Semi-vagile II
	Prionurus punctatus	Herbivore	Semi-vagile II
Balistidae	Balistes polylepis	Invertivore	Semi-vagile I
	Sufflamen verres	Invertivore	Semi-vagile I
	Psuedobalistes naufragium	Invertivore	Semi-vagile I
Chaetodontidae	Chaetodon humeralis	Herb/Invertivore	Semi-vagile I
	Johnrandallia nigrirostris	Herb/Invertivore	Semi-vagile I
Cirrhitidae	Cirrhitus rivulatus	Pisc/Invertivore	Resident
Diodontidae	Diodon holocanthus	Invertivore	Semi-vagile I
Fistularidae	Fistularia commersonii	Piscivore	Semi-vagile I
Haemulidae	Anisotremus interruptus	Invertivore	Semi-vagile I
	Haemulon flaviguttatum	Invertivore	Semi-vagile I
	Haemulon sexfasciatum	Pisc/Invertivore	Semi-vagile I
Kyphosidae	Girella simplicidens	Herb/Invertivore	Semi-vagile II
	Kyphosus analogus	Herb/Invertivore	Semi-vagile II
Labridae	Bodianus diplotaenia	Pisc/Invertivore	Semi-vagile II
	Halichoeres nicholsi	Invertivore	Semi-vagile I
	Halichoeres notospilus	Invertivore	Semi-vagile I
	Halichoeres chierchiae	Invertivore	Semi-vagile I
	Labridae	na	na
	Thalassoma grammaticum	Invertivore	Semi-vagile I
	Thalassoma lucasanum	Plank/Invertivore	Semi-vagile I
Lutjanidae	Hoplopagrus guentherii	Pisc/Invertivore	Semi-vagile I
	Lutjanus argentiventris	Pisc/Invertivore	Semi-vagile I
	Lutjanus novemfasciatus	Pisc/Invertivore	Semi-vagile I
	Lutjanus viridis	Pisc/Invertivore	Semi-vagile I
Mugilidae	Mulloidichthys dentatus	Invertivore	Semi-vagile I
Pomacanthidae	Holacanthus passer	Herb/Invertivore	Semi-vagile I
	Holacanthus clarionensis	Herb/Invertivore	Semi-vagile I
	Pomacanthus zonipectus	Herb/Invertivore	Semi-vagile I
Pomacentridae	Abudefduf troschelii	Plank/Invertivore	Semi-vagile I
	Chromis atrilobata	Planktivore	Semi-vagile I
	Chromis limbaughi	Planktivore	Resident
	Microspathadon bairdii	Herb/Invertivore	Resident
	Microspathadon dorsalis	Herbivore	Resident
	Stegastes spp	Herb/Invertivore	Resident
Scaridae	Nicholsina denticulata	Herbivore	Semi-vagile I
	Scarus compressus	Herbivore	Semi-vagile II
	Scarus ghobban	Herbivore	Semi-vagile II
	Scarus perrico	Herbivore	Semi-vagile II
	Scarus rubroviolaceus	Herbivore	Semi-vagile II
	Scarus sp.	na	na
Serranidae	Alphestes immaculatus	Invertivore	Resident
	Epinephelus labriformis	Pisc/Invertivore	Resident
	Epinephelus panamensis	Pisc/Invertivore	Resident
	Mycteroperca rosacea	Piscivore	Semi-vagile I
	Mycteroperca sp.	na	na
	Paranthias colonus	Planktivore	Semi-vagile I
	Serranus psittacinus	Pisc/Invertivore	Resident
Sparidae	Calamus brachysomas	Invertivore	Semi-vagile I
Tetradontidae	Arothron meleagris	Herbivore	Semi-vagile I
	Sphoeroides annulatus	Herb/Invertivore	Semi-vagile I
	Ostracion meleagris	na	na
	Tetradontidae	na	na
Zanclidae	Zanclus cornutus	Herb/Invertivore	Semi-vagile I

Table 2. Comparison between video and visual survey methods. Asterisks indicate significant differences between methods (P > 0.05). SD is standard deviation.

Comparison Between Video and Visual Survey Methods						
	Method					
Species	Video			Visual		
	n	Mean	SD	n	Mean	SD
Species Richness	15	9.33	2.53	15	8.67	2.32
Diversity (H')	15	1.59	0.32	15	1.57	0.33
Fish Abundance*	15	75.40	50.74	15	53.27	36.20
Abudefduf troschelii	6	16.50	14.65	7	12.43	13.21
Acanthurus xanthopterus	1	1.00	-	1	1.00	-
Arothron meleagris	1	1.00	-	1	-	-
Balistes polylepis	1	1.00	-	1	1.00	-
Bodianus diplotaenia	15	1.93	1.10	12	1.75	1.22
Calamus brachysomas	2	2.50	2.12	2	2.50	2.12
Chromis atrilobata	5	70.00	38.23	5	43.00	7.58
Diodon holacanthus	1	1.00	-	3	1.00	0.00
Epinephelus panamensis	1	1.00	-	1	1.00	-
Haemulon maculicauda	1	44.00	-	1	50.00	-
Haemulon sexfasciatum	2	1.00	0.00	3	1.33	0.58
Halichoeres dispilus	2	3.50	2.12	-	-	-
Halichoeres nicholsi	3	1.67	0.58	4	1.25	0.50
Halichoeres sp.	-	-	-	3	1.00	0.00
Holacanthus passer	13	2.77	1.24	13	2.23	1.09
Johnrandallia nigrirostris	4	1.75	0.96	3	1.33	0.58
Kyphosus analogus	1	6.00	-	1	13.00	-
Labridae	1	3.00	-	-	-	-
Lutjanus argentiventris	4	2.50	1.29	5	2.20	2.17
Microspathadon dorsalis	2	1.00	-	1	1.00	-
Microlepidotus inornatus	1	1.50	0.71	1	2.00	-
Mulloidichthys dentatus	1	4.00	-	-	-	-
*Mycteroperca rosacea**	15	6.40	3.00	15	4.00	2.00
Paranthias colonus	6	6.17	5.42	6	5.67	7.74
Pomacanthus zonipectus	-	-		1	2.00	-
Prionurus punctatus	5	10.40	6.31	5	6.00	3.67
Scarus compressus	1	1.00	-	1	1.00	-
Scarus ghobban	8	6.50	4.72	7	7.29	4.89
Scarus rubroviolaceus	4	5.25	4.99	3	4.33	3.21
Scarus sp.	-	-	-	2	13.00	16.97
Serranus psittacinus	6	1.17	0.41	5	1.40	0.55
*Stegastes spp.**	15	9.73	5.31	15	3.94	2.46
Sufflamen verres	1	1.00	-	2	2.00	0.00
Thalassoma lucasanum	6	16.17	16.27	6	14.17	10.53
unidentified	5	1.00	0.00	-	-	-

Table 3. Species rank frequency of occurrence (%FO) and relative abundance (%N). Species for all locations and individual locations are ranked based on the percentage of transects in which they occur. Ties in %FO are then ranked %N.

Species Rank Frequency of Occurence (%FO) and Relative Abundance (%N)															
	Overall			Carmen			Coronados			Danzante			Pulmo		
Species	Rank	%FO	%N	Rank	%FO	%N	Rank	%FO	%N	Rank	%FO	%N	Rank	%FO	%N
S spp	1	100	14.0	1	100	16.1	2	100	9.9	2	100	19.0	3	100	9.6
H pas	2	97.8	2.6	3	100	2.7	5	100	2.9	8	85.7	1.0	5	100	3.2
T luc	3	93.3	16.5	4	90.9	9.3	1	100	26.8	6	85.7	1.7	2	100	32.5
B dip	4	93.3	1.5	7	86.4	1.0	6	100	1.9	4	100	1.8	6	100	2.0
M ros	5	86.7	2.9	2	100	4.4	3	100	3.5	5	100	1.4	17	33.3	0.4
J nig	6	77.8	0.7	5	90.9	0.9	8	100	1.0	16	57.1	0.3	15	44.4	0.5
S gho	7	71.1	3.6	6	86.4	6.4	11	85.7	2.3	3	100	2.1	NP	0.0	0.0
Labridae	8	71.1	1.5	11	68.2	1.9	21	42.9	1.4	10	71.4	0.9	9	100	1.3
C atr	9	64.4	18.2	12	63.6	18.6	18	57.1	8.4	25	28.6	2.5	1	100	35.7
L arg	10	64.4	1.6	9	72.7	2.5	13	85.7	1.5	7	85.7	1.4	30	11.1	0.0
H sex	11	62.2	1.7	8	77.3	2.8	12	85.7	1.6	9	71.4	1.2	NP	0.0	0.0
P pun	12	60.0	4.2	18	50.0	3.2	19	57.1	6.5	18	42.9	0.7	4	100	6.9
S rub	13	60.0	0.6	14	63.6	0.8	23	42.9	0.3	14	57.1	0.5	11	66.7	0.4
A tro	14	55.6	13.6	16	54.5	9.7	9	85.7	13.7	1	100	45.5	NP	0.0	0.0
P col	15	55.6	2.3	19	45.5	3.1	4	100	3.5	13	57.1	0.6	14	44.4	0.6
S com	16	53.3	1.7	13	63.6	3.3	7	100	1.1	36	14.3	0.1	20	22.2	0.1
S ver	17	51.1	0.6	17	54.5	0.4	33	28.6	0.1	NP	0.0	0.0	7	100.0	1.8
E pan	18	51.1	0.2	25	27.3	0.1	15	85.7	0.3	15	57.1	0.3	10	77.8	0.3
S psi	19	48.9	0.7	10	72.7	1.5	35	14.3	0.1	32	28.6	0.1	18	33.3	0.2
E lab	20	46.7	0.2	23	40.9	0.2	17	71.4	0.3	29	28.6	0.1	13	55.6	0.2
M den	21	44.4	2.2	15	59.1	3.2	10	85.7	4.1	34	14.3	0.3	NP	0.0	0.0
K ana	22	44.4	1.3	20	45.5	1.7	16	71.4	0.9	12	57.1	1.5	23	11.1	0.7
S per	23	37.8	0.5	22	40.9	0.7	30	28.6	0.1	21	42.9	0.2	16	33.3	0.8
D hol	24	37.8	0.2	30	22.7	0.1	14	85.7	0.4	20	42.9	0.2	19	33.3	0.1
T gra	25	26.7	0.4	NP	0.0		NP	0.0	0.0	22	42.9	0.2	8	100	1.7
B pol	26	26.7	0.1	21	45.5	0.3	NP	0.0	0.0	37	14.3	0.1	28	11.1	0.0
M dor	27	24.4	0.3	28	22.7	0.4	26	42.9	0.2	19	42.9	0.3	NP	0.0	0.0
P zon	28	24.4	0.1	33	18.2	0.1	24	42.9	0.2	17	57.1	0.2	NP	0.0	0.0
A int	29	22.2	0.2	24	27.3	0.2	22	42.9	0.5	39	14.3	0.0	NP	0.0	0.0
C riv	30	22.2	0.1	26	27.3	0.1	25	42.9	0.2	40	14.3	0.0	NP	0.0	0.0
L vir	31	20.0	2.6	27	22.7	3.1	28	28.6	2.9	24	28.6	4.6	NP	0.0	0.0
C lim	32	20.0	1.9	36	9.1	0.3	20	42.9	1.9	11	57.1	9.2	NP	0.0	0.0
H nic	33	17.8	0.1	32	18.2	0.1	32	28.6	0.1	41	14.3	0.0	25	11.1	0.1
H gue	34	15.6	0.1	29	22.7	0.1	31	28.6	0.1	NP	0.0	0.0	NP	0.0	0.0
F com	35	13.3	0.1	34	13.6	0.1	34	14.3	0.1	30	28.6	0.1	NP	0.0	0.0
H chi	36	13.3	0.1	NP	0.0		NP	0.0	0.0	NP	0.0	0.0	12	66.7	0.2
A imm	37	13.3	<0.1	35	13.6	0.0	NP	0.0	0.0	23	42.9	0.1	NP	0.0	0.0
G sim	38	11.1	<0.1	NP	0.0		27	42.9	0.1	27	28.6	0.1	NP	0.0	0.0
C bra	39	8.9	0.1	31	18.2	0.3	NP	0.0	0.0	NP	0.0	0.0	NP	0.0	0.0
M bai	40	8.9	<0.1	39	4.5	0.0	36	14.3	0.0	28	28.6	0.1	NP	0.0	0.0
N den	41	8.9	<0.1	37	9.1	0.0	NP	0.0	0.0	31	28.6	0.1	NP	0.0	0.0
A xan	42	6.7	0.2	NP	0.0		29	28.6	1.2	38	14.3	0.0	NP	0.0	0.0
C hum	43	6.7	<0.1	NP	0.0		NP	0.0	0.0	26	28.6	0.1	24	11.1	0.1
A mel	44	6.7	<0.1	40	4.5	0.0	NP	0.0	0.0	NP	0.0	0.0	22	22.2	0.1
H not	45	4.4	<0.1	NP	0.0		NP	0.0	0.0	35	14.3	0.1	26	11.1	0.1
P nau	46	4.4	<0.1	NP	0.0		NP	0.0	0.0	NP	0.0	0.0	21	22.2	0.1
S sp	47	4.4	<0.1	42	4.5	0.0	NP	0.0	0.0	42	14.3	0.0	NP	0.0	0.0
S ann	48	4.4	<0.1	NP	0.0		37	14.3	0.0	NP	0.0	0.0	32	11.1	0.0
H fla	49	2.2	0.2	NP	0.0		NP	0.0	0.0	33	14.3	1.0	NP	0.0	0.0
L nov	50	2.2	0.1	38	4.5	0.1	NP	0.0	0.0	NP	0.0	0.0	NP	0.0	0.0
Z cor	51	2.2	<0.1	NP	0.0		NP	0.0	0.0	NP	0.0	0.0	27	11.1	0.1
H cla	52	2.2	<0.1	NP	0.0		NP	0.0	0.0	NP	0.0	0.0	29	11.1	0.0
M sp	53	2.2	<0.1	41	4.5	0.0	NP	0.0	0.0	NP	0.0	0.0	NP	0.0	0.0
O mel	54	2.2	<0.1	NP	0.0		NP	0.0	0.0	NP	0.0	0.0	31	11.1	0.0
Tetradontidae	55	2.2	<0.1	43	4.5	0.0	NP	0.0	0.0	NP	0.0	0.0	NP	0.0	0.0

Table 4. Percentage Similarity Indices (PSI) between the four sampling locations.

PSI Between Locations				
	Location			
	Carmen	Coronados	Danzante	Pulmo
Carmen	1.000			
Coronados	0.687	1.000		
Danzante	0.477	0.471	1.000	
Pulmo	0.504	0.611	0.199	1.000

Table 5. Percentage Similarity Indices (PSI) for the four habitat types at Isla Carmen.

PSI between Habitats at Isla Carmen				
	Habitat			
	Lava	Lg Bould	Sm Bould	Mixed
Lava	1.000			
Lg Bould	0.516	1.000		
Sm Bould	0.960	0.629	1.000	
Mixed	0.613	0.636	0.583	1.000

Table 6. Summary of pRDA analysis of species and habitats at Isla Carmen.

Summary of pRDA analysis of species and habitats at Isla Carmen

Axes	1	2	3	4	Total variance
Eigenvalues	.153	.061	.039	.035	1.000
Species-environment correlations	.918	.848	.809	.813	
Cumulative percentage variance					
of species data	16.2	22.7	26.8	30.6	
of species-environment relation	52.9	74.1	87.7	100.0	
Sum of all unconstrained eigenvalues					.943
Sum of all canonical eigenvalues					.288

Table 7. Top five most dominant fishes among various locations in the Gulf of California. The sharpnosed puffer, *Canthigaster punctatissima*, was excluded because it was considered cryptic in the present study. Dominance here is considered frequent and abundant. Where possible only data collected during the autumn season was used.

Top five most dominant fishes among various locations in the Gulf of California							
Location							
Pto. San Carlos[1]	Cueva de León[2]	Ensenada Grande[2]	Candelero[2]	San Gabriel[2]	Los Islotes[3]	La Gallina[4]	El Gallo[4]
Abudefduf troschelii	*Stegastes spp*	*Stegastes spp*	*Stegastes spp*	*Stegastes spp*	*Chromis atrilobata*	*Abudefduf troschelii*	*Abudefduf troschelii*
Bodianus diplotaenia	*Thalassoma lucasanum*	*Chromis atrilobata*	*Abudefduf troschelii*	*Thalassoma lucasanum*	*Thalassoma lucasanum*	*Stegastes rectifraenum*	*Chromis atrilobata*
Stegastes rectifraenum	*Chromis atrilobata*	*Abudefduf troschelii*	*Thalassoma lucasanum*	*Abudefduf troschelii*	*Paranthias colonus*	*Bodianus diplotaenia*	*Stegastes rectifraenum*
Thalassoma lucasanum	*Abudefduf troschelii*	*Thalassoma lucasanum*	*Scarus ghobban*	*Holacanthus passer*	*Stegastes rectifraenum*	*Holacanthus passer*	*Chromis limbaughi*
Holacanthus passer	*Microspathodon dorsalis*	*Scarus rubroviolaceus*	*Chromis atrilobata*	*Bodianus diplotaenia*	*Holacanthus passer*	*Thalassoma lucasanum*	*Scarus ghobban*

[1] Gilligan (1980). Central eastern Gulf.
[2] Peréz-España et al. (1996). Near Bahía de La Paz.
[3] Aburto-Oropeza and Balart (2001). Near Bahía de La Paz.

Table 7 (cont.). Top five most dominant fishes among various locations in the Gulf of California.

Top five most dominant fishes among various locations in the Gulf of California (cont.)								
Location								
El Gallo[4]	La Ballena[4]	Los Islotes[4]	Las Animas[4]	Pecio Salvatierra[4]	I. Carmen[5]	I. Coronados[5]	I. Danzante[5]	Cabo Pulmo[5]
Abudefduf troschelii	*Abudefduf troschelii*	*Chromis atrilobata*	*Chromis atrilobata*	*Chromis limbaughi*	*Stegastes spp*	*Thalassoma lucasanum*	*Abudefduf troschelii*	*Chromis atrilobata*
Chromis atrilobata	*Stegastes rectifraenum*	*Thalassoma lucasanum*	*Paranthias colonus*	*Haemulon sexfasciatum*	*Mycteroperca rosacea*	*Stegastes spp*	*Stegastes spp*	*Thalassoma lucasanum*
Stegastes rectifraenum	*Chromis atrilobata*	*Holacanthus passer*	*Thalassoma lucasanum*	*Paranthias colonus*	*Holacanthus passer*	*Mycteroperca rosacea*	*Scarus ghobban*	*Stegastes spp*
Chromis limbaughi	*Thalassoma lucasanum*	*Stegastes rectifraenum*	*Holacanthus passer*	*Mulloidichthys dentatus*	*Thalassoma lucasanum*	*Paranthias colonus*	*Paranthias colonus*	*Prionurus punctatus*
Scarus ghobban	*Chromis limbaughi*	*Prionurus punctatus*	*Bodianus diplotaenia*	*Holacanthus passer*	*Johnrandallia nigrirostrus*	*Holacanthus passer*	*Mycteroperca rosacea*	*Holacanthus passer*

[4] Arreola-Robles and Elorduy-Garay (2002). Near Bahía de La Paz. Pecio Salvatierra is an artificial reef created by a sunken ship.
[5] Present study.

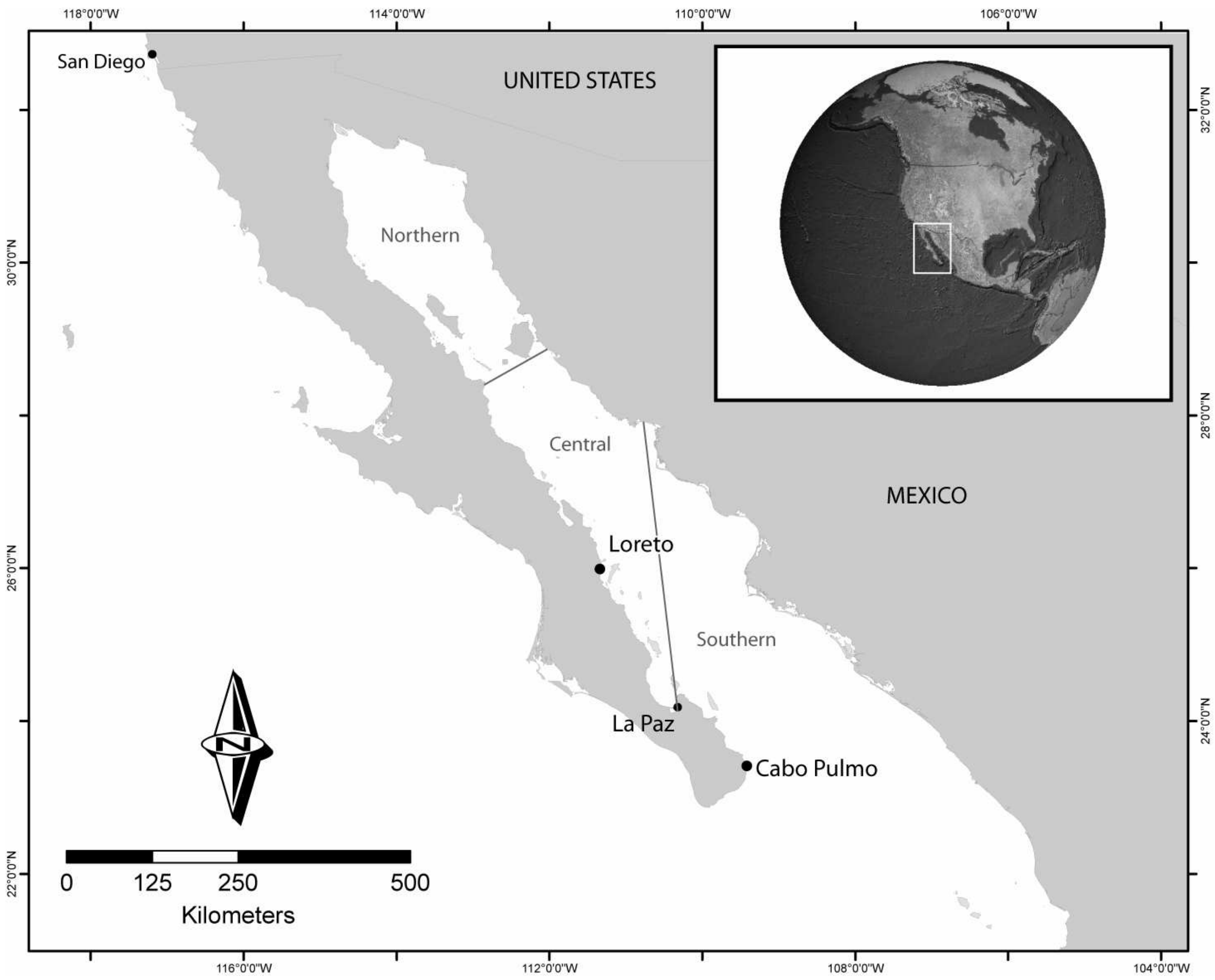

Figure 1. Overview map of the Gulf of California with the three bioregions. Based on Walker (1960) and Thomson et. al (2000).

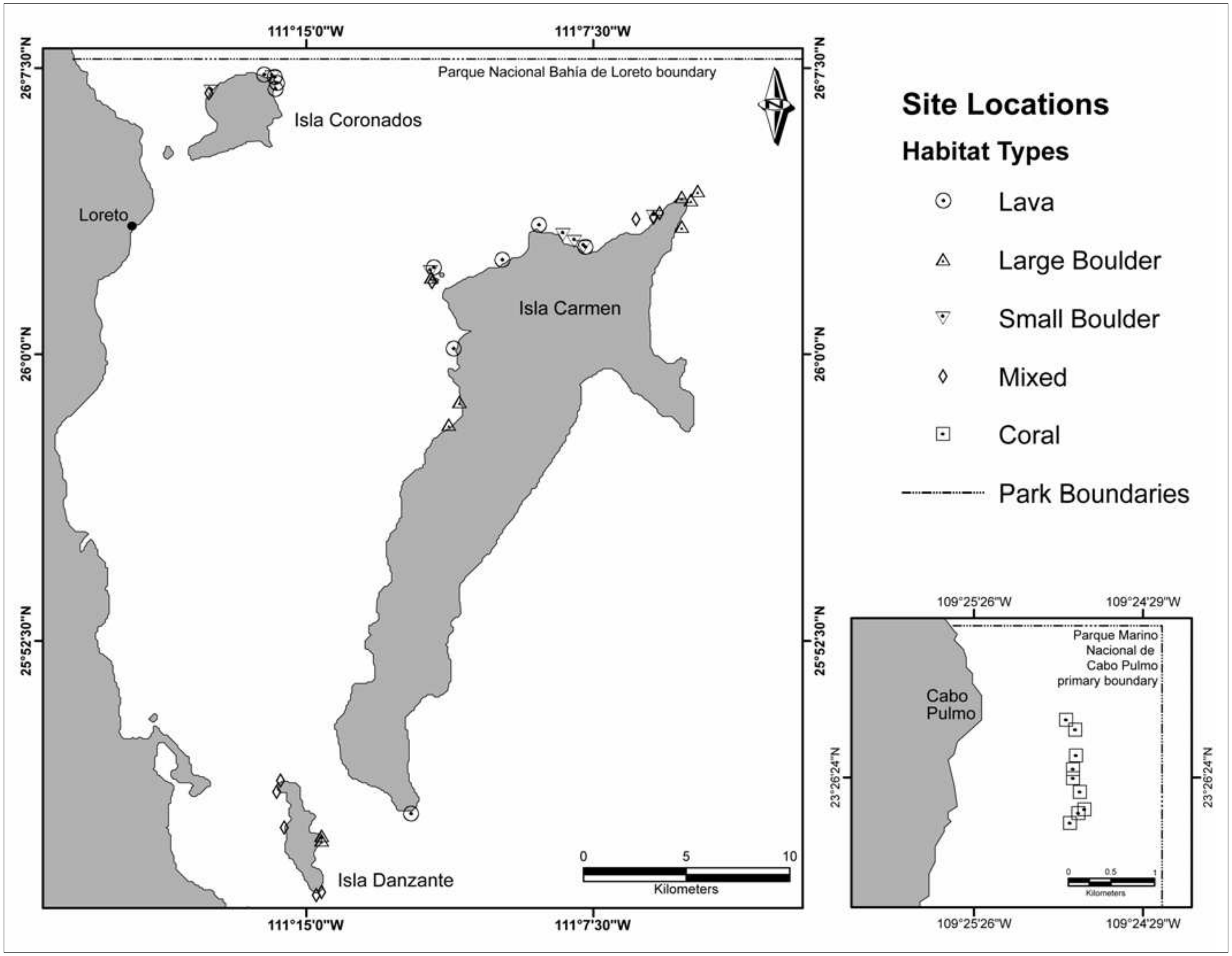

Figure 2. Sampling locations and sites within the Parque Nacional Bahía de Loreto and the Parque Marino Nacional de Cabo Pulmo. Symbols indicate the type of habitat sampled.

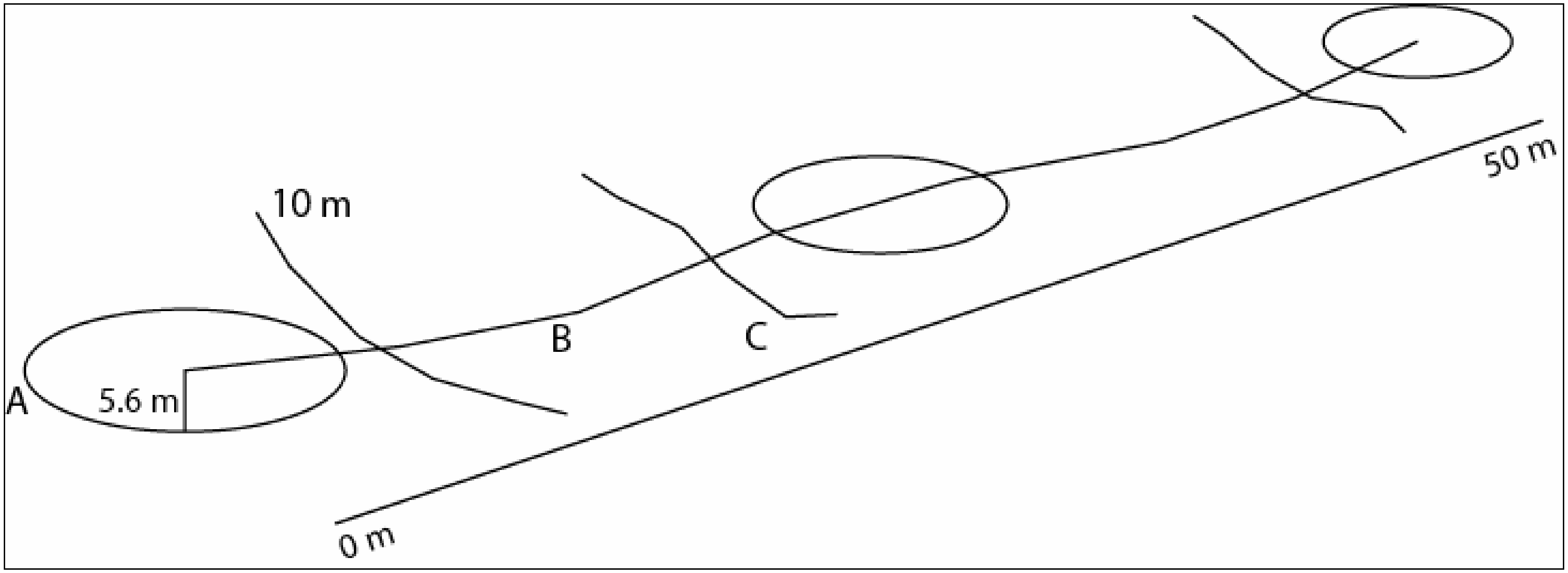

Figure 3. Diagram of sampling method. At 10 meters depth three stationary video surveys (A) were conducted 25 meters apart along a 50 meter transect (B). Immediately following video surveys, habitat variables of rugosity, relief, boulder complexity, and percent cover of encrusting organisms were measured along three randomly chosen 10 meter transects (C) placed across the 50 m transect.

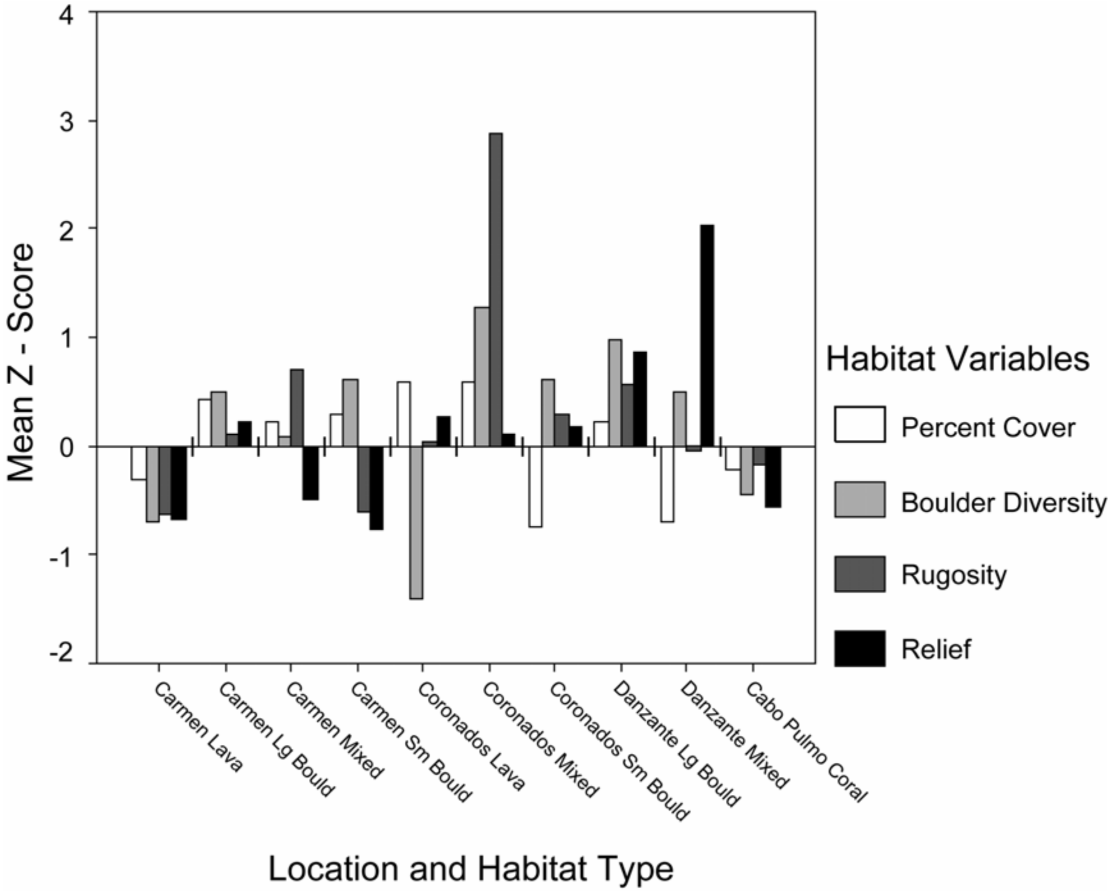

Figure 4. Habitat variables standardized by z-scores for habitats and location.

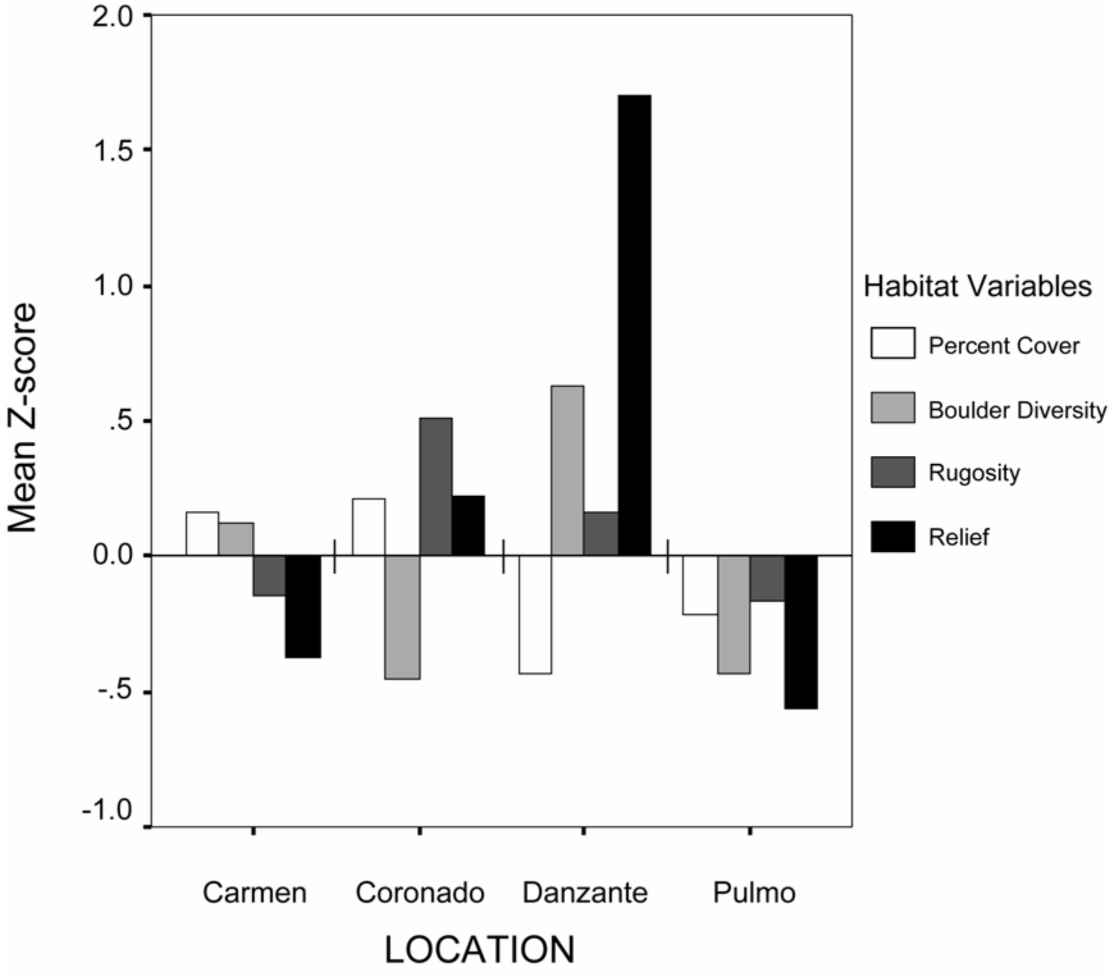

Figure 5. Habitat variables standardized by z-scores for each location.

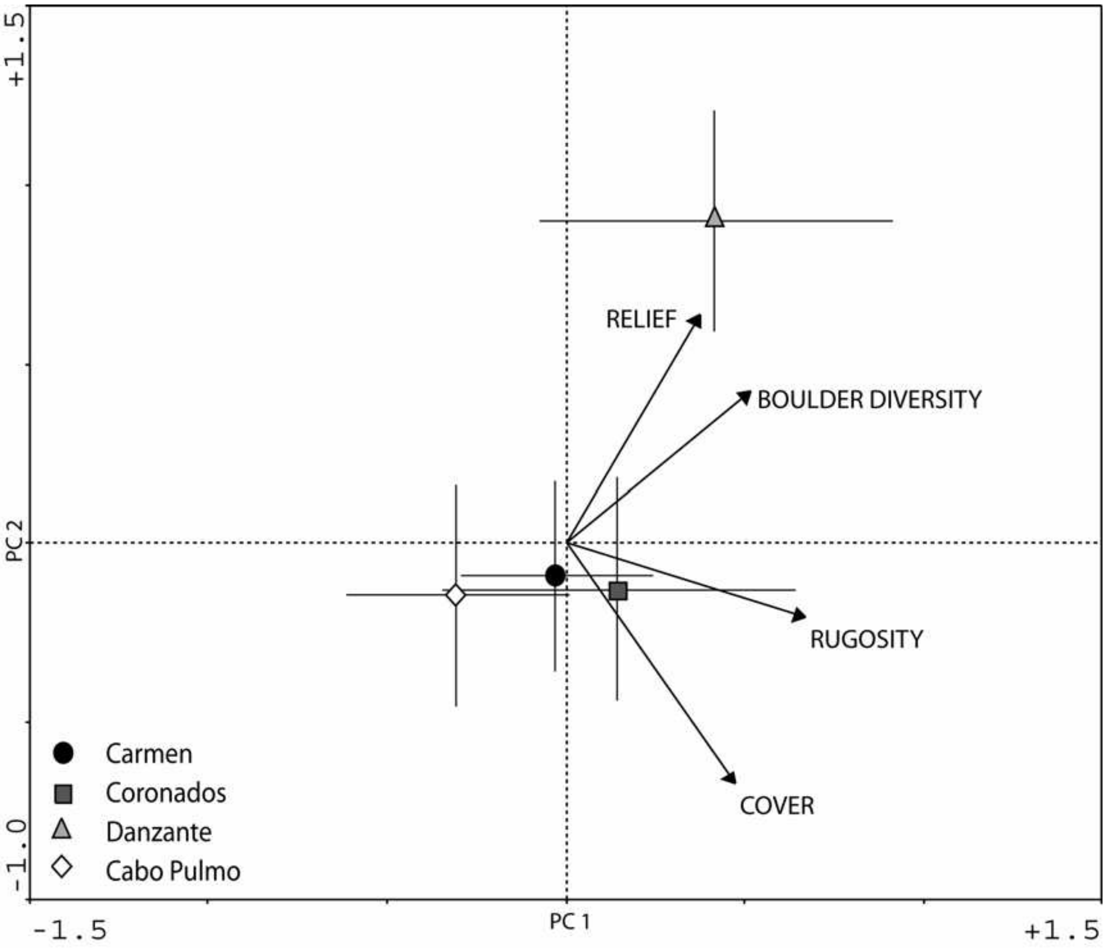

Figure 6. Habitat variables – location biplot. Symbols represent the mean and 95% confidence interval (bars) of site scores at each location.

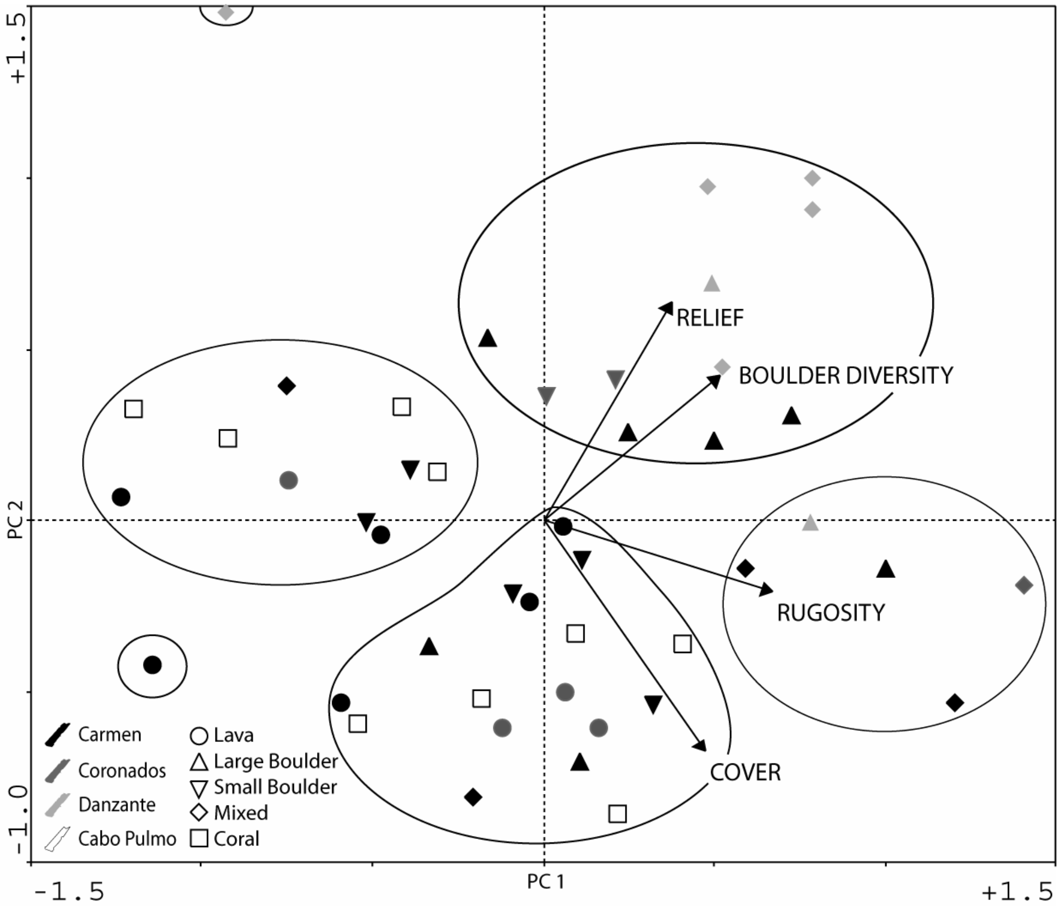

Figure 7. Habitat variable site scores indicating the presence of habitat patches (grouped symbols). Transect scores are represented by symbols; locations differ by color and habitat types differ by shape.

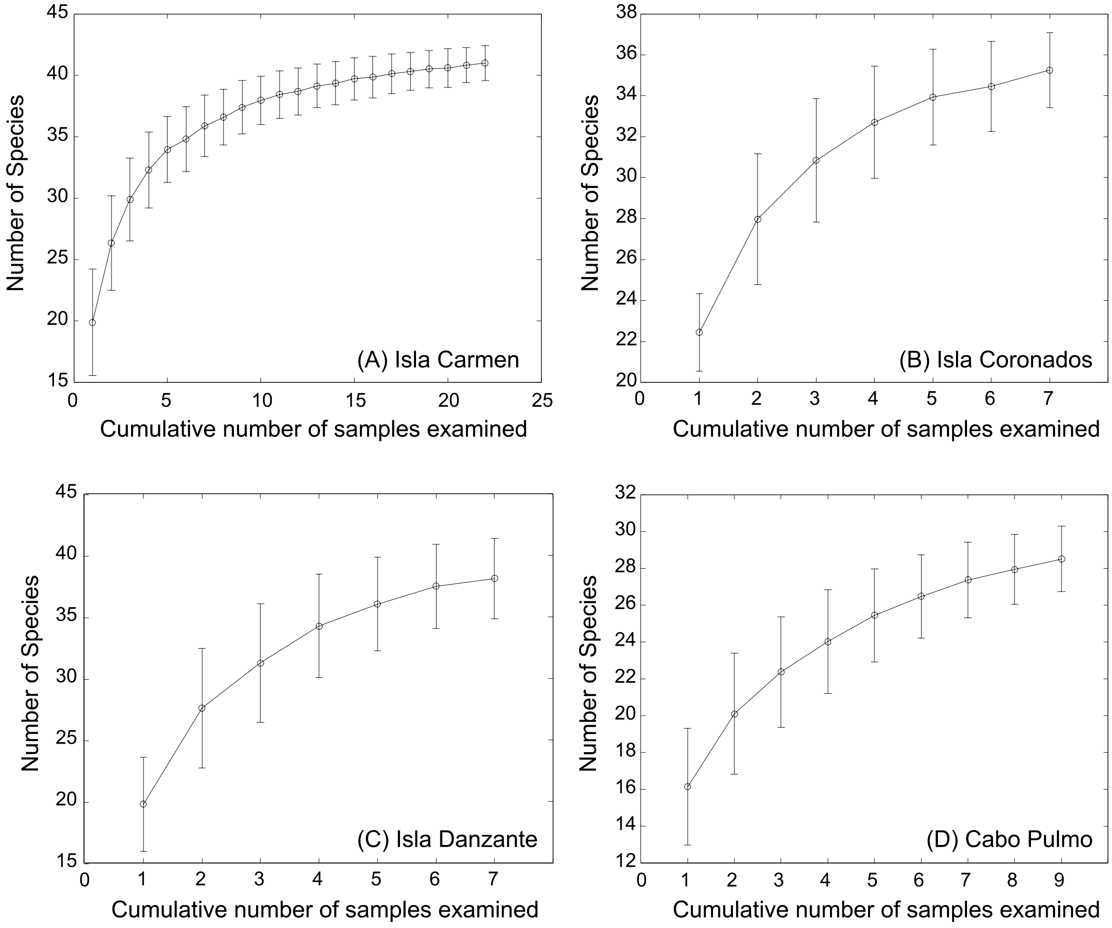

Figure 8. Cumulative species curves for a) Isla Carmen, b) Isla Coronados, c) Isla Danzante, and d) Cabo Pulmo. Note that numbers of species scales are not identical.

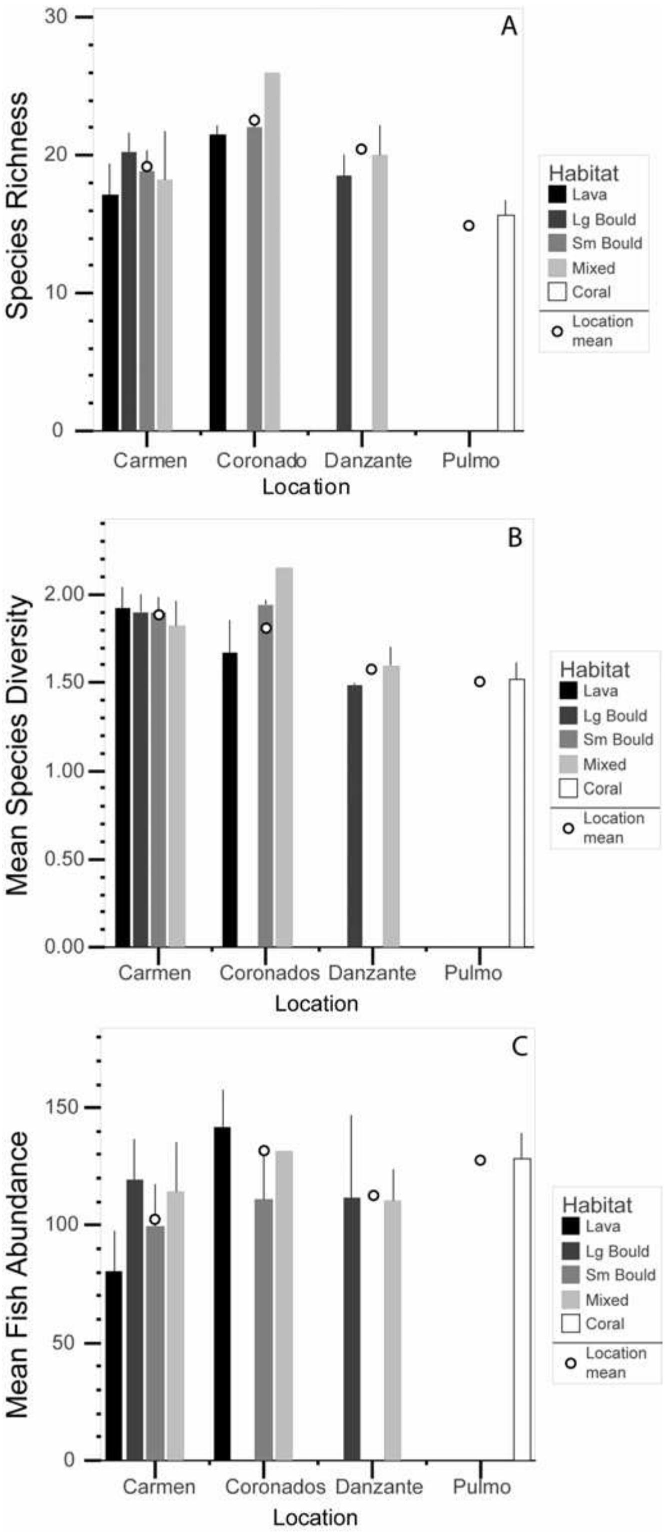

Figure 9. Mean species richness (A), diversity (B), and abundance (C) at each location. Bars are values for each habitat at that location. Means (white dots) were compared. Isla Coronados had greater species richness than Cabo Pulmo (P= 0.011). Species diversity at Isla Carmen was greater than at Isla Danzante (P=0.025) and Cabo Pulmo (P=0.004). There were no differences in fish abundance among locations.

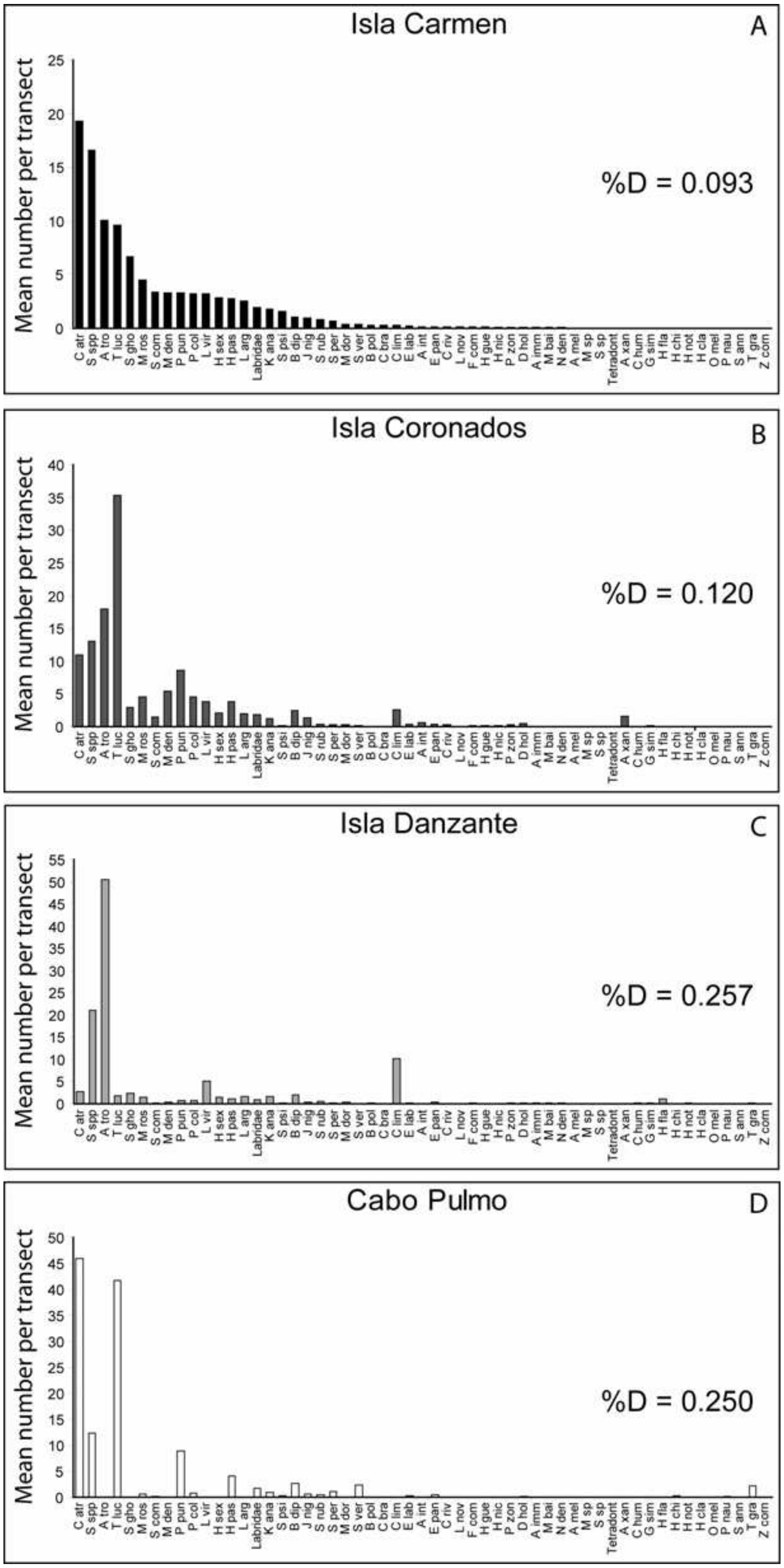

Figure 10. Species abundance histograms for a) Isla Carmen, b) Isla Coronados, c) Isla Danzante, and d) Cabo Pulmo. %D indicates calculated Dominance for that location.

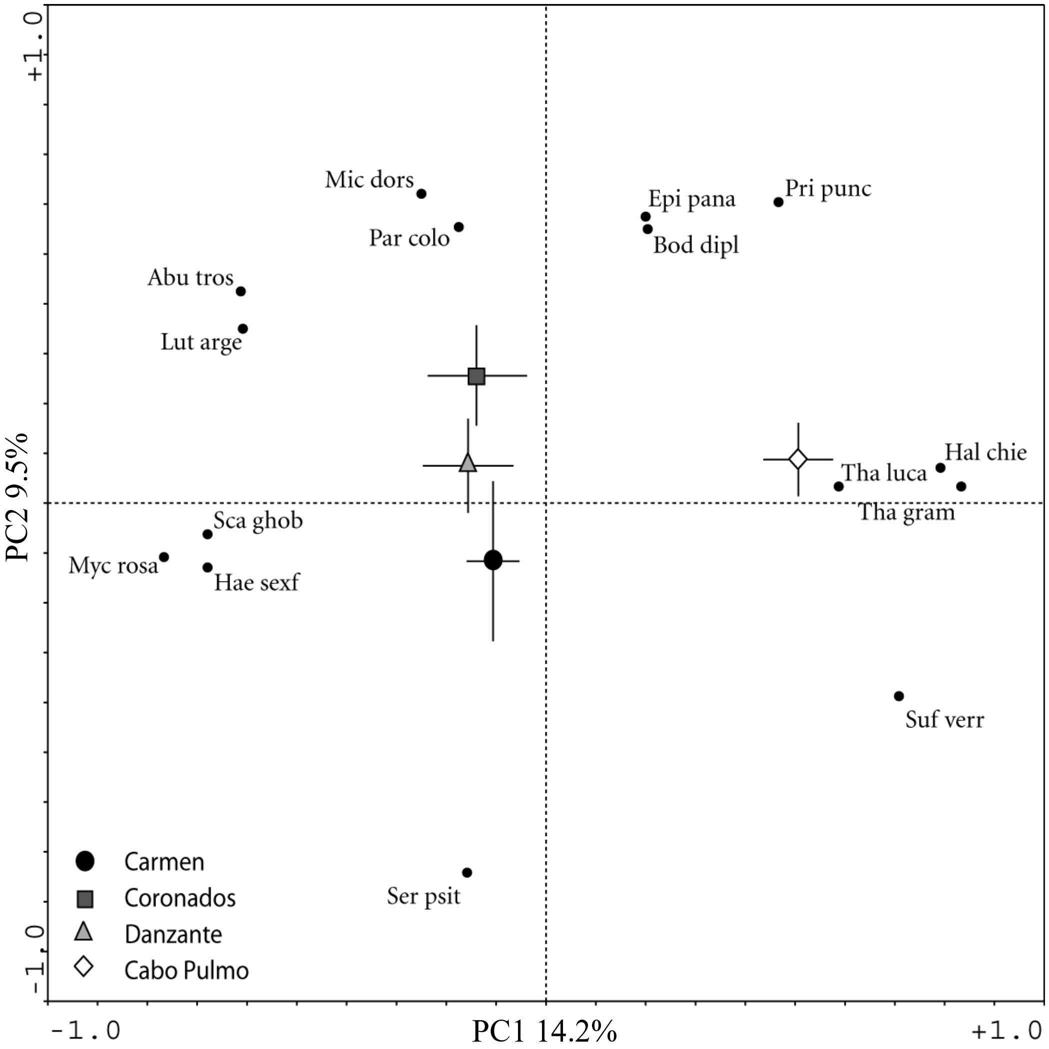

Figure 11. PCA biplot of fish species. Symbols represent the mean and 95% Confidence Interval of transect scores at each location. Axis label indicates amount of variation attributable to the distribution of fishes along that axis. Only those species with sufficiently explained variation (see text) were plotted.

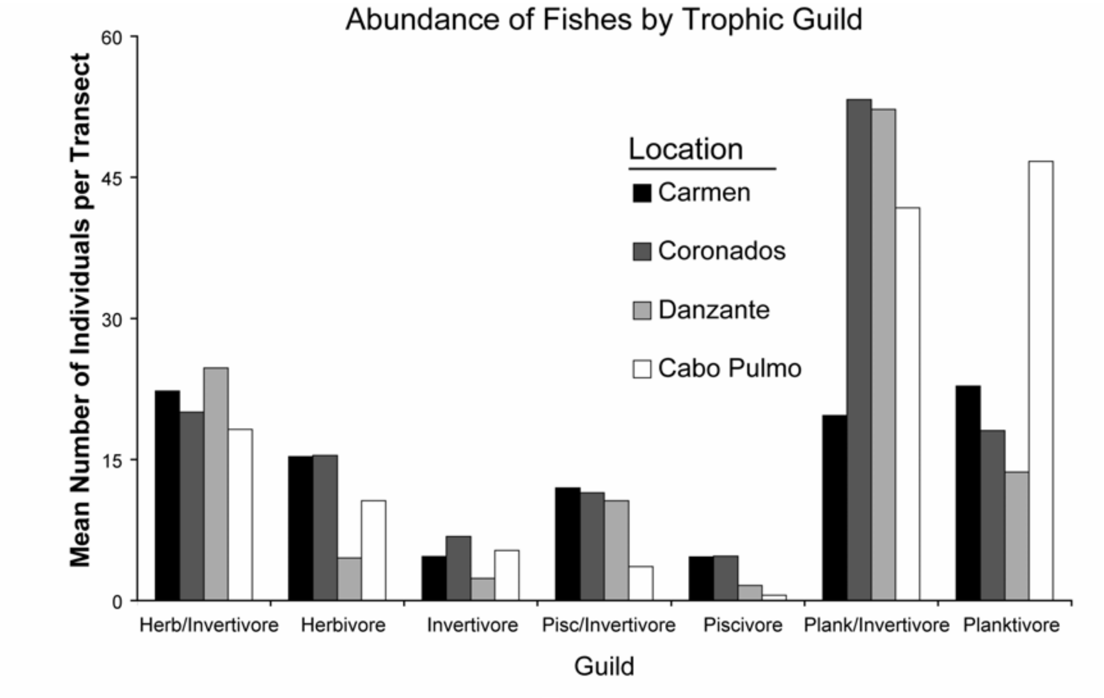

Figure 12. Abundance of fishes by trophic guild. Significant differences were detected among locations in abundance of invertivores (P=0.036), piscivore/invertivores (P=0.005), piscivores (P=0.000), planktivore/invertivores (P=0.002), and planktivores (P=0.013).

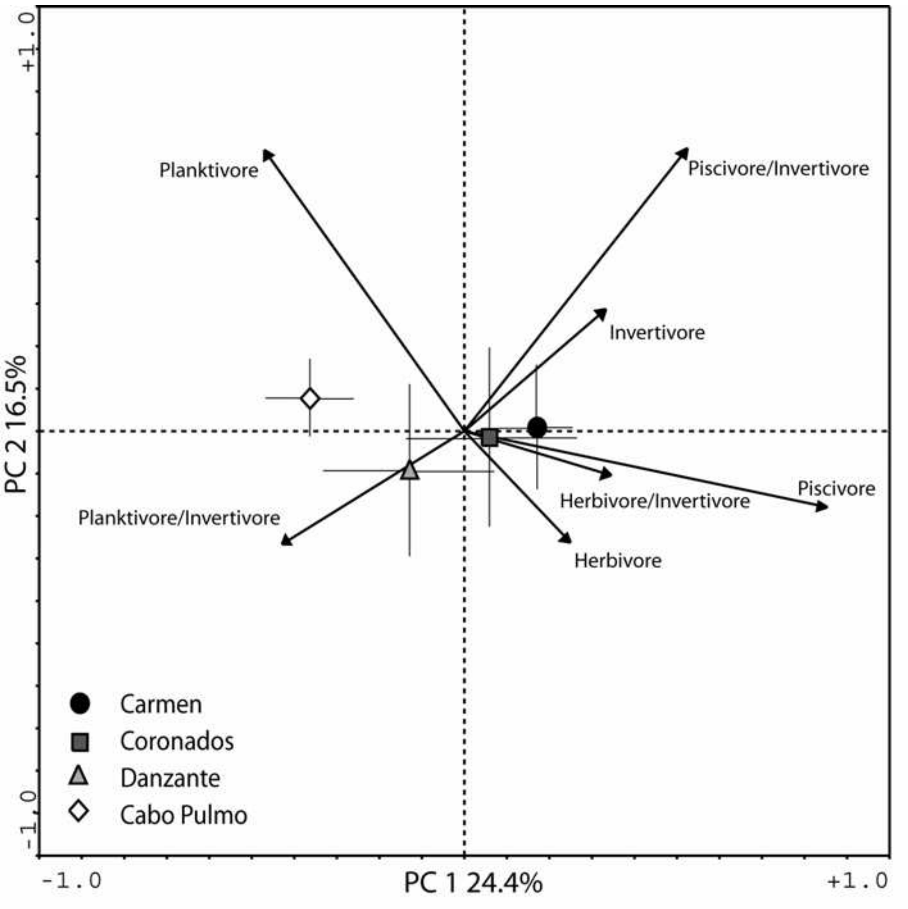

Figure 13. PCA biplot of trophic guilds.

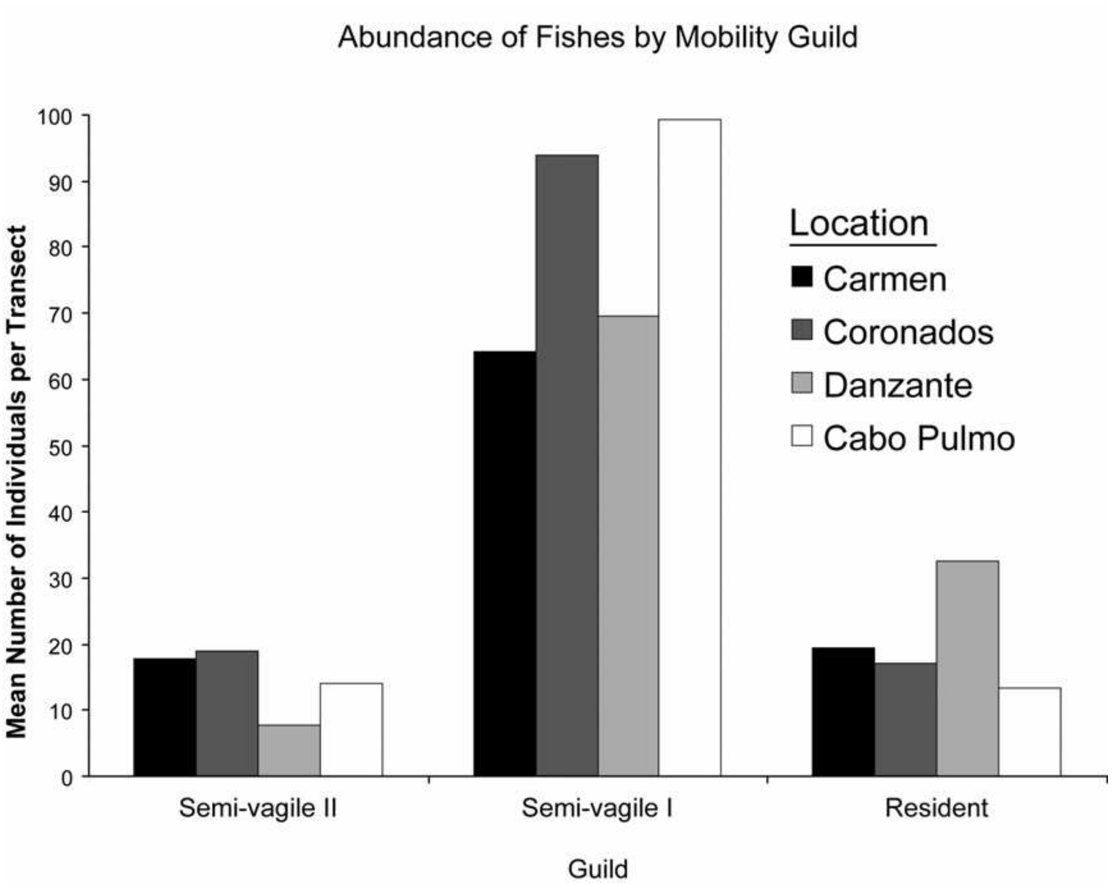

Figure 14. Abundance of fishes by mobility guild among locations. Locations differ significantly in resident fish abundance (P=0.009).

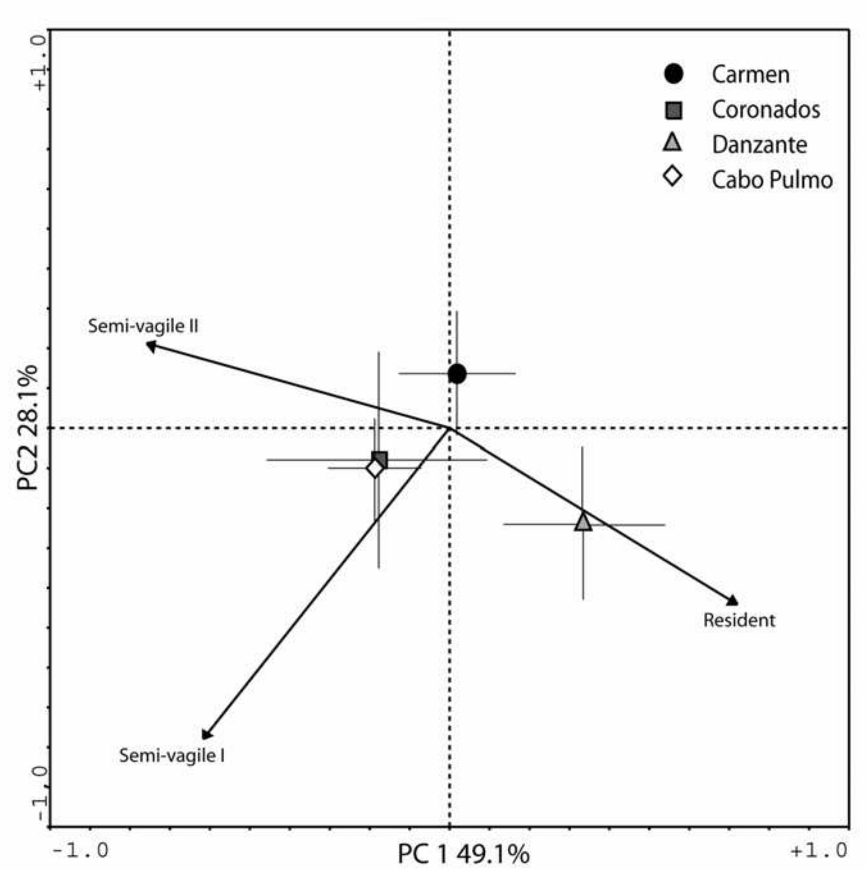

Figure 15. Mobility guilds PCA. Axes explain 77.2% of the variation in mobility guild fishes among locations.

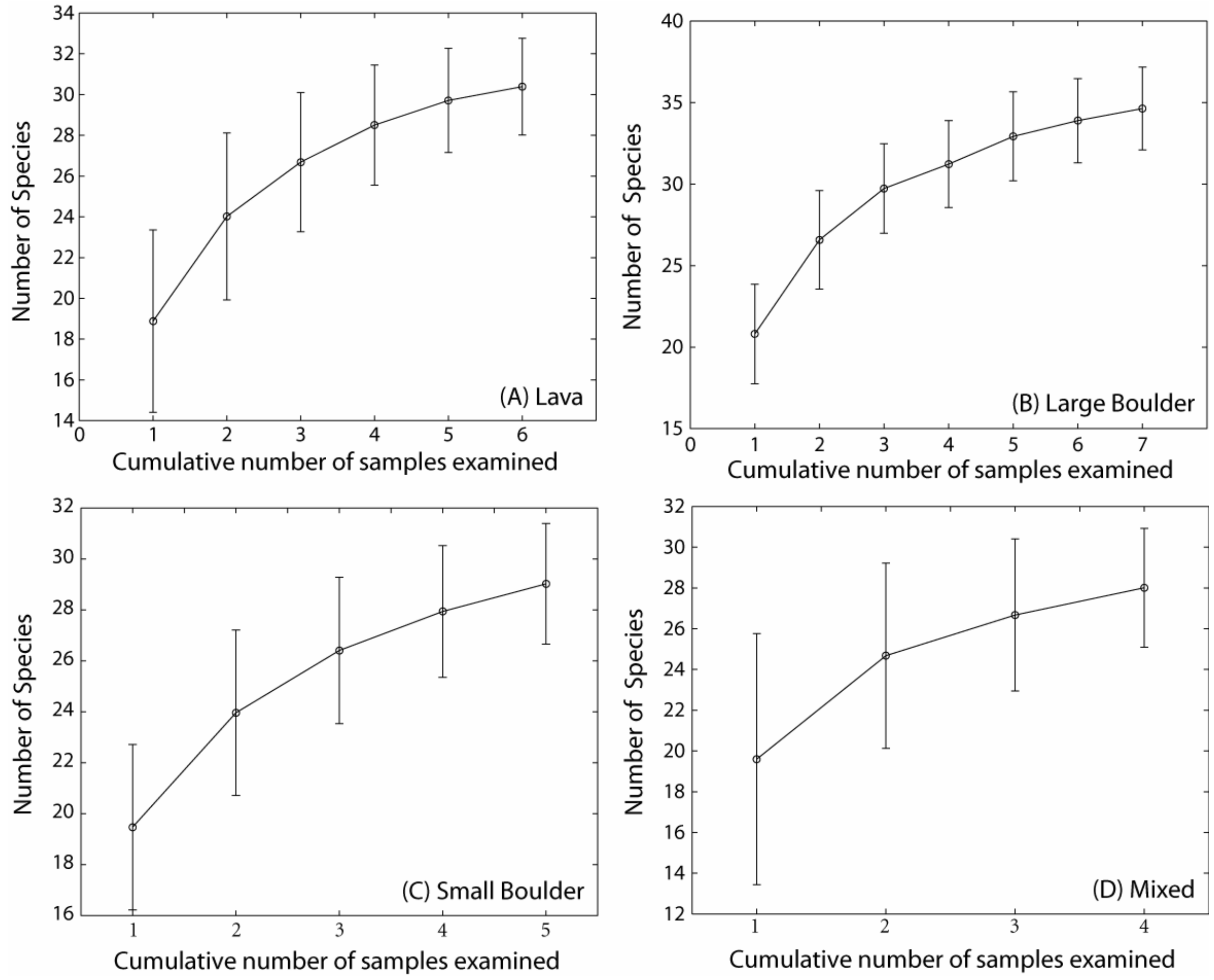

Figure 16. Cumulative species curves for a) lava habitat, b) large boulder, c) small boulder, and d) mixed habitats at Isla Carmen. Note that numbers of species scales are not identical.

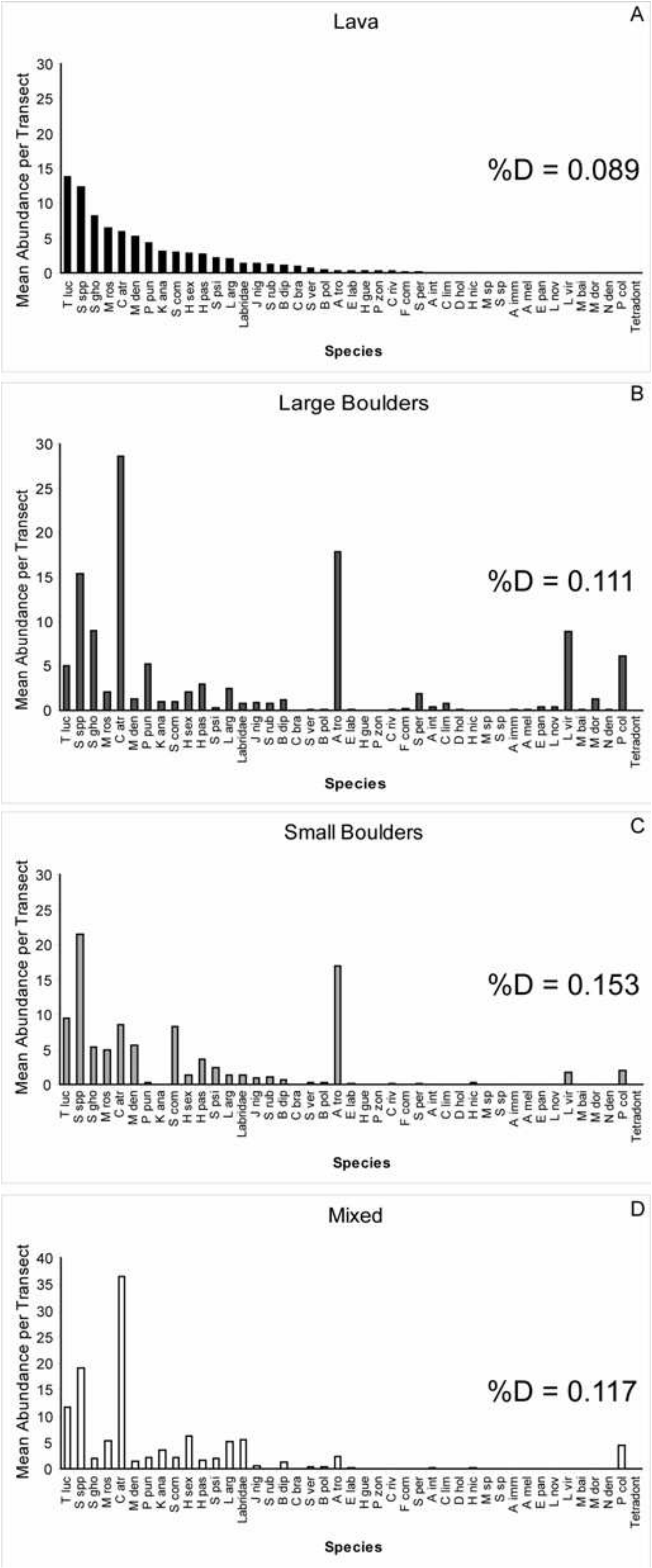

Figure 17. Species abundance histograms and dominance for a) lava habitat, b) large boulder, c) small boulder, and d) mixed habitats at Isla Carmen.

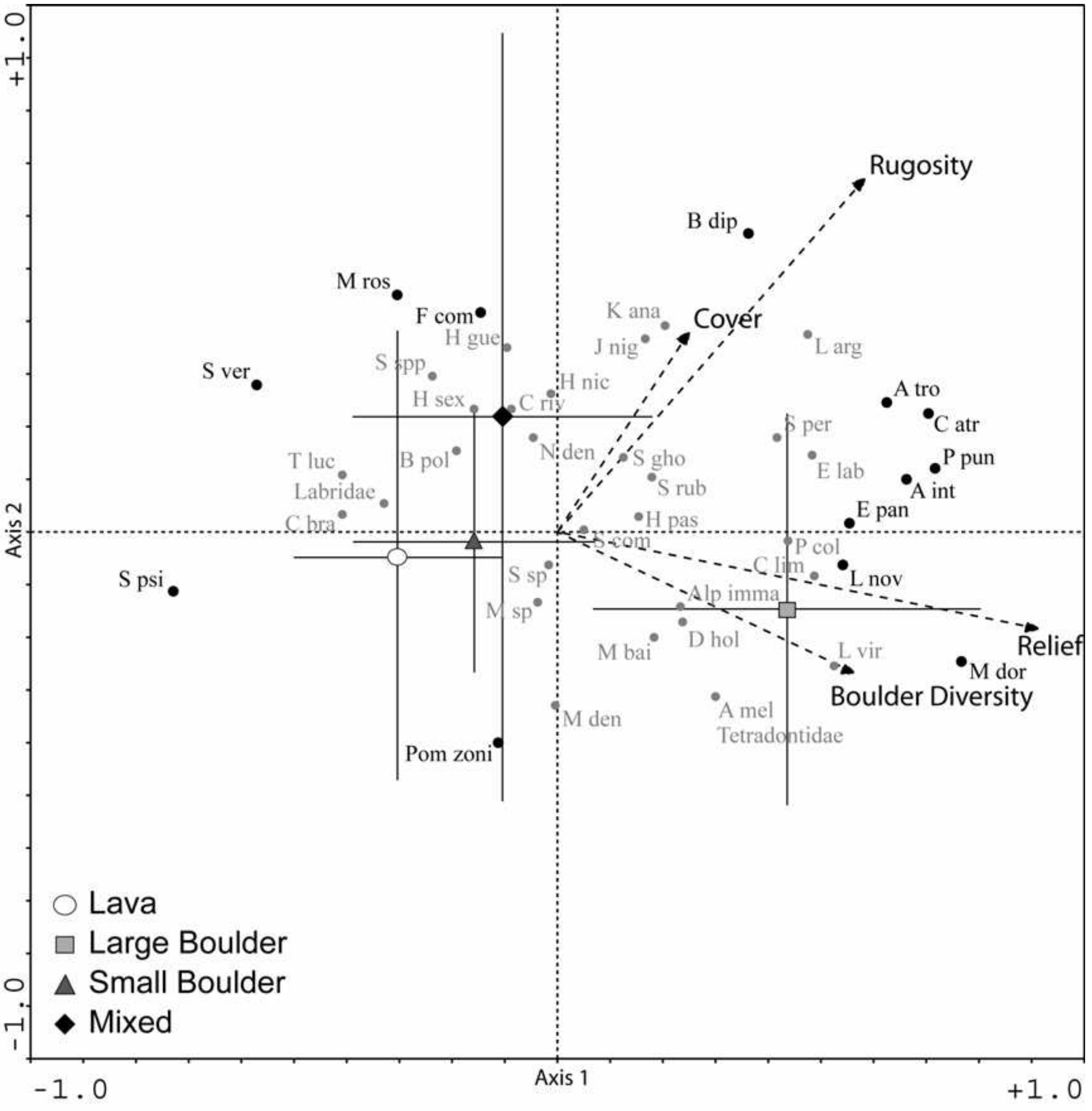

Figure 18. Partial RDA triplot of species and habitats at Isla Carmen. Bold species are those that have sufficient variation explained by the analysis as determined by Mardia's cutoff (see text). Arrows point in the direction of greatest change in the abundance of a given species. The length of the arrow indicates the intensity of that change. The closer the species is to the arrow, the greater the correlation with that variable.

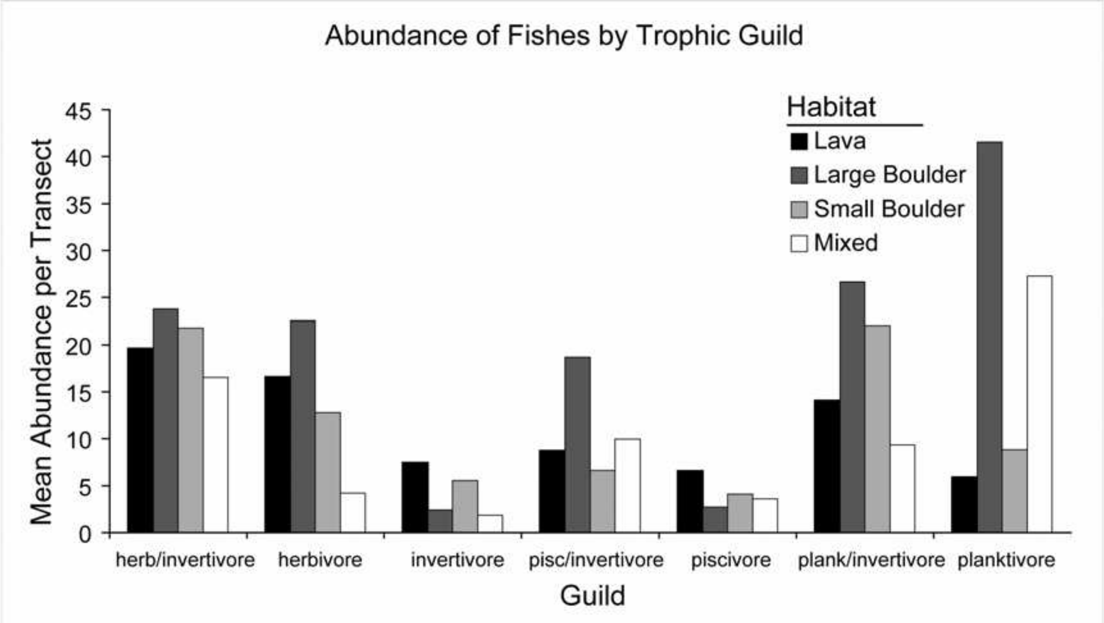

Figure 19. Abundance of fishes by trophic guild for habitats at Isla Carmen. Piscivores and planktivores were significantly different among locations (P = 0.036 and P = 0.044 respectively).

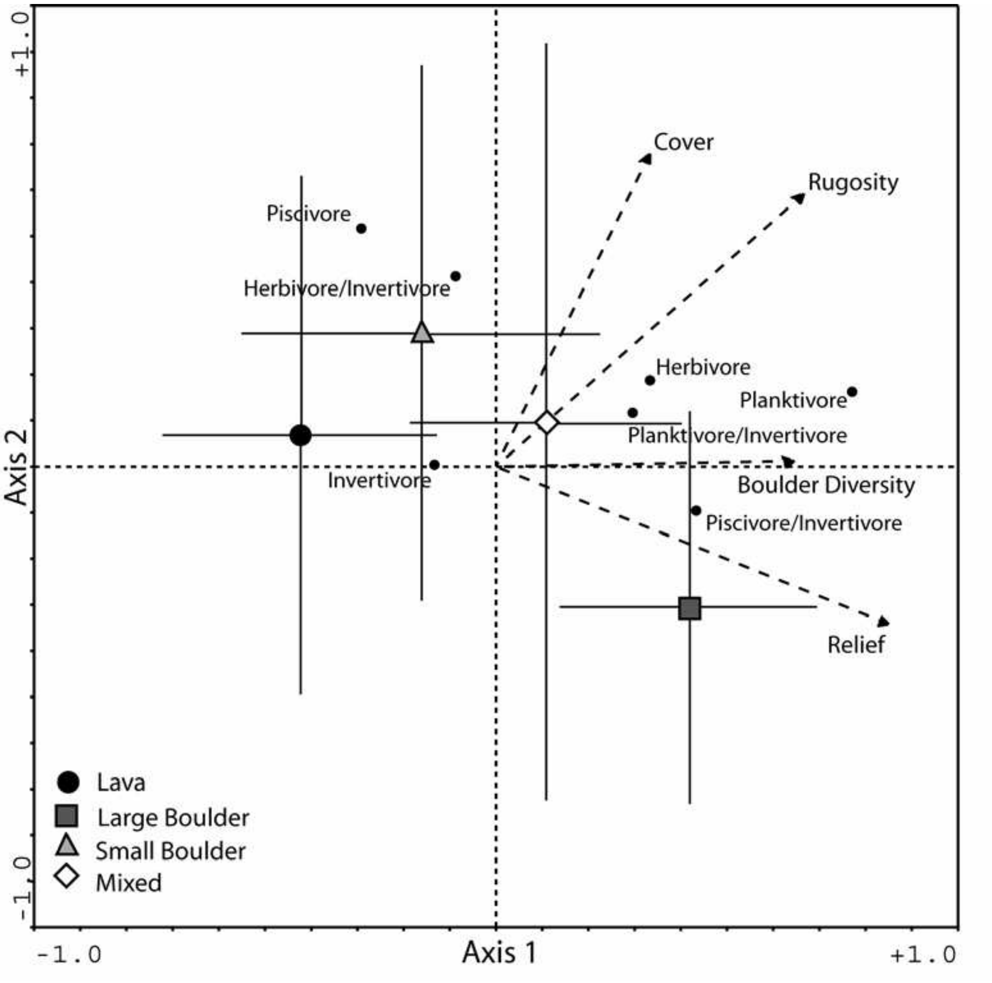

Figure 20. Partial RDA of trophic guilds at Isla Carmen. The first axis, the linear combination of rugosity and boulder diversity, is significant in determining the distribution of guilds (Monte Carlo randomization test P = 0.029).

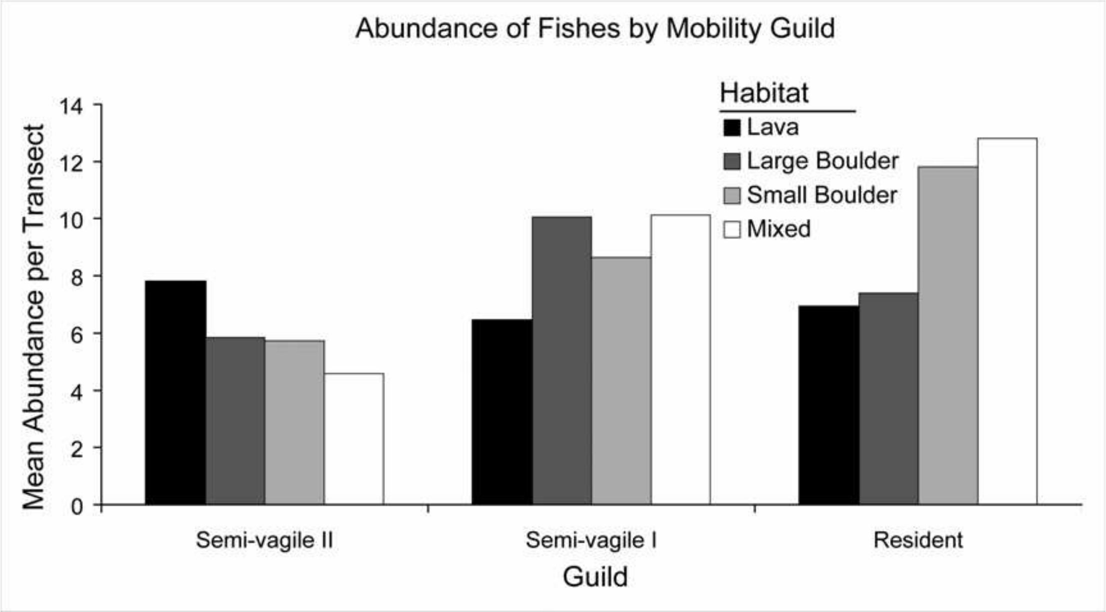

Figure 21. Abundance of fishes by mobility guild for habitats at Isla Carmen. No differences were detected among habitats.

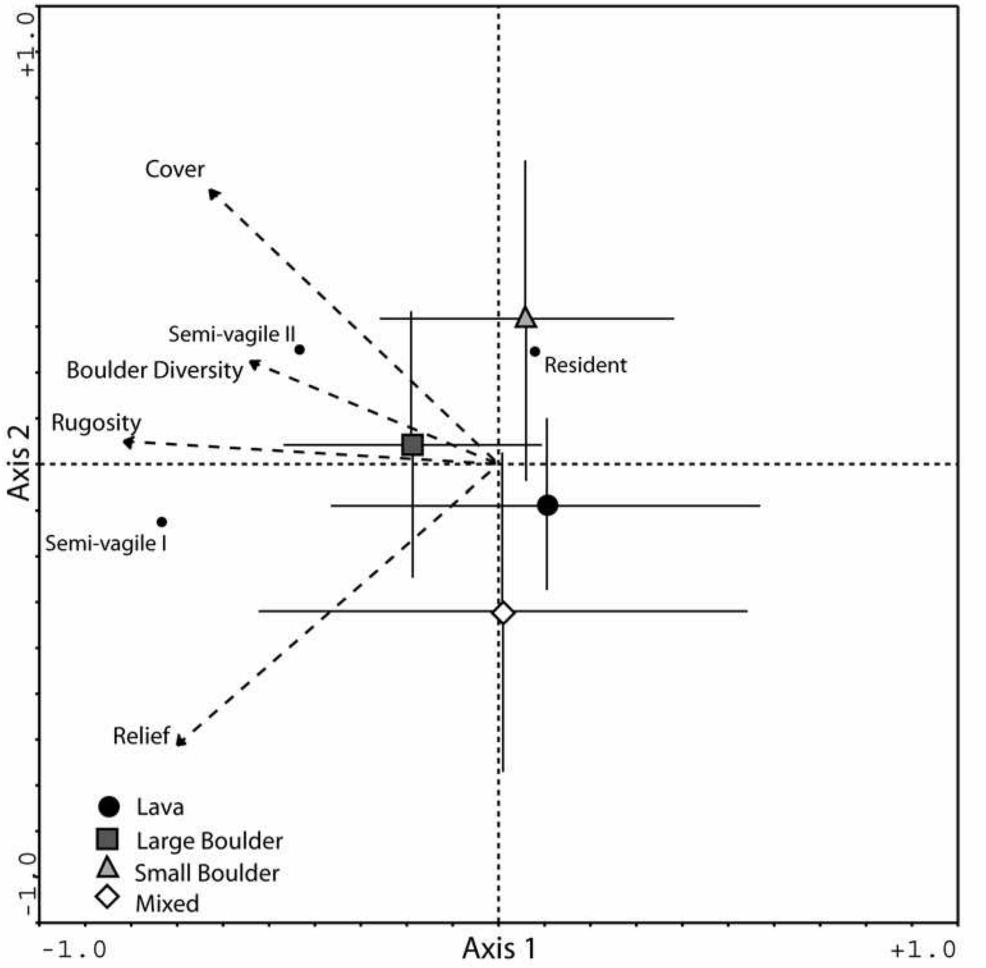

Figure 22. Partial RDA of mobility guilds at Isla Carmen. The first axis, the linear combination of rugosity, boulder diversity, relief, and percent cover, is significant in explaining the distribution of mobility guilds (Monte Carlo randomization tests P = 0.015).