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COMMUNITY STRUCTURE OF EASTERN PACIFIC REEF FISHES (GULF OF PAPAGAYO, COSTA RICA)

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ABSTRACT

We assessed the relative abundance of reef fishes and its relation with physical parameters and habitat at four sites in Culebra Bay, a human disturbed area in Gulf of Papagayo, Costa Rica (eastern Pacific) from March to October 1997. Based on 64 visual counts, we recorded 75 species of 28 families of reef fishes. Four pomacentrids, two labrids and one haemulid comprised the top seven most abundant species, ranked as follows: *Chromis atrilobata, Thalassoma lucasanum, Abudefduf troschelii, Haemulon steindachneri, Halichoeres dispilus, Stegastes acapulcoensis,* and *Stegastes flavilatus.* Densities of many of the species varied significantly with variable site depth. Our results reflect higher Beta diversity than other studies, altough only 22% of the species were found at all the study sites. The type of substrate, the complexity, and the exposure of the reef may have a strong influence on the distribution of many of the species of reef fishes in the Gulf of Papagayo. Four possible groups of fish species were observed suggesting that spatial patterns were stronger than seasonal trends. The shallowest site was characterized by *Ophioblennius steindachneri, Microspathodon bairdii, M. dorsalis and Abudefduf troschelii.* An intermediate site with a more heterogeneous substrate, was composed by *S. acapulcoensis, Canthigaster punctatissima, H. nicholsi, H. chierchiae, T. lucasanum, Sufflamen verres and Serranus psittacinus.* A slightly deeper site than the previous was represented by *H. dispilus, Johnrandallia nigrirostris, Pomacanthus zonipectus, Holacanthus passer, and S. flavilatus.* Finally the deepest site habitat, had a distinctive assemblage composed by *C. atrilobata, Chaetodon* *humeralis, Diodon holocanthus, H. steindachneri, and H. maculicauda.* In terms of trophic groups, our results shows trends have more affinities to temperate regions were planktívores and invertebrates feeders are the most abundant than herbivores.

KEYWORDS

Diversity, spatial variation, trophic groups, upwelling, reef fishes.

RESUMEN

Este trabajo investigó sobre la abundancia de peces de arrecifes de coral y su relación con los parámetros físicos así como su hábitat en cuatro sitios en Culebra Bay, un área afectada por actividad humana en el Golfo de Papagayo, Costa Rica (Este del Pacífico), desde marzo a octubre de 1997. Basado en 64 conteos visuales, nosotros registramos 75 especies distribuidas en 28 familias de peces de arrecifes de coral. Las siete especies más abundantes incluyeron cuatro pomacentridos, dos labridos y un haemulido, los cuales se distribuyeron jerárquicamente de la siguiente manera *Chromis atrilobata, Thalassoma lucasanum, Abudefduf troschelii, Haemulon steindachneri, Halichoeres dispilus, Stegastes acapulcoensis, y Stegastes flavilatus.* Las densidades de distintas especies variaron significativamente de acuerdo a la profundidad. Nuestros resultados reflejan una diversidad Beta bastante alta comparada con otros estudios, aunque solamente el 22% de las especies fueron colectadas con todos los sitios. La distribución de la mayoría de las especies de peces de arrecife de coral fueron afectadas significativamente por el tipo de sustrato, la complejidad y la exposición. El sitio menos profundo se caracteriza por la presencia de *Ophioblennius steindachneri, Microspathodon bairdii, M. dorsalis y Abudefduf troschelii.* Un sitio intermedio (entre aguas profundas y somera) con un sustrato heterogéneo estaba compuesto de: *S. acapulcoensis, Canthigaster punctatissima, H. nicholsi, H. chierchiae, T. lucasanum, Sufflamen verres y Serranus psittacinus.* Un sitio ligeramente profundo que el anterior fue representada por *H. dispilus, Johnrandallia nigrirostris, Pomacanthus zonipectus, Holacanthus passer, y S. flavilatus.* Finalmente el sitio más profundo, tuvo una composición de *C. atrilobata, Chaetodon humeralis, Diodon holocanthus, H. steindachneri, y H. maculicauda.* Desde el punto de vista de los grupos tróficas, nuestros resultados demuestren una tendencia hacia regiones templadas con planctivoros y carnívoras de invertebrados, los cuales fueron los más abundantes comparados con los herbívoros.

PALABRAS CLAVES

Diversidad, variación espacial, grupos tróficos, afloramiento, peces de arrecifes de coral.

INTRODUCTION

The interspecific relationships among fishes and their habitat determine important aspects of population cycles, densities, and dynamics (Choat & Bellwood 1991). In reef fishes, abundance, distribution and trophic structure of the community may be influenced by biotic and abiotic factors such as temperature, depth, habitat complexity, currents, availability of larval recruits, and accessibility of food (Gladfelter et al., 1980, Williams 1991, Sale et al., 1994). The central and eastern Pacific ichthyofauna has more affinity with the western Pacific, with a species richness decline from west to east, the Philippines and Malayan archipelago being considered as centers of distribution (Kay 1980, Springer 1982, Woodland 1983, Thresher 1991). The tropical eastern Pacific (TEP) is one of the most isolated areas in the world oceans, and is exposed to extreme changes in temperature, salinity and nutrients (Cortés 1997). The seasonal upwelling characteristic of the region is a consequence of the trade winds, which are more prevalent in the Gulf of Tehuantepec, Gulf of Papagayo and Gulf of Panamá (Cortés 1997, D`Croz & Robertson 1997). Studies on local coral reef fish communities in the TEP are scare (Guzmán & Robertson 1989, Guzmán & López 1991). There have been some studies of rocky reef fishes from the Gulf of California (e.g Arburto-Oropeza & Balart 2001, Thomsom & Lehner 1976, Molles 1978, Gilligan 1980, Thomsom & Gilligan 1983) as well as in Gorgona Island, off the Pacific coast of Colombia (Zapata & Morales 1997). The main objective of this paper is to present information on the structure of the reef fish community, its relationship to some physical parameters, in the Gulf of Papagayo, Costa Rica in the tropical eastern Pacific. The study aims at a characterization of fish assemblages (including taxonomical component, abundance and species richness) and the composition in terms of fish trophic groups.

MATERIAL AND METHODS

Study site description

This study was conducted in the Gulf of Papagayo (Fig.1), located at 10°45' N and 85° 45' W in the Pacific coast of Costa Rica. Two areas divided into four study sites were located at the entrance of Culebra Bay: Pelonas Islands (10°35' N and 85°43'W) and Viradores Islands (10°36' N and 85°42'W). "Punta Argentina" (P), "Bajo Virador" (V) and "Cabeza de Mono" (C) were considered shallow sites (8-10 m depth) while "Bajo Sorpresa" (S) was the deep station (~20 m).

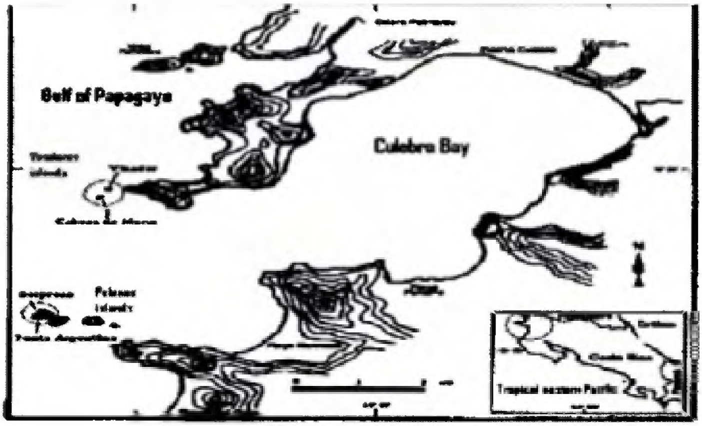

Fig. 1. Study sites in the Gulf of Papagayo, Guanacaste, Costa Rica.

Data collection and analysis

We conducted 64 monthly fish surveys (16 replicates per site with 2 replicates per site/month) between March and October 1997 at four study sites. We recorded the water temperature at the bottom depth, and visibility (horizontal distance of a white acrylic plate). For estimation of substratum we use a sampling unit consisted of a 6-m radius (~ 113 m^2). Substrate types were classified on eight categories after Samoilys & Carlos (1992), and their corresponding percent cover was estimated at 64 sampling units for the site description. For the relative fish density estimation and fish distribution and identification, we used the point count method adapted from Bohnsack & Bannerot (1986), Samoilys & Carlos (1992) and Samoilys (1997). We performed a total of 64 counts (16 counts per site from March to October 1997). Correlation analyses of fish densities with substrate coverage were performed on 64 of the samples. Each count takes an average of 50 minutes between 10:00 to 17:00 hours. The densities were calculated as number of individuals (Juveniles and adults) per square meter ($ind*m^{-2}$). We determined the Shannon-Winner diversity index to compare spatial variation on the different study sites. The non-parametric tests (Kruskal-Wallis) was used to compare, temporal variations of physical conditions (temperature and visibility), and differences in fish diversity and density with a p value of significance of 0.05. An additional Student-Newman-Keuls (SNK) test of multiple-comparisons of means was applied as a post-hoc test (Zar 1996). Relationships among diversity indices, species density and physical parameters were analyzed with Spearman correlations (Sokal & Rohlf 1980, Zar 1996). Fish and habitat relationships were analyzed with a Canonical Correspondance Analysis (CCA) using MVSP 3.1 sofware. (Ter Braak & Verdonschot 1995): We adapted a trophic classification of fish species from Ferreira et al. (2001) and Harmelin-Vivien (2002).

RESULTS

Water temperature varied seasonally on all Culebra Bay (Fig. 2) (Kruskal–Wallis, n= 8, gl=7, H= 53.34, p < 0.001), between a mean of 24°C (February) and 30°C (July). Temperature, however, was not significantly different among study sites. The lowest visibility occurred in February, March and May; higher values were found from July to October. Visibility showed no significant differences among study sites, but it differed significantly through moths (Fig. 2. n=8, df=7, H= 35.79, p<0.001).

Site depths ranged from 8 to 20 m. We classified the substrates into medium size rocks, and rock-sand were the main substrate found at the three shallow sites (Bajo Virador; Cabeza de Mono and Punta Argentina), whit live coral colonies of *Pocillopora* spp. Octocoral colonies of *Carijoa* (27.7 %) and the ahermatypic coral *Tubastrea coccinea* (10.3 %) occurred only at the deep site Bajo Sorpresa.

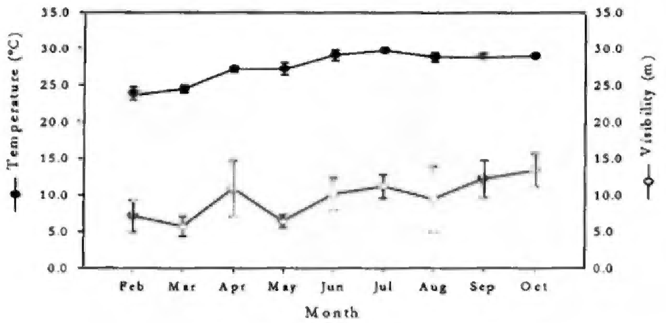

Fig. 2. Variation in temperature and visibility from February to October 1997, Gulf of Papagayo, Guanacaste, Costa Rica.

The Spearman correlation analysis ($p < 0.05$, n= 187) showed a positive correlation between temperature and visibility (Fig. 2. r = 0.55,). The highest fish diversity was found in Cabeza de Mono (H´ = 0.87) followed by Bajo Virador (H´ = 0.80), Bajo Sorpresa (H´ = 0.68) and Punta Argentina (H´ = 0.66), with significant differences among sites (Kruskal-Wallis, n= 64, df=3, H=8.25, $p<0.04$). There was also a low positive correlation between the Shannon-Wiener index and the percent of coverage of rubble (Table 3). Richness ranged from 6.27 (Cabeza de Mono) to 8.1 (Bajo Virador), with no significant differences among sites. Evenness ranks in the same order as the Shannon-Wiener´s diversity index, and also differed significantly among sites (n=64,df=3, H= 8.79, $p<0.03$). There is a positive correlation between evenness and the coverage of medium-sized rocks, substrate that also predominates in Cabeza de Mono (Table 3). The composition of trophic groups seemed to be similar between all sites (Fig. 3) with the majority of fishes being mobile invertebrates feeders and planktivores. All herbivores (roving and territorial) show low percent of occurrence, along with the piscivores and the sessile invertebrate feeders. The carnivores also show a relatively low percent of frequency, however they have the highest number of species.

We found 75 taxa of reef fishes, 70 of which were positively identified to species level, belonging to 28 families (Table 1. cf. Allen & Robertson 1994). In terms of total abundance over all months and sites, four pomacentrids, two labrids and one haemulid comprise the top seven most abundant species their density vary significantly among sites (Table 2). The densities of 6 fish species increased with depth, while other 6 were inversely correlated with this parameter (Table 3). Densities of 11 fish species were positively or negatively correlated to rubble cover, 7 other fishes were positively associated with *Pocillopora* spp., while 11 were with *Carijoa* sp.(Table 3).

In the CCA,the most important habitat variables are represented by arrows and the top 27 most abundant fish species by points in the ordination diagram for the four study sites (Fig. 4.). Both variables account for 65%, 91.7% and 100% for the variance in the weigthed average and the sums of eigenvalues being 0.3, 0.1 and 0.04. The axis 1 clearly represents a depth gradient shallow environments on the left side (P, C and V sites) increasing to the right side closer to axis 2 representing deep reefs (S) (Fig. 4).

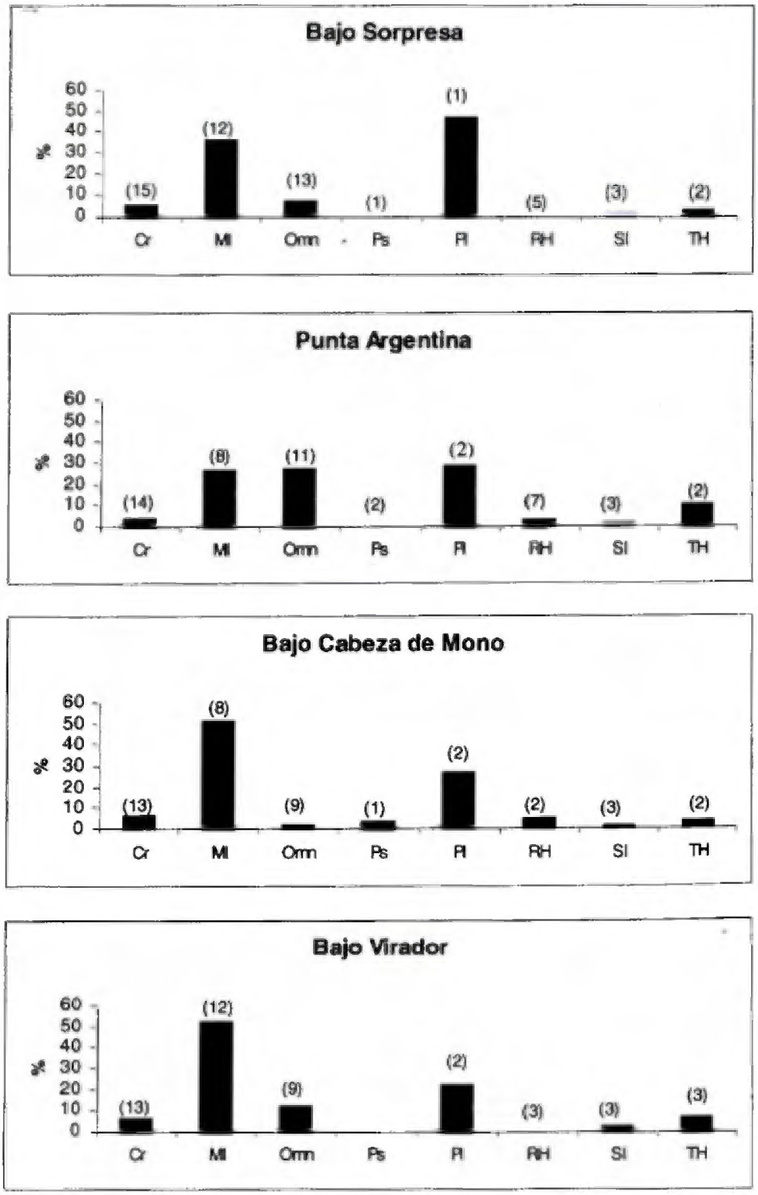

Fig. 3. Percentage of major trophic groups of fishes (from total numbers) within study sites. Number in parenthesis indicate the number of species in each group. Cr=Carnivores, MI=Mobile invertebrate feeders, Omn=omnivores, Ps=Piscivores, Pl=Planktivores, RH=Roving herbivores, SI=Sessile invertebrate feeders, TH=Territorial herbivores.

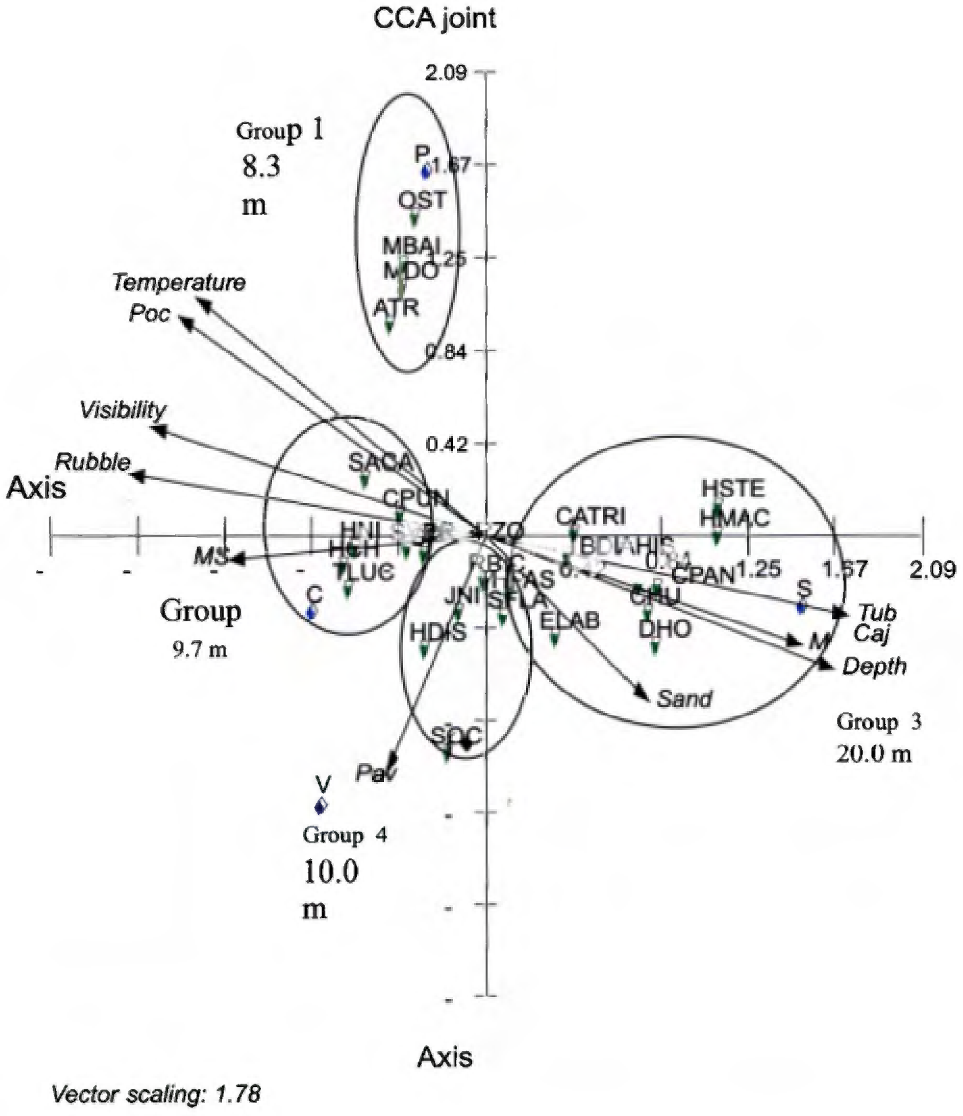

Fig. 4. Canonical correspondance analysis (CCA) of fish abundance vs habitat variables obtained from visual point count census and substrate estimation along the study sites in the Gulf of Papagayo, Guanacaste, Costa Rica. (♦ Sites: C: Cabeza de Mono., P: Punta Argentina.,S: Bajo Sorpresa., V: Bajo Virador ;▼ spp, Fish codes in text, Substrate codes: *Caj: Carijoa* sp *MR: Massive rocks.,MSR*: Medium size rocks., *Pav*: *Pavona* spp.,*Poc*: *Pocillopora* spp.,*Tub*: *Tubastrea coccinea*.)

Table 1. List of eastern Pacific fish species found in Culebra Bay, Gulf of Papagayo,Costa Rica in 1997 and reported by Allen & Robertson (1994). Trophic groups: Cr = Carnivore, MI = Mobile invertebrate feeder Omn=Omnivorous Ps = Piscivorous, Pl = Planktivorous, RH = Roving herbivore, SI= Sessile invertebrates, TH=Territorial herbivore. Study sites: P = Punta Argentina; S = Bajo Sorpresa; C = Bajo Cabeza de Mono; V = Bajo Virador. Sampling months (March to October 1997): Mar= March, A= April, Ma= May, J= June, Ju= July, Au= August, S= September, O= October. D = Average density (ind m^{-2}) SD = standard deviation. + = Important for the ornamental fish trade in Costa Rica (Fournier & Vitola 1994). ** $x < 0.01$ ind m^{-2}

Family/Genus	Trophic level	Study site	Months	D ± SD
Ginglymostomatidae				
Ginglymostoma cirratum	Cr	P	Ju	**
Myliobatidae				
Aeeobatus narinari	MI	S	S	**
Muraenidae				
Gymnothorax castaneus	Cr	C	M	**
+*Gymnomuraena zebra*	Cr	C	Ju	**
+*Muraena lentiginosa*	Cr	S, V, C	M, A, Ma	**
Holocentridae				
Myripristis sp.	Pl	C, P	Ma, O	**
Sergocentron suborbitalis	Cr	All	A, Ma, J, Ju, Au, S,O	0.01±0.04
Fistularidae				
Fistularia commersonii	Cr	C, P	M, J, O	**
Serranidae				
Alphestes inmacualtus	Cr	P	Au, O	**
Epinephelus acanthistius	Cr	V	Ma, O	**
Epinephelus labriformis	Cr	All	All	**
Cephalopholis panamensis	Cr	All	All	0.01±0.04
Paranthias colonus	Pl	V	M	**
+ *Serranus psittacinus*	Cr	All	All	0.01±0.02
Grammistidae				
Rypticus bicolor	Cr	S, C, P	Ma, J, Ju, Au, O	**
Malacanthidae				
Malacanthus brevirostris	Cr	V	O	**
Carangidae				
Caranx spp.	Ps	C	M, O	0.02±0.11
Seriola rivoliana	Ps	P, S	A, Ma, Au	**
Lutjanidae				
Lutjanus argentiventris	Cr	V, S	J, O	**
Haemulidae				
+*Anisostremus taeniatus*	MI	S	Ju, S, O	**

Haemulon sp.1	MI	S	J, O	0.07±0.55
Haemulon flaviguttatum	MI	S	J, S, O	**
Haemulon maculicauda	MI	C, S, P	M, A, J, S, O	0.07±0.27
Haemulon scudderi	MI	S	M	**
Haemulon steindachneri	MI	S,V, P	M, Ma, Au, O,S	0.12±0.58
Haemulon sexfasciatum	MI	S	A	**
Sciaenidae				
Odontoscion xanthops	Cr	S	S	**
+*Pareques viola*	Cr	S	M, Au	**
Kyphosidae				
Kyphosus analogus	Omn	P	J, S, O	**
Kyphosus elegans	Omn	S	A, J	**
Sectator ocyurus	Omn	S, V	M, A, M, J, Ju	**
Ephippididae				
Ephippididae sp. 1	Omn	S	O	**
Chaetodipterus zonatus	Omn	S	M	0.01±0.08
Chaetodontidae				
Chaetodon humeralis	SI	All	All	0.01±0.01
Johnrandallia nigrirostris	SI	All	All	0.01±0.03
Pomacanthidae				
+*Holacanthus passer*	Omn	All	All	0.01±0.01
+*Pomacanthus zonipectus*	Omn	All	All	0.01±0.01
Pomacentridae				
+*Abudefduf troschelii*	Omn	C, P, V	All	0.14±0.52
+*Chromis atrilobata*	Pl	All	All	0.68±1.21
+*Microspathodon dorsalis*	TH	P, V, C	M, J, Ju, Au, S,O	0.02±0.7
+*Microspathodon bairdii*	TH	P, C	A, Ma, J	**
+*Stegastes acapulcoensis*	TH	All	All	0.07±0.09
+*Stegastes flavilatus*	TH	All	All	0.05±0.05
Cirrhitidae				
+*Cirrhitus rivulatus*	Cr	V, C, P	Ma, Ju, Au, O	**
+*Cirrhitichthys oxycephalus*	Cr	P	J	**
Labridae				
+*Bodianus diplotaenia*	MI	All	All	0.03±0.03
+*Halichoeres chierchiae*	MI	V, C, P	All	0.01±0.01
+*Halichoeres dispilus*	MI	All	All	0.08±0.15
Halichoeres melanotis	MI	V, C, P	All	**
Halichoeres nicholsi	MI	All	A, Ma, J, Ju, Au, S,O	0.03±0.05
Halichoeres notospilus	MI	C, V	M, Au	**
Novaculichthys taeniourus	MI	V, C, P	M, Au	**
+*Thalassoma lucasanum*	MI	All	All	0.43±0.66
Xyrichtys victori	MI	V	O	**
Scaridae				
Nicholsina denticulata	RH	P	Ma, J	**
Scarus sp. 1	RH	V, P	J, S	**

Scarus compressus	RH	C, P	Ju, O	**
Scarus ghobban	RH	P, S, C	Ma, J, Ju,O	**
Scarus perrico	RH	S	Au, O	**
Scarus rubroviolaceus	RH	S	S	**
Blennidae				
+*Ophioblennius steindachneri*	TH	P, C	M, A, Ma,J, O	**
Plagiotremus azaleus	Ps	P	M, A, Ma,J,O	**
Acanthuridae				
Prionurus laticlavius	RH	P, C	A, O	0.03±0.22
Scombridae				
Scomberomorus sierra	Ps	P	O	**
Balistidae				
Balistes polylepis	Omn	P, C	A, J	**
Melichthys niger	Omn	P	A, J	**
Pseudobalistes naufragium	Omn	All	M, A, J, Ju	**
Sufflamen verres	SI	All	All	0.01±0.01
Monacanthidae				
Aluterus scriptus	Omn	S	A, S	**
Ostraciidae				
Ostracion meleagris	Omn	V, S, C	J, A, O	**
Tetraodontidae				
Arothron hispidus	Omn	All	All	**
+*Arothron meleagris*	Omn	S, P	A, Ju, Au, O	**
+*Canthigaster punctatissima*	Omn	All	All	0.01±0.01
Diodontidae				
+*Diodon holocanthus*	MI	All	All	**
Diodon hystrix	MI	P, V, S	Ma, S,O	**

Table 2. Densities averages individuals (±SD) (ind m^{-2}) of the most common species found in Culebra Bay, Pacific coast, Costa Rica, in each reef community. Kruskal Wallis: n= 64, df=3 p=0.05. Code: ns = Not significant differences between sites were it was present. A = Species that appear in all the study months; B = Species that appear between 5 to 7 months. ** $x < 0.01$ ind m^{-2}

Species	p value	H value	Bajo Sorpresa	Punta Argentina	Cabeza de Mono	Bajo Virador
C. atrilobata	ns	ns	1.24 ± 1.65	0.56 ± 1.08	0.52 ± 1.12	0.40 ± 0.70
T. lucasanum	0.01	11.31	0.15 ± 0.23	0.28 ± 0.31	0.88 ± 1.05	0.43 ± 0.51
A. troschelii	0.001	17.44	0	0.38 ± 1.01	0.15 ± 0.20	0.02 ± 0.04
H. dispilus	0.01	10.90	0.06 ± 1.14	0.04 ± 0.05	0.05 ± 1.11	0.17 ± 0.23
S. acapulcoensis	0.00	21.12	**	0.11 ± 0.13	0.09 ± 0.09	0.06 ± 0.08
S. flavilatus	0.037	8.47	0.07 ± 0.06	0.02 ± 0.02	0.05 ± 0.03	0.05 ± 0.07
B. diplotaenia	0.04	7.99	0.06 ± 0.05	0.02 ± 0.02	0.02 ± 0.02	0.02 ± 0.02
H. passer	0.00	23.84	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.02
C. panamensis	0.00	18.78	0.04 ± 0.09	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
S. verres	0.05	12.97	**	0.02 ± 0.1	0.01 ± 0.01	0.02 ± 0.01
P. zonipectus	0.002	14.43	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
S. psittacinus	ns	ns	**	0.01 ± 0.02	0.01 ± 0.02	0.02 ± 0.04
J. nigrirostris	0.036	8.56	0.01 ± 0.01	**	0.01 ± 0.05	0.01 ± 0.03
H. chierchiae	0.012	17.89	0	0.01 ± 0.01	0.02 ± 0.02	0.01 ± 0.01
C. punctatissima	ns	ns	**	0.01 ± 0.01	0.01 ± 0.01	**
C. humeralis	0.00	21.67	0.02 ± 0.02	**	**	**
E. labriformis	0.05	12.65	0.01 ± 0.01	**	**	**
D. holocanthus	0.00	18.03	**	**	**	**
A. hispidus	0.001	15.81	**	**	**	**
H. steindachneri	ns	ns	0.15 ± 0.31	0.04 ± 0.18	0	0.28 ± 1.10
S. suborbitalis	ns	ns	0.02 ± 0.06	**	0.01 ± 0.01	0.02 ± 0.4
S. ocyurus	0.04	7.91	0.01 ± 0.04	0	0	0.02 ± 0.05
F. commersonii	ns	ns	**	**	**	**
O. steindachneri	0.01	10.7	0	0.01 ± 0.02	**	0
R. bicolor	ns	ns	**	**	**	0
C. rivulatus	ns	ns	0	**	**	**
M. lentiginosa	ns	ns	0	**	0	0

Table 3. Correlations between species and type of substrate, physical parameters and live coral coverage (p = 0.05, n = 64, value of r> 0.24). Notation: Dp = Depth (m); MR = Massive rock; MSR = Medium size rocks; Rubb= Rubble; Poc = *Pocillopora* spp.; Pav = *Pavona* spp.; Caj = *Carijoa* sp.; Tub = *Tubastrea coccinea* . Numbers in bolds are significant correlations.

	Dp	MR	MSR	Rubb	Sand	Poc	Pav	Caj	Tub
Diversity index (H')	-0.07	-0.19	0.19	**0.24**	0.02	-0.01	0.11	-0.23	-0.13
Species richness	-0.05	-0.14	0.17	0.17	0.03	0.04	0.20	-0.21	-0.09
Evenness	-0.02	-0.18	**0.24**	0.18	0.00	-0.06	0.07	-0.17	-0.09
S. suborbitalis	-0.01	0.05	0.18	-0.11	-0.08	0.15	0.01	-0.03	0.07
E. labriformis	**0.48**	0.12	-0.09	**-0.33**	-0.06	**-0.31**	0.07	**0.43**	**0.49**
E. panamensis	**0.56**	0.10	**0.28**	**-0.44**	-0.00	**-0.31**	0.01	**0.48**	**0.32**
S. psittacinus	0.12	-0.16	**-0.33**	**0.45**	0.18	-0.11	0.07	-0.06	-0.17
R. bicolor	0.11	-0.00	0.20	-0.14	-0.14	-0.12	-0.07	0.15	**0.25**
H. maculicauda	0.16	0.12	0.03	-0.23	-0.09	**-0.25**	-0.07	**0.32**	**0.27**
H. scudderi	-0.21	-0.16	-0.07	-0.09	-0.08	-0.15	-0.02	**0.28**	**0.38**
H. steindachneri	0.15	0.09	-0.13	-0.01	-0.05	-0.22	-0.08	**0.31**	**0.34**
S. ocyurus	0.21	-0.09	0.12	-0.07	0.13	**-0.28**	-0.07	**0.29**	0.22
C. humeralis	**0.56**	0.21	-0.23	-0.05	0.03	**-0.52**	0.10	**0.43**	**0.43**
J. nigrirostris	0.13	0.09	-0.23	**-0.26**	-0.09	-0.23	-0.19	**0.28**	**0.32**
A.troschelii	**-0.33**	**-0.38**	**0.39**	0.22	-0.04	**0.35**	-0.17	**-0.43**	-0.03
M. dorsalis	**-0.41**	0.04	0.10	-0.20	-0.05	**0.40**	-0.01	**-0.34**	-0.10
M. bairdii	-0.16	-0.16	**0.33**	-0.11	0.20	0.23	-0.07	-0.17	-0.10
S. acapulcoensis	**-0.64**	-0.23	**0.27**	-0.18	0.02	**0.74**	0.01	**-0.53**	**-0.34**
S. flavilatus	**0.40**	0.04	0.04	0.18	-0.09	**-0.38**	-0.00	**0.24**	**0.40**
C. rivulatus	-0.16	-0.00	0.22	**-0.25**	0.08	0.23	-0.07	-0.19	-0.11
B. diplotaenia	0.20	**0.28**	0.16	**-0.40**	-0.11	**-0.24**	-0.08	**0.27**	**0.41**
	-0.37	**-0.33**	0.04	**0.24**	-0.00	**0.30**	0.12	**-0.48**	**-0.28**

H. chierchiae									
H. dispilus	-0.07	0.05	-0.08	0.15	0.13	0.11	**0.30**	**-0.26**	**-0.38**
H. nicholsi	**-0.53**	**-0.24**	0.04	**0.24**	0.23	**0.57**	0.04	**-0.50**	**-0.28**
T. lucasanum	**-0.52**	0.12	0.00	-0.12	-0.05	**0.59**	-0.01	**-0.31**	-0.00
S. verres	0.08	0.20	0.14	**0.24**	0.04	**0.28**	**0.24**	**- 0.38**	**-0.39**
A. hispidus	**0.43**	0.13	-0.21	-0.17	0.06	**-0.41**	0.05	**0.44**	**0.30**
C. punctatissima	0.12	-0.11	-0.20	**0.45**	0.06	0.04	-0.02	**-0.28**	-0.05
D. holocanthus	**0.34**	-0.04	-0.09	0.08	0.11	**-0.28**	0.13	0.20	**0.43**

Four possible groups of fish species suggesting that each site has its own particular fish assemblage. Punta Argentina (P), the shallowest site, is characterized by *Ophioblennius steindachneri* (OSTE), *Microspathodon bairdii* (MBAI), *Microspathodon dorsalis* (MDOR), and *Abudefduf troschelii* (ATRO). The second assemblage is Cabeza de Mono (C), close to axis 2 and with a more heterogeneous substrate, composed by *Stegastes acapulcoensis* (SACA), *Canthigaster punctatissima* (CPUN), *Halichoeres nicholsi* (HNIC), *Halichoeres chierchiae* (HCHI), *Thalassoma lucasanum* (TLUC), *Sufflamen verres* (SVER), and *Serranus Psittacinus* (SPSI). The third group, composed by *J. nigrirostris* (JNIG), *H. dispilus* (HDIS), *S. ocyurus* (SOCY), *S. flavilatus* (SFLA), *R. bicolor* (RB), *H.passer* (HPAS) and *P.zonipectus* (PZON) is represented by fishes that were more abundant on Bajo Virador, a slightly deeper site with higher coverage of rocky substrate, higher coverage of the scleractinean coral *Pavona* spp and less coverage of the coral *Pocillopora* sp. Site S, the deep habitat, has a distinctive assemblage composed by pomacentrid *Chromis atrilobata* (CATRI), *Chaetodon humeralis* (CHUM), *Diodon holocanthus* (DHOL), *Haemulon steindachneri* (HSTE) and *Haemulon maculicauda* (HMAC), *Bodianus diplotaenia* (BDIP), *Cephalopholis panamensis* (CPAN) This ordination diagram shows a clear pattern of distribution of the reef fishes on a local scale, that give us an idea on the Beta diversity patterns and a composition of fishes in the Gulf of Papagayo.

DISCUSSION

Water temperature and visibility in our study reflect, taking in account only two months of the dry season, the typical seasonal pattern associated with coastal upwelling during the dry months. *Pocillopora* sp. percent cover was higher in shallower waters, concurring with Glynn et al. (1972) and (Coles & Jokiel 1977). On the contrary, the octocoral *Carijoa* spp. and the ahermatypic *Tubastrea coccinea* showed a similar zonification of increased percent cover with depth, as Jiménez 1998 and Yoshioka & Yoshioka 1989 also described.

In Culebra Bay, we found a total of 75 species of reef fishes belonging to 28 families. On the Colombian Pacific coast, Zapata and Morales (1997) found 71 species of 30 families of reef fishes. These two studies suggest a low species number in the eastern Pacific compared to other sites, such as Hawaii (129 spp., Friedlander & Parrish 1998) and The Red Sea (198 spp., Khalaf & Kochzius 2002). However, in recent surveys conducted at Bahia Honda, a non upwelling area in the Gulf of Chiriqui, Panama, the number of species is higher than the other TEP regions mentioned above (126 spp Dominici-Arosemena & Wolff in prep). Some authors consider that the coral species richness limits the richness of coral reef but there appears to be no strong taxonomic division between many reef and non-reef faunas (Robertson 1998, Bellwood 1998; Ferreira et al., 2001). Species composition has been found to vary among differing habitats within a region (Williams 1991, McGehee 1994). In the Gulf of Papagayo, higher diversity and evenness occurred in shallow sites, where medium-sized rocks and *Pocillopora* spp. were more abundant (Fig. 4). It seems that the structure of corals and rocks (complex topography and variable shapes) probably provide shelter and feeding areas (Hixon & Beets 1989). In Gorgona Island on Colombia's Pacific coast, species richness and evenness were lower in the slope of the reef in deeper areas, the strongest contribution to the difference in evenness in the area was given by *Chromis atrilobata* and *Thalassoma lucasanum* (Zapata & Morales 1997). These two species were the same that affected eveness in our study. In Hawaii, fish diversity variables tended to have higher values where reef sustratum was more structurally or topographically complex and closer to reef edges (Friedlander & Parrish 1998). Twenty-six species of our study had a significant correlation with at least one given kind of substrate rather than depth even that this last mentioned factor is highly variable in the Tropical Eastern Pacific with tidal ranges of more that 3 meters. In some studies of the Indo-Pacific and in the north of the eastern Pacific, the diversity between habitats (Beta-diversity) is large, indicating that there is a high contribution of the diversity of each one of the habitats to the total diversity (Goldman & Talbot 1976, Gilligan 1980, Sale 1980). In the study at Gorgona Island, Colombia, 60% of the species were found in all areas of the reef and just 11% of the species were found only in four of the studied zones. The authors attribute this low Beta diversity to the structural homogeneity of the reef (Zapata & Morales 1997). Our results show a different situation with diversity and evenness. Only 22.8% of the species were found in all study sites, while many of the species were restricted to a specific reef community. The trophic structure of the fish community here described differs from trends reported in other tropical regions. Our results indicate that mobile invertebrate feeders and planktivorous fishes were consistently more abundant at the study sites with low relative abundance of territorial and roving herbivores (Fig. 3). If we consider this case, our results shows trends have more affinities to temperate regions were planktívores and invertebrates feeders are the most abundant than herbivores (Floeter et al., 2004): These differences in trophic group proportions probably result from local events (e.g., upwelling, lower temperatures) in the TEP (D'Croz & Robertson 1997). Herbivores (both roving and territorial) are present with very low abundance in TEP when compared to the Tropical western Atlantic and including many Brazilian areas (Ferreira et al., 2004). Given this discrepancy, we question whether the trend toward the use of low-caloric food resources among tropical coral reef fishes, as proposed by Harmelin-Vivien (2002), can be applied to a marginal region like the TEP where the localized upwelling causes dramatic seasonal changes or pulses in water temperature, nutrient contents, and abundances of phytoplankton and zooplankton.

Recent studies show fish associations according to the physical conditions of the area. McGehee (1994) found particular fish organizations in Puerto Rican waters that are similar to our associations in the level of genus. The 4 fish associations of our work are-site specific and show some trophic structure. Even the shallow-water groups from nearby sites had different species assemblages. One was characterized by omnivores and invertebrate feeders, the other with mobile invertebrate feeders (labrids). The Punta Argentina assemblage was mostly composed by territorial herbivores (blennids and pomacentrids), while the deep assemblage was represented by invertebrate feeders.

The Gulf of Papagayo is of high economic and social importance for the local coastal communities. Due to its easy access, the area is exposed to exploitation by artisan, commercial, and ornamental fisheries (Fournier & Vitola 1994, Gutiérrez 1994). Some studies have evaluated the negative effect of extractive activities in detriment of the tourism industry (Ibarra 1996).

Dominici-Arosemena et al., 2001 report that the ornamental trade may have an effect on all the reef fish community. In species like *T. lucasanum,* where colored terminal phases are heavily extracted, the absence of terminal males triggers the sex transformation of females into terminal phase males. Some studies suggest the need of a follow-up research for developing and management plans on the Gulf of

Papagayo based on marine protected areas, zoning for controlled use and levels of exploitation is recommended (Dominici-Arosemena 1999).

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