

Food resource partitioning among five dominant fish species in the Los Frailes reef, south-western Gulf of California, Mexico

Reparto de recursos tróficos entre cinco especies de peces dominantes del arrecife de Los Frailes, suroeste del Golfo de California, México.

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Abstract.

Partitioning of the food resources among five dominant fish species in the Los Frailes reef, Baja California Sur, Mexico: *Arothron meleagris* (Tetraodontidae), *Stegastes rectifraenum* (Pomacentridae), *Thalassoma lucasanum* (Labridae), *Acanthurus triostegus* and *Prionurus punctatus* (Acanthuridae) was investigated. Stomach contents were analyzed and quantified using the index of relative importance (IRI), diet width was calculated with Levin's index, and trophic overlap was

calculated with the Morisita-Horn index. A total of 94 benthic food items were identified, which consisted mainly of algae (green, red, brown), crustaceans and molluscs. *P. punctatus* (n= 85) and *A. triostegus* (n= 50) can be categorized as herbivores, while *A. meleagris* (n= 101), *S. rectifraenum* (n= 50) and *T. lucasanum* (n=246) can be categorized as omnivores. The diet breadth index (Bi) as well as the overlap index (C λ) indicated that the five analyzed species had a specialized trophic behavior (Bi= <0.6) and low trophic overlap (C λ = \leq 0.1). Based on these results, we conclude that each species has a preference for particular food components, a narrow diet width, and that there is low trophic overlap among them, which allows them to coexist on the reef in high numerical abundances and with minimal interspecific competition for food.

Keywords: Gulf of California, diet, reef fish, trophic interactions, rocky reef, trophic overlap.

Resumen.

Se determinó el reparto de recursos tróficos entre cinco especies de peces dominantes del arrecife de los Frailes, Baja California Sur, México: *Arothron meleagris* (Tetraodontidae), *Stegastes rectifraenum* (Pomacentridae), *Thalassoma lucasanum* (Labridae), *Acanthurus triostegus* y *Prionurus punctatus* (Acanthuridae). Para el análisis y cuantificación de los contenidos estomacales de cada especie se empleó el índice de importancia relativa (IIR) y se determinó la amplitud y la sobreposición de las dietas utilizando el Índice de Levin y Morisita-Horn respectivamente.

Se identificaron un total de 94 componentes alimenticios bénticos, los cuales se constituyeron principalmente por algas (verdes, rojas, cafés), crustáceos y moluscos. *Prionurus punctatus* (n= 85) y *A. triostegus* (n= 50) se categorizaron como especies herbívoras, mientras *A. meleagris* (n= 101), *S. rectifraenum* (n= 50) y *T. lucasanum* (n=246) como especies omnívoras. Tanto el índice de Levin (*Bi*) como el índice de Morisita-Horn (*Cl*) indicaron que todas las especies de consumidores analizados son especialistas ($Bi = <0.6$) y que el traslapamiento trófico entre sus dietas es bajo ($Cl = \leq 0.1$). Los resultados indican que cada especie tiene preferencia por algunos componentes alimenticios específicos, una amplitud de dieta estrecha y un bajo traslape trófico entre ellas, lo cual les permite coexistir en el arrecife con abundancias altas y competencia mínima entre ellas.

Palabras clave: Golfo de California, dieta, Peces arrecifales, Interacciones Tróficas, Arrecife Rocoso, traslape trófico.

INTRODUCTION

The Gulf of California, also known as the Sea of Cortes, is a highly diverse biological area with abundant marine life (Case & Cody, 1983). The highest underwater diversity of this sea is found on rocky bottoms, at less than 50 m depth, mainly along the coasts of the Baja California Peninsula (Thomson *et al.*, 2000).

The Los Frailes reef belongs to the Cabo Pulmo Marine Park, in the south-western Gulf of California (Reyes-Bonilla, 1997). This reef has a high fish diversity (236 species, Villareal-Cavazos *et al.*, 2000), including species that are very abundant and that remain spatio-temporally on the reef, such as *Arothron*

meleagris (Lacèpede, 1798) (Tetraodontidae), *Stegastes rectifraenum* (Gill, 1862) (Pomacentridae), *Thalassoma lucasanum* (Gill, 1862) (Labridae), *Acanthurus triostegus* (Linnaeus, 1758) and *Prionurus punctatus* Gill, 1862 (Acanthuridae). These species generally dominate reef systems in the south-western Gulf of California (Pérez-España *et al.*, 1996; Aburto-Oropeza & Balart, 2001).

There are few studies on the trophic ecology of reef fishes in the Gulf of California (*e.g.* Hobson, 1968; Montgomery *et al.*, 1980, 1980a; Moreno-Sánchez *et al.*, 2009, 2011; Abitia-Cárdenas *et al.*, 2011). These studies have described the general food composition of species without taking into account interspecific trophic interactions, which are fundamental for understanding biological interactions and energy flow in ecosystems (Gulland, 1983; Pauly, 1984; Caddy, 1988; Soares *et al.*, 1992). The analysis of diet overlap among the dominant species in an ecosystem allows the identification of strategies (generalist, specialist or opportunist) that favour species coexistence, minimizing competition among species and allowing their establishment and dominance (Caragistou & Papaconstantinou, 1994; Cruz-Escalona *et al.*, 2000). Several authors have also mentioned that trophic overlap measures among fish species that coexist in a given habitat are useful for comparing the use of food resources (Farnsworth & Ellison, 1996; Cruz-Escalona *et al.*, 2000).

In this context, the present study described the diet of *T. lucasanum* in the Los Frailes reef, BCS, analyzing it in conjunction with the diets of *A. meleagris*, *S. rectifraenum*, *A. triostegus*, and *P. punctatus* (Moreno-Sanchez *et al.*, 2009, 2011;

Abitia-Cardenas *et al.*, 2011; Moreno-Sanchez *et al.*, 2014), in order to determine diet breadth and dietary overlap, and establish whether there was partitioning of food resources among the five dominant fish species.

MATERIALS AND METHODS

Sampling trips were carried out monthly from November 2004 to October 2006, at the Los Frailes rocky reef, south-western Gulf of California (23° 22' 54.44" N; 109° 25' 4.04" W). Specimens of *A. meleagris*, *S. rectifraenum*, *A. triostegus*, and *P. punctatus* were captured using basic scuba gear and a polespear (Moreno-Sánchez *et al.*, 2009, 2011; Abitia-Cárdenas *et al.*, 2011; Moreno-Sánchez *et al.*, 2014), while *T. lucasanum* specimens were caught using a cylindrical net (Clifton, 1996). All samples were obtained between 10:00 a.m. and 16:00 p.m., since all species have diurnal feeding habits.

The length (TL) of each collected organism was recorded, and the stomach was removed. Stomach contents were kept in tagged plastic bags and frozen until later analysis at the Fish Ecology laboratory at the Centro Interdisciplinario de Ciencias Marinas (CICIMAR-IPN). The different food items were separated according to taxonomic group, and identified to the lowest possible taxonomic level, depending on the type and digestion state of prey items.

For taxonomic identification of crustaceans and molluscs the keys by Brusca (1980), Morris *et al.* (1980) and Fischer *et al.* (1995) were used; for algal identification the keys by Dawson (1944, 1961), Abbott and Hollenberg (1976), Dawes (1986) and Espinoza-Avalos

(1993) were used. Once the taxonomic identification was complete, stomach contents of all species were analyzed quantitatively, using the following indices: frequency of occurrence (%FO), percent by number (%N) and percent by weight (%W) (Pinkas *et al.*, 1971). In order to standardize and evaluate the information obtained from the five species, the Index of Relative Importance was used (Pinkas *et al.*, 1971):

$$IIR = (\%W + \%N) * \%FO$$

where IRI = index of relative importance, %W = percent weight, %N = percent number, and %FO = percent frequency of occurrence.

This index combines information from the component indices above and contains information on the contribution of each prey item to the predator (Liao *et al.*, 2001). The IRI was also expressed as a percentage (%IRI) (Cortés, 1997), using the following formula:

$$\%IIR = \frac{100IIR_i}{\sum_{i=1}^n IIR_i}$$

The diet breadth (Bi) was calculated using the standardized Levin's index (Hurlbert, 1978) using the absolute values obtained with the IRI. This index gives values ranging from 0 to 1. Low values (< 0.6) indicate a specialist predator that uses few prey resources and prefers certain prey (specialist predator), and high values (> 0.6) indicate a generalist predator that uses all resources without preference (Labropoulou & Eleftheriou, 1997; Escobar-Sanchez *et al.*, 2006).

$$B_i = \frac{1}{n-1} \left(\frac{1}{\sum_j p_{ij}^2} - 1 \right)$$

Where B_i = Levin's standardized index for predator i ; p_{ij} = proportion of diet of predator i that is made up by prey j ; and n = number of prey.

The interspecies dietary overlap was estimated using the Morisita-Horn Index employing the absolute IRI values (Smith & Zaret, 1982).

$$C\lambda = \frac{2 \sum_{i=1}^n (P_{xi} * P_{yi})}{\left(\sum_{i=1}^n P_{xi}^2 + \sum_{i=1}^n P_{yi}^2 \right)}$$

Where $C\lambda$ = Morisita-Horn index of overlap between predator x and predator y . P_{xi} = Proportion of prey i of the total prey used by predator x . P_{yi} = Proportion of prey i of the total prey used by predator y . n = Total number of prey.

$C\lambda$ values vary from 0, when no elements of the diet are alike, to 1 when all elements occur in equal abundance. The trophic overlap was classified according to the scale proposed by Langton (1982): low overlap = 0.0 to 0.29, middle overlap = 0.30 to 0.65, high overlap = 0.66 to 1.

RESULTS

The trophic spectra of *A. meleagris*, *S. rectifraenum*, *A. triostegus* and *P. punctatus* were obtained from studies published by Moreno-Sánchez *et al.* (2009, 2011, 2014), and Abitia-

Cárdenas *et al.* (2011), which characterized the diet of these species using the Index of Relative Importance.

Quantitative descriptions of the *T. lucasanum* diet were carried out during the present study. A total of 300 stomachs of this species were analyzed (82% contained food and 18% were empty), and 378 prey items were counted, belonging to 15 food components. These groups included algae, invertebrates (molluscs, crustaceans and others), and fish scales. Gastropods were the most numerous group, followed by ostracods; these two groups comprised 52.9 % of the diet (Table 1). The most important component by weight (47.8 g) and frequency (52.23%) was unidentified organic matter (UOM), followed by copepods, which constituted 29.2 g and 29.9% FO (Table 1). According to the IRI, the food components that made up 98% of the diet were UOM, gastropods, ostracods, shell remains and isopoda. The estimated IRI values for each recorded item in the diet of the five species are presented in Table 2.

Levin's index indicated that *A. triostegus* ($B_i = 0.10$) and *P. punctatus* are specialists ($B_i = 0.13$), as are the omnivorous species *A. meleagris* ($B_i = 0.12$), *S. rectifraenum* ($B_i = 0.30$), and *T. lucasanum* ($B_i = 0.08$). Trophic overlap values were low among all analyzed species (≤ 0.1) (Table 3). Specifically, *A. triostegus* and *P. punctatus* had several food items in common, such as *Cladophora* spp., *Codium simulans*, *Amphiroa valonioides*, *Ceramium* spp., *Gracilaria* spp., *Jania mexicana*, *Dictyota crenulata*, *Padina conrescens*, and *Sphacelaria* spp. *A. triostegus* and *S. rectifraenum* had the following algae in common: *Bryopsis* spp., *Cladophora* spp., *Rhizoclonium*

Reef fish trophic interactions

Table 1. Trophic spectrum composition of the Cortez rainbow wrasse, *Thalassoma lucasanum* in the Los Frailes reef, B.C.S., presented as absolute and percent values by number (N), weight (W), frequency of occurrence (FO) and index of relative importance (IRI). UOM = Unidentified organic matter.

Tabla 1. Composición del espectro trófico de la arcoiris de Cortés, *Thalassoma lucasanum* en el arrecife de Los Frailes, B.C.S., se presentan los valores absolutos y los porcentajes por número (N), peso (W), frecuencia de ocurrencia (FO) y el índice de importancia relativa (IRI). UOM= Materia orgánica no identificada.

Species	W	%W	FO	%FO	N	%N	IRI	%IRI
Phaeophyceae	3.4	3.04	5	2.02	0	0	6.16	0.18
Rhodophyceae	0.3	0.27	1	0.4	0	0	0.11	0
Chlorophyceae	2.1	1.88	7	2.83	0	0	5.33	0.15
Benthic copepods	0.4	0.36	1	0.4	13	3.44	1.54	0.04
Phylum Porifera	0.8	0.72	3	1.21	0	0	0.87	0.03
Class Gastropoda	3.5	3.13	11	4.45	113	29.89	147.09	4.25
Fish eggs	0.4	0.36	2	0.81	30	7.94	6.72	0.19
Isopoda	1.6	1.43	5	2.02	75	19.84	43.06	1.24
UOM	47.8	42.79	129	52.23	0	0	2234.95	64.58
Ostracoda	9.4	8.42	10	4.05	87	23.02	127.25	3.68
Copepoda	29.2	26.14	74	29.96	0	0	783.19	22.63
Shell remains	3.9	3.49	10	4.05	60	15.87	78.4	2.27
Phylum Crustacea	0.3	0.27	1	0.4	0	0	0.11	0
Phylum Echinoder- mata	3.4	3.04	9	3.64	0	0	11.09	0.32
Fish scales	5.2	4.66	8	3.24	0	0	15.08	0.44
TOTAL	111.7	100	247		378	100	3460.93	100

Table 2. Stomach contents of the dominant fish species in the Los Frailes rocky reef, B.C.S., Mexico, according to the index of relative importance (%IRI).

Tabla 2. Resumen del contenido estomacal de las especies dominantes del arrecife rocoso de Los Frailes, B.C.S., México, de acuerdo con el Índice de Importancia Relativa (%IIR).

Species	<i>Acanthurus triostegus</i>		<i>Prionurus punctatus</i>		<i>Arothron meleagris</i>		<i>Stegastes rectifraenum</i>		<i>Thalassoma lucasanum</i>	
	IRI	%IRI	IRI	%IRI	IRI	%IRI	IRI	%IRI	IRI	%IRI
Unidentified alga					7.79	0.13				
Chlorophyceae									5.33	0.15
<i>Bryopsis</i> spp.	28.53	0.62					961.59	11.08		
<i>Caulerpa racemosa</i>	0.13	0								
<i>Cladophora</i> spp.	48.94	1.07	3.7	0.05	0.52	0.01	115.01	1.33		
<i>Cladophoropsis fasciculatus</i>	0.08	0								
<i>Codium simulans</i>	0.5	0.01	5.22	0.07						
<i>Derbesia marina</i>	13.11	0.29								
<i>Enteromorpha</i> spp.	0.07	0								
<i>Rhizoclonium</i> spp.	13.43	0.29					601.99	6.94		
<i>Ulva lactuca</i>	19.41	0.42			2.39	0.04	5.39	0.06		
<i>Ulva linza</i>	2356.4	51.5					619.87	7.14		
Rhodophyceae									0.11	0.003
<i>Ahnfeltia</i> spp.	0.18	0								
<i>Amphiroa beauvoisii</i>			13.76	0.17	34.22	0.56				
<i>Amphiroa misakiensis</i>			87.41	1.1						
<i>Amphiroa valonioides</i>	119.54	2.61	57.56	0.73			7.172	0.083		
<i>Centroceras</i> spp.	0.1	0								
<i>Ceramium flaccidum</i>					1.02	0.02				
<i>Ceramium</i> spp.	1.29	0.03	20.3	0.26						
<i>Corallina vancouverensis</i>			5.56	0.07						
<i>Champia</i> spp.	41.04	0.9								
<i>Erythrotrichia</i> spp.	0.05	0								

Reef fish trophic interactions

Table 2 Continued...

Species	<i>Acanthurus triostegus</i>		<i>Prionurus punctatus</i>		<i>Arothron meleagris</i>		<i>Stegastes rectifraenum</i>		<i>Thalassoma lucasanum</i>	
	IRI	%IRI	IRI	%IRI	IRI	%IRI	IRI	%IRI	IRI	%IRI
<i>Galaxaura</i> spp.			4.68	0.06						
<i>Gelidiella aerea</i>			11.84	0.15						
<i>Gelidiella</i> spp.	667.68	14.59								
<i>Goniotrichum alsidi</i>	0.06	0								
<i>Gracilaria</i> spp.	16.18	0.35	1209.35	15.24	0.45	0.01	191.62	2.21		
<i>Herposiphonia tenella</i> f. <i>secunda</i>			197.82	2.49						
<i>Herposiphonia</i> spp.	5.98	0.13					199.53	2.3		
<i>Hypnea musciformis</i>	38.19	0.84	681.01	8.58						
<i>Hypnea</i> spp.					9.39	0.15				
<i>Jania adhaerens</i>					1.86	0.03				
<i>Jania mexicana</i>	32.08	0.7	459.17	5.79			494	5.69		
<i>Laurencia</i> spp.	115.72	2.53								
<i>Neogoniolithon trichotomum</i>			154.19	1.94						
<i>Pitophilium</i> spp.	0.74	0.02								
<i>Polysiphonia simplex</i> spp.	395.12	8.64								
<i>Polysiphonia pacifica</i>					6.37	0.1				
<i>Polysiphonia</i> spp.			173.25	2.18						
<i>Porphyra</i> spp.	47.05	1.03								
<i>Pterocladia capillacea</i>			168.19	2.12						
<i>Pterocladia</i> spp.	1.03	0.02								
Phaeophyceae									6.16	0.18
<i>Dictyopteris delicatula</i>	2.62	0.06								
<i>Dictyopteris undulata</i>					1.97	0.03				
<i>Dictyopteris</i> spp. A			133.07	1.68						

Table 2 Continued...

Species	<i>Acanthurus trios-</i>		<i>Prionurus puncta-</i>		<i>Arottrhon me-</i>		<i>Stegastes recti-</i>		<i>Thalassoma luca-</i>	
	IRI	%IRI	IRI	%IRI	IRI	%IRI	IRI	%IRI	IRI	%IRI
<i>Dictyopteris</i> spp. B			3.33	0.04						
<i>Dictyota crenulata</i>	26.61	0.58	192.62	2.43			99.91	1.151		
<i>Dictyota dichotoma</i>					1.69	0.03				
<i>Dictyota flabellata</i>			306.91	3.87						
<i>Ectocarpus</i> spp.	6.52	0.14					650.12	7.49		
<i>Lobophora</i> spp.	8.45	0.19								
<i>Padina conrescens</i>	0.01	0	85.38	1.08						
<i>Padina durvillaei</i>					19.16	0.31				
<i>Sphacelaria</i> spp.	17.14	0.38	317.85	4						
PHYLUM CNIDARIA										
<i>Pocillopora</i> spp.					728.51	11.85				
PHYLUM CRUSTA-									0.11	0.003
BALANIDAE										
<i>Balanus</i> spp.					5.35	0.09				
PALINURIDAE										
<i>Panulirus inflatus</i>					11.2	0.18				
<i>Panulirus interruptus</i>					1.54	0.03				
PHYLUM MOLLUSCA										
CLASS GASTROPODA					1.7	0.03			147.09	4.25
<i>Cerithium</i> spp.							868.14	10		
<i>Olivella</i> spp.							843.16	9.72		
<i>Notoacmea fascicularis</i>					25.58	0.42				

Reef fish trophic interactions

Table 2 Continued...

Species	<i>Acanthurus triostegus</i>		<i>Prionurus punctatus</i>		<i>Arotrhon meleagris</i>		<i>Stegastes rectifraenum</i>		<i>Thalassoma lucasanum</i>	
	IRI	%IRI	IRI	%IRI	IRI	%IRI	IRI	%IRI	IRI	%IRI
<i>Phenacolepas malonei</i>					12.57	0.2				
HIPPONICIDAE										
<i>Hipponix panamensis</i>					18.7	0.3				
CALYPTRAEACEA										
<i>Crepidula aculeata</i>					7.03	0.11				
<i>Crepidula arenata</i>					235.07	3.82				
CLASS PELECYPODA										
MYTILIDAE										
<i>Lithophaga</i> spp.					22.52	0.37				
OSTREIDAE										
<i>Ostrea fisheri</i>					0.79	0.01				
CLASS BIVALVIA					3.83	0.06				
Bivalves							3.49	0.04		
Shell remains							307.03	3.54	78.4	2.27
TELLINIDAE										
<i>Tellina</i> spp.					98.86	1.61				
CRUSTACEA										
COPEPODA									783.19	22.63
Benthic copepods							2418.5	27.87	1.54	0.04
BRACHYURA										
<i>Eriphia verrucosa</i>							92.5	1.07		
Phylum Echinodermata									11.09	0.32
CIDARIDAE										

Table 2 Continued...

Species	<i>Acanthurus triostegus</i>		<i>Prionorus punctatus</i>		<i>Arottrhon meleagris</i>		<i>Stegastes rectifraenum</i>		<i>Thalassoma lucasanum</i>	
	IRI	%IRI	IRI	%IRI	IRI	%IRI	IRI	%IRI	IRI	%IRI
<i>Eucidaris thouarsii</i>					1.09	0.02	4.97	0.06		
ECHINOMETRIDAE										
<i>Echinometra vanbrunti</i>					1614.49	26.26				
ASTEROIDEA										
<i>Phataria unifascialis</i>					1.72	0.03				
ORDER SCLERACTINIA										
PORITIDAE										
<i>Porites</i> spp.					297.06	4.83				
ANNELIDA										
POLICHAETA					0.92	0.01				
BRYOZOA					330.3	5.37				
ISOPODA									43.06	1.24
OSTRACODA									127.25	3.68
PHYLUM PORIFERA					770.48	12.53			0.87	0.03
UROCHORDATA (tunicates)										
Tunicates							79.87	0.92		
Fish scales							0.64	0.01	15.08	0.44
Fish eggs									6.72	0.19
Sand							42.73	0.49		
UOM	551.7	12.05	3644.58	45.92	1872.07	30.45	69.79	0.8	2234.95	64.58
TOTAL	4576	100		100	6148.2	100	8677.45	100	3460.93	100

Reef fish trophic interactions

Table 3. Trophic overlap among the five dominant fish species of the Los Frailes reef, BCS, Mexico. Overlap was calculated with the Morisita-Horn index.

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Tabla 3. Traslape trófico entre las cinco especies de peces dominantes del arrecife de Los Frailes Baja California Sur, México. El traslapamiento fue calculado con el índice de Morisita-Horn.

	<i>A. triostegus</i>	<i>P. punctatus</i>	<i>A. meleagris</i>	<i>S. rectifraenum</i>	<i>T. lucasanum</i>
<i>A. triostegus</i>	*				
<i>P. punctatus</i>	0.03 *				
<i>A. meleagris</i>	0.002	0.005 *			
<i>S. rectifraenum</i>	0.17	0.1	0.0004 *		
<i>T. lucasanum</i>	0	0	0.0005	0.009 *	

spp., *Ulva lactuca*, *U. linza*, *A. valonioides*, *Gracilaria* spp., *Heterosiphonia* spp., *J. mexicana*, and *D. crenulata*. *S. rectifraenum* and *P. punctatus* both fed on *Cladophora* spp., *A. valonioides*, *Gracilaria* spp., *J. mexicana*, *D. crenulata*. The omnivores *A. meleagris* and *S. rectifraenum* consumed *Cladophora* spp., *Ulva lactuca*, *Gracilaria* spp., and *Eucidaris thouarsii*. Despite having diet items in common, diet overlap was low, because the proportions of these shared items were minimal in the diet. Additionally, *T. lucasanum* did not have any species in common with *A. triostegus* or *P. punctatus*.

DISCUSSION

Although there are previous studies of the feeding habits of reef fish in the Gulf of California (e.g., Hobson, 1968; Montgomery *et al.*, 1980; Pérez-España & Abitia-Cárdenas, 1996; Aburto-Oropeza *et al.*, 2000; Abitia-Cárdenas *et al.*, 2011; Moreno-Sánchez *et al.*, 2009, 2011, 2012), few studies have focused on resource partitioning or on interactions among coexisting species (Cruz-Escalona *et al.*, 2000, 2010). This information is vital to understand the mechanisms that favour coexistence and energy flow in ecosystems, as well as interspecific trophic interactions (Gulland, 1983; Pauly, 1984; Caddy, 1988; Soares *et al.*, 1992; Cruz-Escalona *et al.*, 2000).

According to stomach content analyses, two fish feeding guilds could be identified: herbivores and omnivores. The herbivores *A. triostegus* and *P. punctatus* fed exclusively on algae; *A. triostegus* consumed 35 algae species and *P. punctatus* consumed 23 algae species, which represented 58% and 36% respectively, of all macroalgae present in the Los Frailes reef (Anaya-Reyna & Riosmena-Rodríguez, 1996).

However, only 3 to 5 algae species were the most important in the diet of these herbivorous fish species, and therefore Levin's index categorized them as specialists. According to Gerking (1994), specialist species feed on a reduced number of food components, independently of the abundance of the resource in the habitat.

Selective feeding habits attenuate competition to a minimum. *A. triostegus* fed mainly on green algae, especially on *Ulva linza*, which can comprise up to 50% of its diet, while *P. punctatus* fed mainly on red algae (which comprised up to 40% of its diet). *P. punctatus* consumed mainly *Gracilaria* spp. as well as brown algae (which makes up 13% of the diet), and this was confirmed by the low diet overlap value between the two species ($C\lambda = 0.03$).

The differentiation of diets allows these species to coexist in the Los Frailes reef. Choat and Bellwood (1985) found that the adaptations that favoured trophic resource distribution between two herbivorous fish species (*Acanthurus lineatus* and *Ctenochaetus striatus*) in a Lizard Island reef were differences in dentition, mandible shape, and digestive tract. Although no description of the mandibular apparatus (dentition) or digestive tract of *A. triostegus* and *P. punctatus* were carried out, it is probable that morphological differences allowed them to select different algae when feeding. In order to clarify this point it would be necessary to conduct studies on the functional morphology of the jaw apparatus and digestive tract of these species.

Species that fed on invertebrates in higher proportion and on algae in lower proportion were catalogued as omnivores (*A. meleagris*,

S. rectifraenum and *T. lucasanum*). The range of food components for these species was large, comprising algae as well as invertebrates such as benthic copepods, barnacles, snails, lobsters, sea stars and polychaetes. However, the trophic overlap among species was almost nil ($C\lambda = \leq 0.009$), since each species had a few important components in the diet, and these important components did not coincide among the analyzed species. The diet of each species was dominated by a few food items, and Levin's index categorized them as specialists.

This differentiation allowed the establishment of *A. meleagris*, *S. rectifraenum* and *T. lucasanum* as the most dominant omnivorous species (by numerical abundance) in the Los Frailes reef. This was facilitated in part by the behaviour of each species on the reef. *A. meleagris* is a solitary wandering species that inhabits waters from 0.5 m to 35 m depth, and has a dentition consisting of 4 plates that allow it to feed on hard food items, such as sea urchins, corals, sponges, molluscs and bryozoans (Robertson & Allen, 2008). These same trophic items have been found in studies carried out in several regions of the Eastern Tropical Pacific (Glynn *et al.*, 1972; Guzmán & López, 1991; Reyes-Bonilla & Calderón-Aguilera, 1999).

Stegastes rectifraenum is a territorial species that occupies specific places on the reef and defends them vigorously from other species, and feeds mainly on benthic copepods, on *Bryopsis* spp., *Cerithium* spp., *Olivella* spp. and *Ectocarpus* spp. Its territorial behaviour restricts its food consumption to certain trophic components, due to the limited mobility it has on the reef, and to the size of its mouth and teeth (Montgomery, 1980b; Thomson *et al.*, 2000; Aguilar-Medrano *et al.*,

2011). *Thalassoma lucasanum* is the most conspicuous, abundant (numerically) and dominant species on the Los Frailes rocky reef. It consumed benthic food items, such as crabs, gastropods, ostracods, isopods, algae and fish scales. According to Hobson (1968), *T. lucasanum* feeds on bottom organisms such as crustaceans, algae, and soft corals, which was also reported in the present study. It should be mentioned that fish scales present in the stomach contents of *T. lucasanum* could be due to this species visiting cleaning stations and probably feeding on the scales of the fish that it cleans (Hobson, 1968). A considerable quantity of UOM in the stomach contents was also recorded, as well as food items very little to not at all digested. This is probably due to *T. lucasanum* feeding all day long, as Hobson (1968) reported in a trophic behaviour study that included 800 hours of filming. Levin's index determined that *T. lucasanum* was a specialist. However, this result should be treated with caution due to the low taxonomic resolution of prey, occasioned by the advanced degree of digestion and small prey size.

In general, the trophic spectrum of the analyzed species spanned the principal benthic fauna of the Los Frailes reef, which is a habitat with high structural complexity (high number of cavities, rugosity, substrate heterogeneity, depth variation, waves) that fosters the existence of highly variable and abundant prey species (e.g., algae, invertebrates) that are the main food source for the dominant fish species (Moreno-Sánchez *et al.*, 2014). Even though there were high numbers of food components in the diet of the dominant fish species, it is clear that there is trophic distribution, with selection of only a few food items, according to the availability of food resources on the reef,

which allows the minimization of interspecific competition and enables species coexistence on the Los Frailes reef.

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REFERENCES

- Abbott IA., GJ Hollenberg (1976). Marine Algae of California. Stanford University. Stanford, California, USA.
- Abitia-Cardenas LA., XG Moreno-Sánchez., DS Palacios-Salgado., O Escobar-Sánchez. (2011). Feeding habits of the convict surgeonfish *Acanthurus triostegus* (Teleostei: Acanthuridae) on the Los Frailes reef, Baja California Sur, México. *Aqua, International Journal of Ichthyology* 17 103-108.
- Aburto-Oropeza O., E Sala., C. Sánchez-Ortiz. (2000). Feeding behavior, habitat use, and abundance of the angelfish *Holocanthus passer* (Pomacanthidae) in the southern Sea of Cortés. *Environmental Biology of Fishes* 57(4) 435-442.
- Aburto-Oropeza O., EF Balart. (2001). Community structure of reef fish in several habitats of rocky reef in the Gulf of California. *Marine Ecology* 22(4) 283-305.
- Aguilar-Medrano R., B Frédérich., E De Luna., EF Balart. (2011). Patterns of morphological evolution of the cephalic region in damselfishes (Perciformes: Pomacentridae) of the Eastern Pacific. *Biological Journal of the Linnean Society* 102, 593-613.
- Allen GR., DR Robertson. (1994). Fishes of the tropical eastern Pacific. Honolulu: University of Hawaii Press. pp. 332.
- Anaya-Reyna G., R Riosmena-Rodríguez. (1996). Macroalgas del arrecife coralino de Cabo Pulmo-Los Frailes, Baja California Sur, México. *Revista de Biología Tropical* 44 (2) 903-906.
- Brusca R. (1980). Common intertidal invertebrates of the Gulf of California. University Arizona. Tucson, Arizona, USA.
- Caddy JF. (1988). A Research strategy in support of stock evaluation of demersals in the Mediterranean Sea, GFCM Technical Consultations on stocks assessment. *FAO Fisheries Research* 112, 116-126.
- Caragistou E., C Papaconstantinou. (1994). Feeding habits of piper (*Trigla lyra*) in the Saronikos Gulf (Greece). *Journal of Applied Ichthyology* 10, 104-113.
- Case J., ML Cody. (1983). Island biogeography in the Sea of Cortez. University of California Press, Berkeley.
- Choat J H., DR Bellwood. (1985). Interaction amongst herbivorous fishes on a coral reef. Influence of spatial variation. *Marine Biology* 89, 221-234.

- Clifton KE (1996). Field methods for the behavioral study of foraging ecology and life history of herbivorous coral-reef fishes. In: M.A. Lang., C.C. Baldwin (eds.), Methods and techniques of underwater research. Proceedings of the American Academy of Underwater Sciences Sixteenth Annual Scientific Diving Symposium. American Academy of Underwater Sciences. Nahant, Massachusetts. pp 75-82.
- Cortés E. (1997). A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Canadian Journal of Fisheries and Aquatic Science 54, 726-738.
- Cruz-Escalona VH., LA Abitia-Cárdenas., L Campos-Dávila., F Galván-Magaña. (2000). Trophic interrelations of the three most abundant fish species from Laguna San Ignacio, Baja California Sur, Mexico. Bulletin of Marine Science, 361-373.
- Cruz-Escalona VH., L Campos-Dávila., LA Abitia-Cárdenas., MJ Zetina-Rejón. (2010). Repartición de recursos alimentarios entre la ictiofauna dominante de una Laguna templada de Baja California Sur, México. CICIMAR Oceanides 25(1) 1-15.
- Dawes CJ. (1986). Botánica Marina. [Marine Botany] Limusa, México.
- Dawson EY. (1944). The marine algae of the Gulf of California. Allan Hancock Pacific Expeditions 3(10) 189- 464.
- Dawson EY. (1961). A guide to the literature and distributions of Pacific benthic algae from Alaska to the Galápagos Islands. Pacific Science 15, 370-461.
- Escobar-Sanchez O., LA Abitia-Cardenas., F Galvan Magaña. (2006). Food habits of the Pacific angel shark *Squatina californica* in the southern Gulf of California, Mexico. Cybium 30(4) 91-97.
- Espinoza-Avalos J. (1993). Macroalgas marinas del Golfo de California. pp. 328-357. In: Salazar-Vallejo SI., González NE. (eds.) Biodiversidad Marina y Costera de México CONABIO. CIQRO.
- Farnsworth JE., MA Ellison. (1996). Scale-dependent spatial and temporal variability in biogeography of mangrove root epibiont communities. Ecological Monographs 66(1) 45-46.
- Fischer W., F Krupp., W Schneider., C Sommer., KE Carpenter., VH Niem. (1995). Guía FAO para la identificación de especies para los fines de pesca, Pacifico Centro-Oriental. FAO, Rome.
- Gerking SD. (1994). Feeding ecology of fish. San Diego, CA: Academic Press.
- Glynn PW., RH Stewart., JE Mccosker. (1972). Pacific coral reefs of Panama: structure, distribution and predators. Geologische Rundschau 61, 483-519.
- Gulland JA. (1983). Fish stock assesment. FAO/Wiley series on food and agriculture, London.
- Guzmán MH., JD López. (1991). Diet of the corallivorous pufferfish *Arothron meleagris* (Pisces: Tetraodontidae) at Gorgona Island, Colombia. Revista de Biología Tropical. 39, 203-206.

- Hobson ES. (1968). Predatory behavior of some shore fishes in the Gulf of California. United States Fish and Wildlife Service Research Reports 72, 1-92.
- Hurlbert SH. (1978). The measurement of niche overlap and some relatives. *Ecology* 59, 67-77.
- Labropoulou M., A Eleftheriou. (1997). The foraging ecology of two pairs of congeneric demersal fish species: importance of morphological characteristics in prey selection. *Journal of Fish Biology* 50, 324-340
- Langton RW. (1982). Diet overlap between the Atlantic cod *Gadus Morhua*, silver hake *Merluccius bilinearis* and fifteen other northwest Atlantic finfish. *Fishery Bulletin* 80, 745-759.
- Liao H., CL Pierce., JG Larscheid. (2001). Empirical assessment of indices of prey importance in the diets of predacious fish. *Transactions of the American Fisheries Society* 130, 583-591.
- Montgomery WL. (1980a). The impact of non-selective grazing by the giant blue damselfish, *Microspathodon dorsalis*, on algal communities in the Gulf of California, Mexico. *Bulletin of Marine Science* 30, 290-303.
- Montgomery WL. (1980b). Comparative feeding ecology of two herbivorous damselfishes (Pomacentridae: Teleostei) from the Gulf of California, Mexico. *Journal of Experimental Marine Biology and Ecology* 47, 9-24.
- Montgomery WL., T Gerrodette., L Marshall. (1980). Effects of grazing by the yellowtail surgeonfish, *Prionurus punctatus*, on algal communities in the Gulf of California, Mexico. *Bulletin of Marine Science* 30 (4), 901-908.
- Moreno-Sanchez XG., LA Abitia-Cardenas., A Favila., FJ Gutiérrez-Sánchez., DS Palacios-Salgado. (2009). Ecología trófica del pez *Arothron meleagris* (Tetraodontiformes: Tetraodontidae) en el arrecife de Los Frailes, Baja California Sur, México. *Revista de Biología Tropical* 57, 113-123.
- Moreno-Sánchez XG., LA Abitia-Cárdenas., O Escobar-Sánchez., DS Palacios-Salgado. (2011). Diet of the Cortez damselfish *Stegastes rectifraenum* (Teleostei: Pomacentridae) from the rocky reef at Los Frailes, Baja California Sur, Mexico. *Marine Biodiversity Records* 4, 1-5.
- Moreno-Sánchez XG., O Escobar-Sánchez., LA Abitia-Cárdenas., VH Cruz-Escalona. (2012). Diet composition of the sicklefin smooth-hound shark *Mustelus lunulatus* caught off El Pardito Island, Baja California Sur, Mexico. *Marine Biodiversity Records*, 5 1-5.
- Moreno-Sánchez XG., LA Abitia-Cárdenas., R Riosmena-Rodríguez., M Cabrera-Huerta., FJ Gutiérrez-Sánchez. (2014). Diet of the yellowtail surgeonfish *Prionurus punctatus* (Gill, 1862) on the rocky reef of Los Frailes, Baja California Sur, México. *Cahiers de Biologie Marine* 55, 1-8.
- Morris RH., DP Abbot., EC Haderlie. (1980). *Intertidal invertebrates of California*. Stanford University, Stanford. Palo Alto, California, USA.

- Pauly D. (1984). Fish population dynamics in tropical waters: a manual for use with programmable calculators. ICLARM Studies and Reviews, Manila 8, 325.
- Pérez-España H., LA Abitia-Cárdenas. (1996). Description of the digestive tract and feeding habits of the king angelfish and the Cortes angelfish. Journal of Fish Biology 48, 807-817.
- Pinkas L., MS Oliphant., LK Iverson. (1971). Food habits of albacore, blue fin tuna and bonito in California waters. California Department of Fish and Game, United States. Fish Bulletin 152, 105.
- Reyes-Bonilla H. (1997). Cabo Pulmo reef: a new marine reserve in the Gulf of California. Conservation Biology 11, 827.
- Reyes-Bonilla H., LE Calderón-Aguilera. (1999). Population density, distribution and consumption rates of three corallivores at Cabo Pulmo Reef, Gulf of California, México. Marine Ecology 20, 347-357.
- Smith PE., MT Zaret. (1982). Bias in estimating niche overlap. Ecology 5, 1248-1253.
- Soares ISH., CLDB Rossi-Wongtschowski., IMC Alvares., EY Muto., MA Gasalla. (1992). Grupos tróficos de peixes demersais da plataforma continental interna de Ubatuba, Brasil. I. Chondrichthyes. Boletim do Institute Oceanográfico 40, 79-85.
- Thomson DA., LT Findley., AN Kerstitch. (2000). Reef fishes of the Sea of Cortez. University of Texas Press, Austin, Texas.
- Villareal-Cavazos A., H Reyes-Bonilla., B Bermúdez-Almada., O Arizpe-Covarrubias. (2000). Los peces del arrecife de Cabo Pulmo, Golfo de California, México: Lista sistemática y aspectos de abundancia y biogeografía. Revista Biología Tropical 48, 413-424.

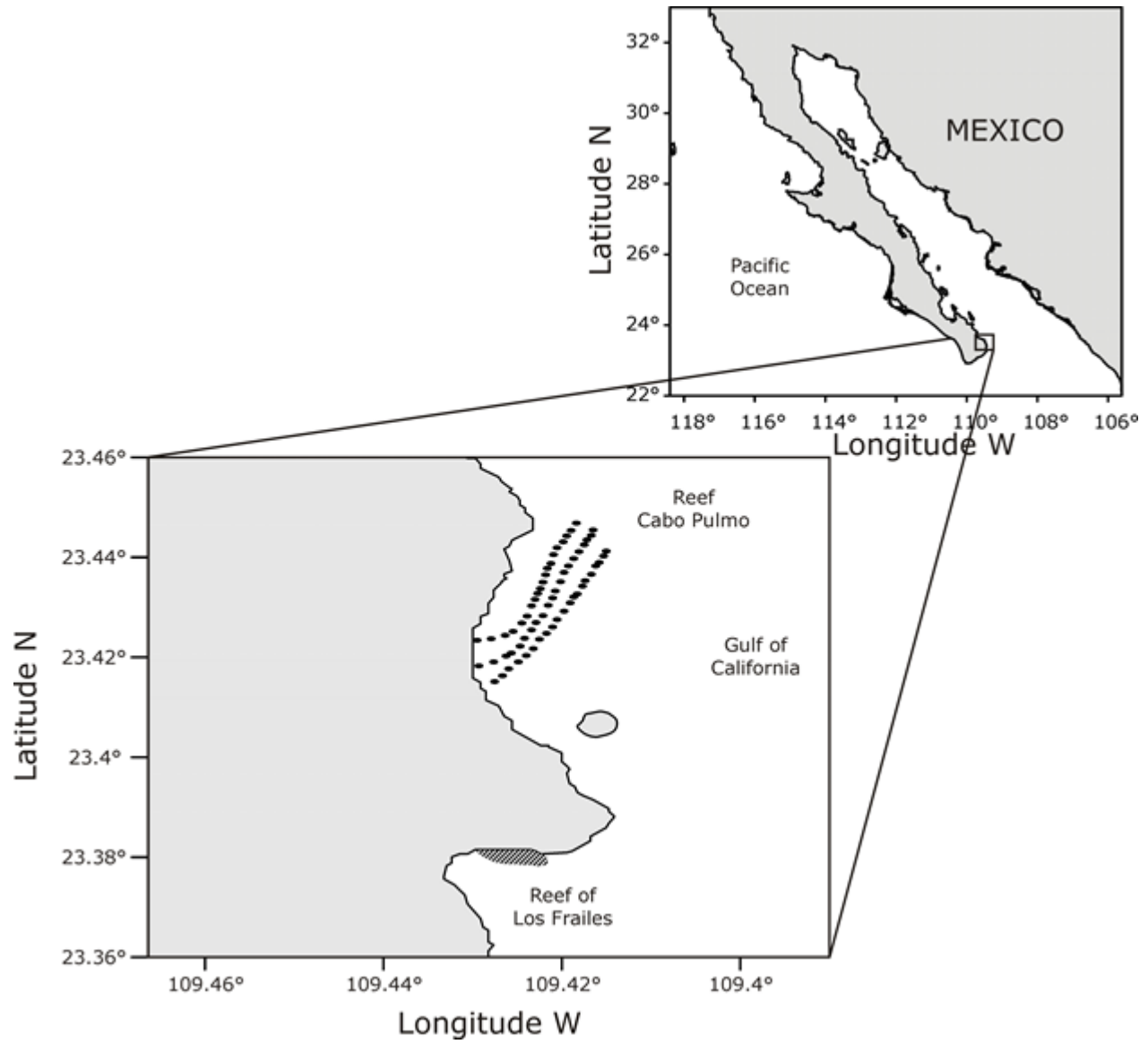


Figure 1. Los Frailes rocky reef, Baja California Sur.
Figura 1. Arrecife rocoso de Los Frailes, Baja California Sur.

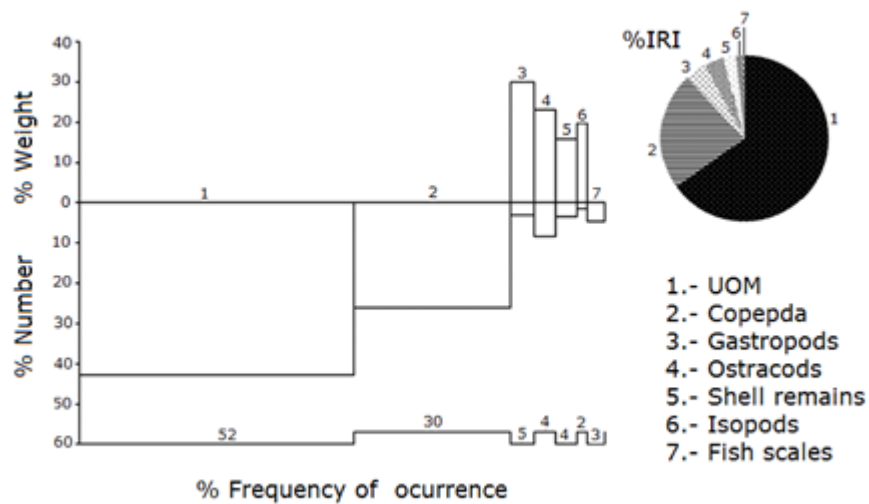


Figure 2. Main prey of the Cortez rainbow wrasse, *Thalassoma lucasanum* shown as percent number, percent weight, frequency of occurrence, and index of relative importance (%IRI). UOM=.Unidentified organic matter.

Figura 2. Presas principales de la arcoiris de Cortés, *Thalassoma lucasanum* mostradas como porcentajes de número, porcentajes de peso, frecuencia de ocurrencia, e índice de importancia relativa (IRI). UOM= Materia orgánica no identificada.