

Food habits and feeding ecology of an estuarine fish assemblage of northern Pacific Coast of Ecuador

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Abstract. In order to analyze trophic relationships occurring within an estuarine fish assemblage in northern Ecuador, 271 stomachs from 12 species were examined. Percent by number (%N) was used to establish trophic organization applying Levins' dietary breadth, Pianka's dietary overlap index and diet Bray Curtis Coefficient to evaluate interespecific relationships. Two planktophagous and 10 carnivorous species were defined with low dietary breadth; the former are species whose diet is based mainly on diatoms. The latter is largely composed by predators of fishes, decapods larvae, shrimps, crabs, polychaetes and bivalves. Of 66 possible dietary overlaps, two were found statistically significant and three functional groups were established. The first one composed by shrimps and mantis shrimp consumption, the second one distinguished by plankton feeders and the third one made up with species, which fed upon shrimps and crabs. These preliminary results suggest partitioning of food resources among these 12 estuarine species, which may favor their coexistence.

Key words: mangrove fishes, diet, trophic structure, resource partitioning.

Resumen: Relaciones tróficas de un ensamble de peces estuarinos en el Pacífico Norte de Ecuador. Se analizaron las relaciones tróficas de un ensamble de peces estuarinos del norte del Pacífico ecuatoriano a partir de las dietas de 271 individuos pertenecientes a 12 especies. A partir del porcentaje en número (N%) se calcularon tres métodos numéricos para establecer la organización trófica: índice de amplitud de nicho de Levins, índice de sobreposición de dietas de Pianka y un análisis de similitud alimenticia utilizando la medida de Bray Curtis para evaluar las relaciones interespecíficas. A partir de las presas identificadas se definieron dos especies de dieta planctófaga y 10 de dieta carnívora con bajos valores de amplitud de dieta. Las especies plantófagas basaron su dieta principalmente en diatomeas. El grupo de los carnívoros está constituido por especies con preferencia por peces, larvas de decápodos, camarones, cangrejos, poliquetos y bivalvos. Solo dos de 66 sobreposiciones de dieta posibles, fueron significativas. Se identificaron tres grupos funcionales, el primero basado en el consumo de camarones y estomatópodos, el segundo en fitoplancton, y el tercer gremio se basó en especies cuya dieta se compuso de camarones y cangrejos. Estos resultados sugieren que el fraccionamiento del recurso alimentario entre estas 12 especies del estuario puede estar favoreciendo su coexistencia.

Palabras clave: peces de manglar, dieta, estructura trófica, partición del recurso.

Introduction

Food habits and feeding ecology research are a fundamental tool to understand fish roles within their ecosystems since they indicate relationships based on feeding resources and indirectly indicate community energy flux (Yánez-Arancibia & Nugent 1977, Hajisamaea *et al.* 2003), which allows inferring competition and predation effects on community structure (Krebs 1999). Other resources such as space and time have also been important for community ecology and the ecological theory predicts that resource partitioning at spatial, temporal and trophic level may increase tolerance of niche overlap reducing competition pressure between co-occurring species. Ross (1986) identified that in aquatic environments food is the main factor and that its partition defines functional groups within the community, which get together in guilds according to trophic similarity.

These trophic guilds (Root 1967) seem to be a consequence of such resource partitioning, which could explain how several species can coexist in the same space by differing in use of several resource dimensions. Several studies have focused on competitive exclusion and resource partitioning in teleost fishes (Zaret & Rand 1971, Hixon 1980, Ross 1986) and have found that habitat partitioning could be related to high dietary overlap among competing species or to interactive competition, where competing species have the same preference by preys (Hixon 1980, Jansen *et al.* 2002).

Little is known about resource partitioning within fish assemblages in Neotropical coastal environments (Arenas-Granados & Acero 1992, Zahorcsak *et al.* 2000, Castellanos & Giraldo 2008) and nothing about trophic organization of ichthyic community of The Cayapas-Mataje Mangroves Ecological Reserve (REMACAM, Spanish abbreviation); therefore, the object of this study was to quantify and compare the diet and trophic interactions of mangrove fishes species from the REMACAM, and to suggest possible mechanisms for their coexistence.

Materials and Methods

Between October 2004 and February 2005, the monitoring of catches by artisanal fishermen was carried out monthly in three places in the REMACAM, which is located in northwestern Ecuador in the Province of Esmeraldas on the border with Colombia (Fig. 1). Sampling comprised 73 effective days as follows: 29 days in San Lorenzo, 22 in Tambillo and 22 in Palma Real. In the area, fishing tasks start early in the morning (about 06:00) and end late in the afternoon (about 18:30). In all monitored catches, driftnets, whose mesh size ranged from $\frac{1}{4}$ to 4 inches (mostly 2 $\frac{3}{4}$ inches) were used.

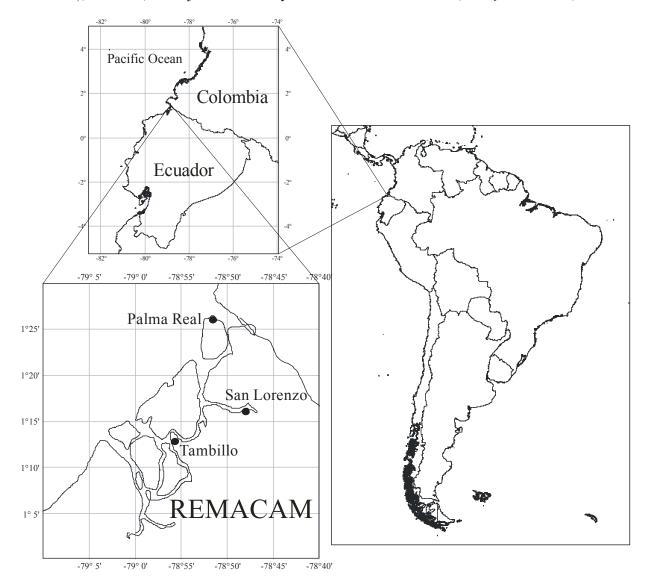


Figure 1. Schematic image from Cayapas-Mataje Mangroves Ecological Reserve (REMACAM) and location of the three monitoring areas (•): Palma Real, San Lorenzo and Tambillo.

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Specimens were identified to species level and their stomachs were extracted and fixed in 10% formalin solution for later analysis. Preys found were identified to the lowest possible taxon and data were quantified using the numerical methods such as percent by frequency of occurrence (%O), percent by number (%N) and percent by weight (%W) revised by Hyslop (1980). In the case of preys such as plankton, items were counted by using a microscope (Olympus CH-20, zoom 40X) and only percent by number was calculated. Cumulative prey curves were constructed for each species to determine if an adequate number of stomachs had been collected to accurately describe diets (Cortés 1997). When the curves reach a stable asymptote, the number of stomachs analyzed is considered sufficient for describing dietary habits.

Contribution of each prey category to fish diets was estimated according to the index of relative importance IRI, since it combines the three indexes indicated above (Hyslop 1980, Cortés 1997). To facilitate diet comparisons among species, IRI was standardized to %IRI (Cortés 1997). For plankton, %IRI was not calculated because weight was not taken. To determine diet specialization of each species, dietary breadth was calculated based on %N for each prey according to standardized Levins' measure which ranges from 0 to 1.0, where values close to 0 indicate specialization while values close to 1.0 show generalization (Hurlbert 1978). To calculate dietary overlap, %N was applied to the index proposed by Pianka (1980) which is a symmetric analysis that allows approximations to overlap between two species in one way; values \geq 0.6 are considered "biologically significant" for teleosts (Pianka 1976). To validate significance of these overlaps, the observed values were compared to a distribution of expected overlap values based on null-model simulations. The distribution of nullmodel data resulted from 1000 randomizations of the diet by using EcoSim v7.42 software (Gotelli & Entsminger 2001). The observed value was considered statistically different from the null distribution if it was greater or less than the simulated index 95% of the time (P<0.05; Winemiller & Pianka 1990). An observed value significantly less than the simulation index would suggest differences in diet or diet partitioning while an observed value significantly higher than the simulation index would suggest similarities in diet or the lack of competition for food resources (Winemiller & Pianka 1990).

Standardized %N data were converted into proportions by using arcsine transformation

function, which is recommended for this data (Gotelli & Ellison 2004). To construct similarity matrix, Bray Curtis Coefficient measure was used, given that such measure is independent from the size sample (Wolda 1981), and the Unweighted Pair Group Method (UPGMA) was used to determine similarity among species using arithmetic averages. To determine dietary similarity level in which a functional group can be defined in an objective way, bootstrapping interactions were used to test for statistical significance of similarity of each branch in the cluster. In each association observed, a resampling of similarity values was run (1000 times) and such null distribution was contrasted with the observed similarity value. The observed value was considered statistically different from the null distribution if it was greater or less than the simulated index 95% of the time. This technique gives greater resolution than those which determine a unique significance value for all studied species together (McKenna 2003).

Results

Stomach analysis: 271 stomachs from 12 species were analyzed. Ontogenetic changes were not determined, since sizes were homogeneous and individuals in different development stages were not collected. Samples varied between eight (*Eugerres periche* (Evermann & Radcliffe, 1917)) and 43 stomachs (*Mugil cephalus* Linnaeus, 1758) (Tab. I).

Prey species accumulation curves. Of the 12 species studied, nine (75%) obtained an insufficient sampling such as *M. cephalus*, *O. libertate*, *S. peruviana*, *L. pacificus*, *E. currani*, *E. periche*, *G. cinereus*, *P. grandisquamis* and *H. leuciscus* (Fig. 2A). According to the remaining cumulative prey curves, 25 stomachs were enough to estimate feeding habits of *C. caninus*; 15 for *L. jordani* and seven for *D. peruvianus* (Fig. 2B).

Food composition. O. libertate and M. cephalus were found to feed on diatoms, mainly on Coscinodiscus sp. (25 %N and 42.34 %N, respectively) (Table II), and the other 10 species were found to be carnivorous. Invertebrates were the main food item for most species studied. Crabs were the most important prey item for L. jordani (100%IRI), H. leuciscus (60.7%IRI) and G. cinereus (64.48%IRI); shrimps contributed more than 90%IRI to the diet of P. grandisquamis and E. currani; whereas, polychaetes comprised the 98.8 %IRI of the diet of E. periche; C. caninus was the only species which fed exclusively on fishes. Insects, cnidarians and gastropods were rare items in the diet of species (Table III and IV).

Feeding ecology. The species E. currani had the broadest diet (0.89), whereas D. peruvianus, H. leuciscus, C. caninus and S. peruviana presented the narrowest feeding spectrum (Table V). Only two out of 66 possible dietary overlap, were biologically significant, which are: O. libertate – M. cephalus and P. grandisquamis – E. currani (Table VI). Simulation results of null model confirmed the low trophic overlap levels within this assemblage given that overlap average observed was not significantly different from expected average (p=0.16) (Gotelli & Graves 1996). Based on common contribution of preys to the species diets, three functional groups were established, based on dietary similarities considered as significant (p<0.05). The first group was composed by *P. grandisquamis* and *E. currani* with similarity higher than 0.8 and an overlap of 0.74, the planktophagous species *M. cephalus* and *O. libertate* whose diet similarity was higher than 0.7 and its overlap was 0.78, made up the second relationship. Due to the fact that *G. cinereus* and *H. leuciscus* had an overlap value near the limit (p=0.048), the cluster analysis identified these species as the third functional group (Fig. 3).

Table I. Sampling data of fish species caught at Palma Real, San Lorenzo and Tambillo (Ecuador), range size and weight (2004-2005).

Family	Species		Weig	ht (g)	Total leng	gth (cm)
	Species	Ν	Average	Range	Average	Range
Mugilidae	Mugil cephalus	43	172.33	35-285	26.23	22-32
Carangidae	Selene peruviana (Guichenot, 1866)	39	100.31	58-190	21.1	18-26
	Caranx caninus Günther, 1867	38	172.45	144-200	23.61	21-25
Clupeidae	Opisthonema libertate (Günther, 1867)	33	114.3	72-150	22.33	20-24
Sciaenidae	Larimus pacificus Jordan & Bollman, 1890	27	102.22	72-142	19.74	18-21
Gerreidae	Eucinostomus currani Yáñez-Aranciba, 1980	22	84.09	56-154	18.32	16-24
Lutjanidae	Lutjanus jordani (Gilbert, 1898)	17	333.41	210-820	27.71	24-39
Mullidae	Pseudupeneus grandisquamis (Gill, 1863)	15	115.27	80-160	20.67	18-23
Haemulidae	Haemulopsis leuciscus(Günther, 1864)	11	195	92-462	23	19-33
Gerreidae	Diapterus peruvianus (Cuvier, 1830)	9	300.86	152-460	24.78	21-29
	Gerres cinereus (Walbaum, 1792)	9	219.33	134-380	24.22	20-32
	Eugerres periche	8	163.63	108-275	22.5	19-27

Discussion

Regardless of variables assessed invertebrates predators have been most of times the main group within coastal systems, i.e. P. grandisquamis and C. caninus have been reported as shrimp feeders (Espinosa 1997. Adames 2000), L. jordani as crustacean predator (López-Peralta & Arcila 2002), G. cinereus with a diet based on polychaeta, tunicates and bivalves (Arenas-Granados & Acero 1992. Layman & Silliman 2002), E. periche has been found to feed upon crustacean (Arroyave 1998) and D. peruvianus was reported to feed mainly upon echinoderms and mollusks (López-Peralta & Arcila 2002). Regarding planktophagous species, M. cephalus and O. libertate have been reported as plankton feeders in similar habitats (De Silva & Wijeyaratne 1976, Gallardo-Cabello et al. 1991. Manrique 2000), which agrees with results obtained in this research. Data on diet of H. leuciscus and E. currani are not available, so this paper presents the first record prey items consumed by these species. Regarding piscivore species, their scarcity (only C. caninus was found to feed merely on fishes) could be related with

environmental impact exerted in the area by anthropogenic activities such as shrimp and palm crops, which have affected water quality due to chemical use (INEFAN-GEF 1999. Noboa 2000), for many carnivorous fishes, vision is the most important sense for prey detection and water clarity is one of the factors affecting their occurrence (Blaber 2000 cited in Hajisamaea et al. 2003). In general, it is not possible to establish feeding habits for any particular species (only prey items reported for two carnivorous species P. grandisquamis and L. jordani agree with our findings), patterns observed are determined by fishes responses to the particular habitat characteristics such as predator-prey assemblage, prey relative abundance in the environment (Labropoulou & Eleftheriou 1997) and water productivity (Blay 1995). Dietary breadth values found were very low for most species (less than 0.5), oscillating between 0 and 0.89 because species had a %N higher than 40% focused only on one resource. One factor upon which breadth is based, is prey availability because when it is abundant, breadth trends to be very low (Hajisamaea et al. 2003) which is related to habitat structural complexity. A greater physical structure creates more micro-habitat types which allow competitors coexistence as well as predator and prey persistency (Crowder & Cooper 1982). It also generates more complex trophic relations in terms of guilds number and functional groups as a result of the breadth of resource utilization (Ángel & Ojeda 2001). On the other hand, Yánez-Arancibia & Sánchez-Gil (1988) proposed that tropical estuarine ecosystems have great habitat heterogeneity, which allows high prey availability and so, greater breadth trophic spectrum. Our hypothesis is that low dietary breadth value in this estuary can be a species response to the decreasing availability of food resources due to artisanal trawl fishery outside and inside the estuary (Solís-Coello & Mendívez 2001). This reduction in dietary breadth would be a specialization mechanism toward the optimums resource of each species; thereby, increasing coexistence possibilities.

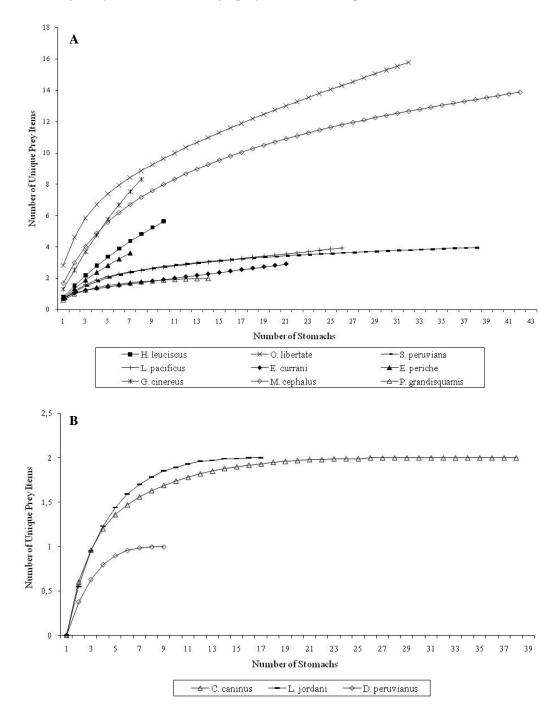


Figure 2. Randomized cumulative prey curves of 12 estuarine fishes. A) Curves showing insufficient sampling. B) Curves showing sufficient sampling (see text).

Table II. Contribution by number (%N) and frequency of occurrence (%O) of the major taxa and identifiable dietary categories to the composition of the overall diet of two planktophagous fishes.

	O. lib	ertate	M. cej	phalus
	%N	%O	%N	%0
Phylum Cyanobacteria (Bacteria)				
Family Merismopediaceae				
Agmenellum sp.			5.86	9.30
Phylum Ochrophyta (Diatoms)				
Family Skeletonemaceae				
Skeletonema costatum	37.53	54.54	14.74	34.88
Family Coscinodiscaceae				
Coscinodiscus perforatus var. cellulosa	0.76	3.03	1.7	6.98
Coscinodiscus sp.	25.00	78.79	42.34	48.84
Family Rhizosoleniaceae				
Proboscia alata	2.13	18.18	0.57	6.98
Rhizosolenia hebetata	15.09	48.48	12.67	34.88
Rhizosolenia setigera	0.15	3.03		
Family Biddulphiaceae				
Biddulphia alternans	0.30	3.03		
Biddulphia sinensis	0.91	9.10		
Family Triceratiaceae				
Odontella mobiliensis	0.30	3.03	0.19	2.32
Odontella regia	5.03	48.48		
Family Fragilariaceae				
Asterionellopsis glacialis	0.15	3.03		
Familiy Lithodesmiaceae				
Lithodesmium undulatum			0.19	2.32
Phylum Bacillariophyta (Plants)				
Family Diploneidaceae				
Diploneis bombus var. bambiformis	0.15	3.03	0.19	2.32
Diploneis sp.	0.15	3.03		
Diploneis smithii var. rhombica			0.76	6.98
Family Rhopalodiaceae				
Epithemia sp.			0.19	2.32
Family Bacillariaceae				
Nitzschia navicularis			0.19	2.32
Unidentified diatom #1	0.15	3.03	13.42	9.30
Phylum Chlorophyta (Green algae)				
Family Scenedesmaceae				
Scenedesmus bijuga	11.74	66.67	6.99	20.93
Phylum Dinophyta (Protozoa)				
Family Peridiniaceae				
Heterocapsa triquetra	0.46	9.10		

*Taxonomic classification according to http://www.catalogueoflife.org/annual-checklist/2007/

		E. pe	E. periche D. peruvianus				G. cinereus			H. leuciscus			L. pacificus		
	%N	%0	%W %]	RI %	6N %O	%W %IRI	%N	%0	%W %IR	[%N	%0	%W %IRI	%N	%0	%W %I
Phylum Rhodophyta (Red Algae)															
Family Delesseriaceae															
Caloglossa sp.							4	11.1	0.2 2.13						
Phylum Chordata															
Unidentified fish										0.66	18.2	3.78 4.3	22	40.7	78.4 66.
Phylum Arthropoda															
Family Squillidae	7.14	12.5	1.32 3.	54											
Family Penaeidae															
Unidentified penaeid shrimps							8	22.2	1.93 10.06	5 1.29	27.3	4.21 8.01			
Unidentified hermit										0.32	9.09	1.63 0.95			
Unidentified decapod zoeae													2	3.7	0.01 0.1
Unidentified crabs							8	22.2	27.8 36.32	0.32	9.09	5.38 2.77			
Unidentified brachyura							8	11.1	2.22 5.19						
Unidentified brachyura larvae													56	33.3	3.59 32.2
Family Calappidae										0.32	9.09	62.1 30.28			
Family Porcellanidae							4	11.1	0.33 2.2						
Unidentified crustaceans eggs										97.09	9.09	13.6 53.7			
Order Hemiptera							8	22.2	0.01 8.13						
Phylum Mollusca															
Familiy Mytilidae				1	00 44.4	95.7 100							20	3.7	0.66 1.2
Family Cerithiidae							4	11.1	0.26 2.16						
Phylum Annelida															
Family Spionidae	42.9	12.5	16.6 25	56											
Unidentified Polychaeta 1	28.6	37.5	13.9 54	.83											
Unidentified Polychaeta 2	21.4	12.5	15.7 15	.97											
Unidentified Polychaeta 3							12	11.1	0.19 6.19						
Phylum Cnidaria															
Unidentified anemone							44	11.1	10.4 27.61						
Digested material			52.5			4.34			56.7			9.34			17.4

Table III. Contribution by number (%N), by weight (%W), frequency of occurrence (%O) and standardized index of relative importance (%IRI) of the major taxa and identifiable dietary categories to the composition of the overall diet of five estuarine fish species.

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	C. caninus		,	S. peruviana		P. grandisquamis				E. currani			L. jordani		
	%N	%0	%W %IRI	%N	%0	%W %IR	[%N	%0	%W %IRI	%N	%0	%W %IRI	%N	%0	%W %IR
Phylum Chordata															
Family Engraulidae	98.9	65.8	82 98.98												
Family Atherinidae	1.06	13.2	8.27 1.02												
Unidentified fish				3.94	20.5	22.4 7.78									
Phylum Arthropoda															
Family Squillidae				1.97	7.69	1.15 0.35	24.1	13.3	3.59 3.43	20	4.54	4.45 17.92			
Family Penaeidae															
Potrachypene precipua				0.49	2.56	24.6 0.93									
Unidentified penaeid shrimps							75.9	66.7	80.5 96.57	40	4.54	20.9 44.62			
Unidentified decapod larvae				93.6	43.6	51.1 90.94									
Unidentified brachyura													80	47.1	26.2 78.74
Family Xanthidae													20	17.7	56.5 21.26
Unidentified crustaceans										40	4.54	11.1 37.46			
Digested material			9.69			0.76			15.9			63.6			17.3

Table IV. Contribution by number (%N), by weight (%W), frequency of occurrence (%O) and standardized index of relative importance (%IRI) of the major taxa and identifiable dietary categories to the composition of the overall diet of five estuarine fish species.

*Taxonomic classification according to http://www.catalogueoflife.org/annual-checklist/2007/

Species	В'
Eucinostomus currani	0.89 (3)
Eugerres periche	0.72 (4)
Pseudupeneus grandisquamis	0.58 (2)
Larimus pacificus	0.50 (4)
Lutjanus jordani	0.47 (2)
Gerres cinereus	0.40 (9)
Mugil cephalus	0.24 (14)
Opisthonema libertate	0.21 (16)
Selene peruviana	0.05 (4)
Caranx caninus	0.02 (2)
Haemulopsis leuciscus	0.01 (6)
Diapterus peruvianus	0.00 (1)

Table V. Dietary breadth values calculated for each species with the standardized Levins' measure (B'). Number within parentheses indicates number of prey for each species.

The two significant dietary overlaps that were found out of 66 possibilities are given by only three prey types (diatoms, shrimps and mantis shrimps), which ratifies the low dietary breadth. According to Schoener (1974) and Ross (1986), our findings suggest in a preliminary basis that among fish species that inhabit this estuary there is food partitioning as the main coexistence mechanism, since this resource is considered the main limiting factor in aquatic environments, avoiding diet overlapping, which in turn avoids competition.

There were two main restrictions for the diet

analyses performed in this research. First, although a high level of prey identification (LPI) was reached for most of the items (32 out of 47 items were identified up to family), niche breadth value could be influenced by such LPI. This effect was considered by Greene & Jaksic (1983) who proposed that the use of LPI could underestimate species dietary breadth, and also influence IRI results (Hansson 1998). In the same way, those values of dietary overlap could have been overestimated by the LPI (Greene & Jaksic 1983).

Table VI. Dietary overlap values between the studied species. The overlap was calculated with Pianka's Index. where 0 and 1 values correspond to the minimum and maximum of dietary overlap respectively. Values equal or greater than 0.6 are considered significant (numbers in bold). *Ol) Opisthonema libertate, Mc) Mugil cephalus, Cc) Caranx caninus, Sp) Selene peruviana, Pg) Pseudupeneus grandisquamis, Hl) Haemulopsis leuciscus, Lj) Lutjanus jordani, Lp) Larimus pacificus; Ec) Eucinostomus currani, Ep) Eugerres periche, Dp) Diapterus peruvianus, Gc) Gerres cinereus.*

	Ol	Мс	Cc	Sp	Pg	Hl	Lj	Lp	Ec	Ер	Dp	Gc
Ol	-											
Мс	0.7764											
Cc	0.0000	0.0000	-									
Sp	0.0000	0.0000	0.0000	-								
Pg	0.0000	0.0000	0.0000	0.0064	-							
Hl	0.0000	0.0000	0.0000	0.0003	0.0127	-						
Lj	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	-					
Lp	0.0000	0.0000	0.0000	0.0146	0.0000	0.0023	0.0000	-				
Ec	0.0000	0.0000	0.0000	0.0070	0.7364	0.0089	0.0000	0.0000				
Ep	0.0000	0.0000	0.0000	0.0000	0.0385	0.0000	0.0000	0.0000	0.0000	-		
Dp	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.3153	0.0000	0.0000	-	
Gc	0.0000	0.0000	0.0000	0.0000	0.1561	0.0027	0.1590	0.0000	0.1092	0.0000	0.0000	-

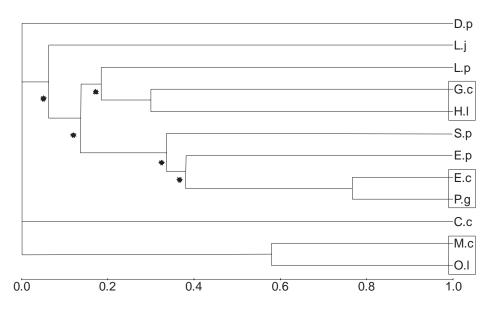


Figure 3. Diet similarity cluster of 12 species that inhabit an estuarine area from Ecuadorian Pacific. Boxes indicate significant grouping and asterisks refer to links not approved by bootclus. *Ol) Opisthonema libertate, Mc) Mugil cephalus, Cc) Caranx caninus, Sp) Selene peruviana, Pg) Pseudupeneus grandisquamis, Hl) Haemulopsis leuciscus, Lj) Lutjanus jordani, Lp) Larimus pacificus; Ec) Eucinostomus currani, Ep) Eugerres periche, Dp) Diapterus peruvianus, Gc) Gerres cinereus*

Indeed, some authors reporting broad dietary overlap as a common characteristic among estuarine fishes have identified preys up to class (Ley *et al.* 1994).

Since this study analyzed commercial fish species, which are destined for selling in local markets and for consumption, getting a high sample number was a difficult task (second restriction), resulting in an insufficient sample size, situation reflected in the cumulative curves, where only three out of 12 species curves reached an asymptote. In this way, as more species are included in the research and prey identification level is improved, it is possible to find greater resource partitioning.

The present findings contribute to an understanding of how resource partitioning could determine species coexistence in highly diverse marine tropical environment (in REMACAM's estuary at least 102 fish species occur, SQUALUS

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Foundation data unpublished) and highlights the need for further studies to evaluate the effect of partitioning on space and time in this area, and also if competitive exclusion principle does occur.

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