Research Article

Feeding ecology of juvenile marine fish in a shallow coastal lagoon of southeastern Mexico

Daniel Arceo-Carranza[1] & Xavier Chiappa-Carrara[1]
[1]Unidad Multidisciplinaria de Docencia e Investigación, Universidad Nacional Autónoma de México
Laboratorio de Ecología, Puerto de Abrigo s/n, CP 97356, Sisal, Hunucmá, Yucatán, México
Corresponding author: Daniel Arceo-Carranza (darceo@ciencias.unam.mx)

ABSTRACT. Many species of marine fish use coastal lagoons during early stages of their life cycles due to the protection provided by their turbid waters and complex structure of the environment, such as mangroves and mudflats, and the availability of food derived from the high productivity of these sites. In this study, we analyzed the diet of six species of juvenile marine fishes that use a karstic lagoon system in the northwest portion of the Yucatan Peninsula, Mexico. Through stomach contents analysis we determined the trophic differences among *Caranx latus*, *Oligoplites saurus*, *Trachinotus falcatus*, *Synodus foetens*, *Lutjanus griseus*, and *Strongylura notata*. *C. latus*, *O. saurus, S. foetens*, and *S. notate*, which are ichthyophagous species (>80% by number). *L. griseus* feeds mainly on crustaceans (>55%) and fish (35%), while *T. falcatus* feeds on mollusks (>50% bivalves, >35% gastropods). The analysis of similarities (ANOSIM) showed differences in the diet of all species. Cluster analysis, based on the Bray-Curtis similarity matrix revealed three groups; one characterized by the ichthyophagous guild (*S. notata*, *S. foetens, C. latus*, and *O. saurus*), other group formed by the crustacean consumers (*L. griseus*), and the third, composed by the mollusk feeder (*T. falcatus*). Species of the ichthyophagous guild showed overlap in their diets, which under conditions of low prey abundance may trigger competition, hence affecting juvenile stages of these marine species that use coastal lagoons to feed and grow.
Keywords: juvenile fish, stomach contents, diet breadth, piscivory, trophic overlap.

Ecología alimentaria de peces marinos juveniles en un sistema lagunar somero del sureste de México

RESUMEN. Muchas especies de peces marinos utilizan las lagunas costeras durante los estadios juveniles de su ciclo de vida, por la protección que les provee las aguas turbias y la complejidad estructural de ambientes como los manglares y planicies lodosas, además de la disponibilidad de alimento originada por la alta productividad de estos sitios. En el presente estudio se analizó la dieta de juveniles de seis especies de peces marinos que utilizan una laguna cárstica en el noroeste de la Península de Yucatán, México, para determinar las diferencias alimentarias en los contenidos estomacales de *Caranx latus*, *Oligoplites saurus*, *Trachinotus falcatus*, *Synodus foetens*, *Lutjanus griseus* y *Strongylura notata. C. latus*, *O. saurus, S. foetens* y *S. notata*, que son especies ictiófagas (>80% en número). *L. griseus* se alimenta principalmente de crustáceos (>55%) y peces (35%), mientras que *T. falcatus* se alimenta de moluscos (>50% bivalvos y >35% gasterópodos). El análisis de similitud (ANOSIM) mostró diferencias en la dieta de todas las especies. El análisis de agrupación, basado en la matriz de similitud de Bray-Curtis mostró tres grupos; uno caracterizado por peces ictiófagos (*S. notata*, *S. foetens*, *C. latus* y *O. saurus*), otro grupo formado por consumidores de crustáceos (*L. griseus*) y el tercer grupo, conformado por consumidores de moluscos (*T. falcatus*). Los resultados indican que existe traslape en las dietas de las especies que forman el grupo de peces piscívoros. Por lo tanto, en condiciones de baja abundancia de presas puede desencadenar la competencia por el alimento afectando las etapas juveniles de estas especies marinas que utilizan las lagunas costeras para alimentarse y crecer.
Palabras clave: peces juveniles, contenidos estomacales, amplitud de dieta, piscivoría, traslape trófico.

Corresponding editor: Claudia Bremec

INTRODUCTION

Coastal lagoons are recognized as high productivity systems that provide shelter for early-life stages of many marine fish species. Juvenile fish spend time in shallow coastal waters where they feed and grow to sub-adults before migrating into deeper waters (Blay *et al*., 2006). Shallow soft-bottom habitats, including mangroves and mudflats, are important nurseries for juvenile fish (Laegdsgaard & Johnson, 1995; Nagelkerken & Van der Velde, 2002; Verweij *et al*., 2006; Tse *et al*., 2008; Arceo-Carranza *et al*., 2009). The productive and structurally complex environment provided by mangrove stands is used as feeding grounds and refuge by juvenile fishes (Ruiz *et al*., 1993; Laegdsgaard & Johnson, 2001) and many juveniles and sub-adults of nocturnal species use these areas as refuge habitats during the day (Cocheret de la Morinière *et al*., 2004; Verweij *et al*., 2006). Even if mudflats are structurally less complex, they hold a great abundance and diversity of invertebrates and are used as feeding grounds for juvenile fishes (Laegdsgaard & Johnson, 2001; Tse *et al*., 2008).

To assess the feeding habits is fundamental for understanding the role of fish within their ecosystems, since they indicate relationships among species based on feeding resources and they indirectly indicate community energy flux (Yáñez-Arancibia & Nugent, 1977; Hajisamaea *et al*., 2003). This allows inferences to be drawn regarding the effects of competition and predation on the community structure (Krebs, 1999). Other resources, such as space, are also important for community ecology. Ecological theory predicts that resource partitioning at the spatial, temporal, and trophic level may reduce niche overlap and thereby reduce competition pressure between co-occurring species. Ross (1986) identified that food is the main limiting factor in aquatic environments, and suggested that the use of similar prey types defines functional groups within the community, so species can be grouped in guilds according to their trophic similarity. Trophic guilds (Root, 1967) seem to be a consequence of resource partitioning and could explain how several species can co-exist in the same space by the differential use of resources in several dimensions, including time. Studies of competitive exclusion and resource partitioning in teleost fishes (Hixon, 1980; Ross, 1986) have found that habitat partitioning could be related to high dietary overlap among competing species or to interactive competition, when competing species have the same preference for prey species (Jansen *et al*., 2002; Ramírez-Luna *et al*., 2008). Under the assumption that juvenile marine fish species use shallow coastal waters as feeding and refuge grounds, the goal of this study was to analyze and compare the diet of six marine fish species that use a shallow karstic lagoon and to assess the trophic overlap among them.

MATERIALS AND METHODS

La Carbonera Lagoon is located in the northeastern part of the Yucatán Peninsula. It is a semi-enclosed water body with an average depth of 30 cm and is surrounded by mangroves, mainly *Rhizophora mangle* and *Avicennia germinans.* The lagoon bottom is dominated by mud flats. It also contains freshwater seeps, although the average salinity is 35. Samples were obtained bimonthly from beach seine landings (40 m in length and mesh size of 2.5 cm) in nine soft-bottom sites (Fig. 1), from April 2008 to December 2010. Collected specimens were euthanized in ice slurry and preserved in formaldehyde (10%). In the laboratory, standard length (SL ± 0.1 cm) of each individual was measured, and the body weight (g ± 0.1) was obtained. Among all landings, juvenile marine species that use the lagoon to feed (Gallardo *et al*., 2012) were selected, since they are important in the transport of matter and energy between coastal environments. Maturity stages were assessed from the available data on length at first sexual maturity (Tzeek-Tuz, 2013; Froese & Pauly, 2014). Furthermore, we choose those species whose abundance was consistently greater than 30 individuals to analyze their stomach contents. According to these criteria, the species analyzed in this study were: *Caranx latus*, *Oligoplites saurus*, *Trachinotus falcatus*, *Synodus foetens*, *Lutjanus griseus* and *Strongylura notata*. A species accumulation curve was obtained to assess the sampling effort representativeness, measured as the number of stomachs analyzed. Parameters of the Clench model (1979) were obtained using Statistica 7.0 (Jiménez-Valverde & Hortal, 2003) considering 500 permutations of data obtained with EstimateS 8.0 (Colwell, 2006). The coefficient of determination was used as an indicator of the goodness of fit, and slope values below 0.1 were considered asymptotic.

Stomach contents

The number (N), weight (W), and frequency of occurrence (FO) of each dietary component were quantified and expressed as percentages (Hyslop, 1980). The index of relative importance (IRI) was calculated for each dietary component as (Pinkas *et al*., 1971).

$$IRI = (\%N + \%W)\% \, FO$$

Cortés (1997) suggested that IRI values should be expressed as percentages (% IRI).

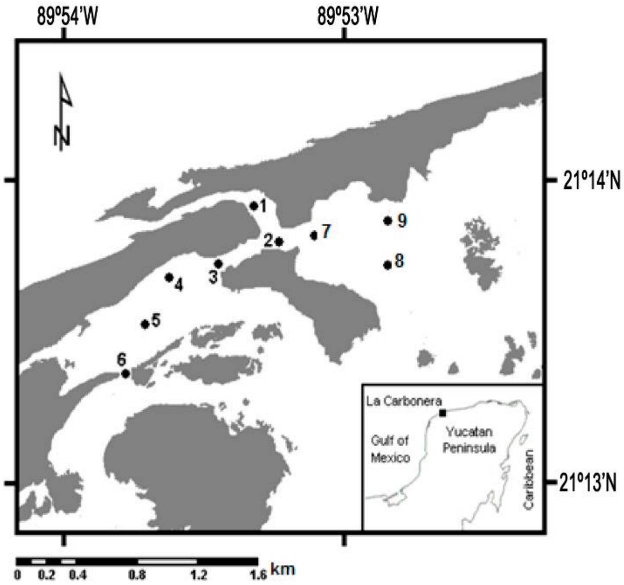

Figure 1. La Carbonera Lagoon (Yucatán, Mexico) and the sampling sites.

Data analysis

Trophic guilds

One-way analysis of similarity (ANOSIM) was used to test the null hypothesis of no differences in the diet composition between the studied species over a Bray-Curtis rank similarity matrix constructed with the fourth-root transformed data. A cluster (using group-average linkage) was generated to determine the trophic guilds based on the diet similarities among species. Analyses were performed using the statistical package PRIMER 6 (Clarke & Warwick, 2001).

Diet breadth

The diet breadth was calculated using the Levin´s standardized index (Krebs, 1999) as:

$$B_i = 1/\text{n} - 1 \ \{(1/\Sigma \ pij^2) - 1)\}$$

where B_i is the Levin index for species *i*; p_{ij} is the proportion of the diet of predator *i* that is made up of prey *j*, and *n* is number of prey species. B_i values range between 0 and 1. Zero indicates that fish feed on only one prey type, representing the minimum diet breadth and high feeding specialization. As the index approaches 1, the species consumes all food resources in the same proportion (p_j = 1/n), representing no selection among prey types and the widest possible trophic niche (Krebs, 1999).

Feeding strategy

The Amundsen *et al*. (1996) method, which is a modification of Costello´s (1990) graphical method, was used to obtain the feeding strategy of each species. This method uses the frequency of occurrence (%FO) and a percent measure of abundance (%N) to provide a description of prey importance (dominant or rare), predator feeding strategy (specialized or generalized), and the degree of homogeneity of feeding in the predator population (Bacha & Amara, 2009). To determine the feeding strategy, prey species were grouped as fish, crustaceans, mollusks, insects, and "others".

Diet overlap index

Shoener's index (Shoener, 1971) of niche overlap (α) was used to assess dietary overlap considering that α = 0 indicates that diets have no common items and α = 1 indicates identical diets (Wallace, 1981).

RESULTS

We analyzed 223 individuals belonging to six species (*C. latus, O. saurus, T. falcatus, S. foetens, L. griseus* and *S. notata*). Of them, 185 (83%) presented some type of food in their stomachs while 38 (17%) were empty (Table 1). *C. latus, O. saurus, T. falcatus, and S. foetens* were caught only as juvenile fish, according to data on length at first sexual maturity (Froese & Pauly, 2014); *S. notata* was captured in juvenile and adult stage (Tzeek-Tuz, 2013), and data of length at first maturity of the lizardfish *S. foetens*, are not available but, according to their sizes (4.0-15 cm), they were considered as juvenile fish (Fig. 2).

Diet composition

Species accumulation curves for each species are shown in Figure 3; slope values of the Clench (1979) model are greater than 0.1, with R^2 values >0.9. *C. latus* fed mainly on fish (78% IRI), but crustaceans were also consumed (20% IRI). *O. saurus* fed on small fish (97% IRI), principally Engraulidae. *T. falcatus* fed on mollusks, mainly bivalves (57% IRI) and gastropods (34% IRI). Crustaceans (7% IRI) such as amphipods, tanaids, and ostracods, were also present. *S. foetens* fed primarily on small fish (86% IRI) such as Gerreidae (*Eucinostomus* spp.), Cyprinodontidae (*Floridich polyommus*), and Clupeidae (*Opisthonema oglinum*); penaeid crustaceans were also present (8% IRI). Small Synodontidae were also found in their stomachs (10% IRI), which may constitute an evidence of cannibalism. The grey snapper (*Lutjanus griseus*), which is a commercially important species, fed on a wide variety of crustaceans (59% IRI), such as penaeid shrimps, amphipods, mysids, and isopods but also on fishes (35% IRI) such as Ariidae, Clupeidae and Cyprino-dontidae. The Needlefish *S. notata* also consumed fishes (91% IRI) (Cyprinodontidae, Clupeidae, Gerreidae, and Atherinopsidae, mainly *Menidia* sp.), as well as decapod crustaceans (8% IRI) (Table 2).

Table 1. Size interval of captured specimens (standard length) and sample size (number of stomachs) of six marine fish species in La Carbonera Lagoon.

Species	Total number of stomachs	Number of empty stomachs	Percentage of empty stomachs (%)	Standard length (cm)
C. latus	42	12	28.57	4.70-23.50
O. saurus	36	0	0	5.09- 8.82
T. falcatus	35	10	28.57	4.70-18.00
S. foetens	34	1	2.94	4.02-15.10
L. griseus	39	5	12.82	3.15-22.50
S. notata	37	10	27.02	3.27-41.50

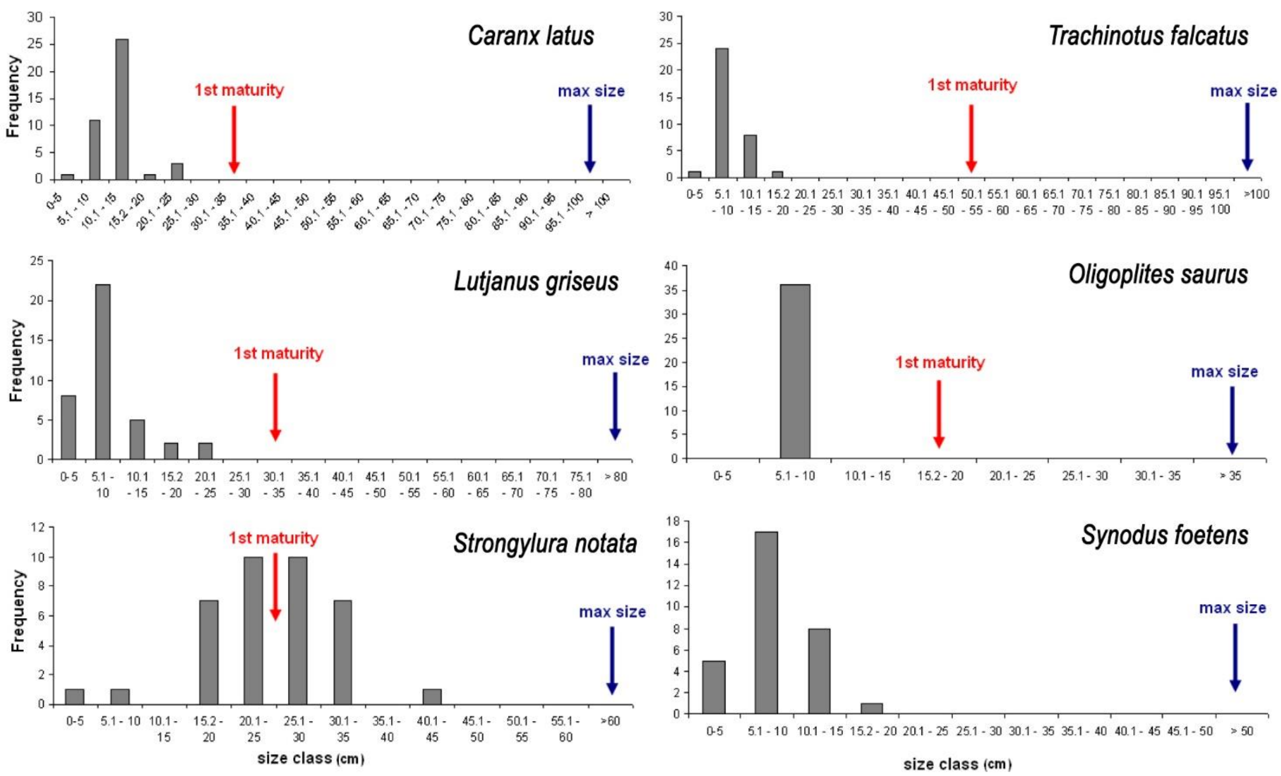

Figure 2. Length-frequency distributions of the fish species analyzed. First maturity and maximum size are shown (Tzeek-Tuz, 2013; Froese & Pauly, 2014).

Trophic guilds

The Bray-Curtis similarity index formed three groups (Fig. 4). The first includes *C. latus*, *O. saurus*, *S. foetens*, and *S. notata* which form the piscivorous trophic guild; the second has *Lutjanus griseus* that displayed a mixed diet composed of fish and crustaceans; while in the third group appears *T. falcatus*, a specialized carnivore whose mouth and dentine adaptations allow it to crush the calcareous shells of mollusks, mainly bivalves.

In the ichthyophagous guild, the analysis of similarities (ANOSIM) showed significant differences between each species (R Global = 0.109; P = 0.001) indicating that the most important prey types in the diet of each species differ (Table 3) even if fish are their main food.

Diet breadth

The diet breadth values indicate that all species display a specialized type of feeding behavior. Values of the Levin's index fall below 0.6 (*O. saurus*, Bi = 0.026; *T. falcatus*, Bi = 0.123; *L. griseus*, Bi = 0.124; *S. notata*, Bi = 0.036; *S. foetens*, Bi = 0.163; *C. latus*, Bi = 0.042), indicating that only a few prey types dominate the diet and predators can be classified as stenophagous species.

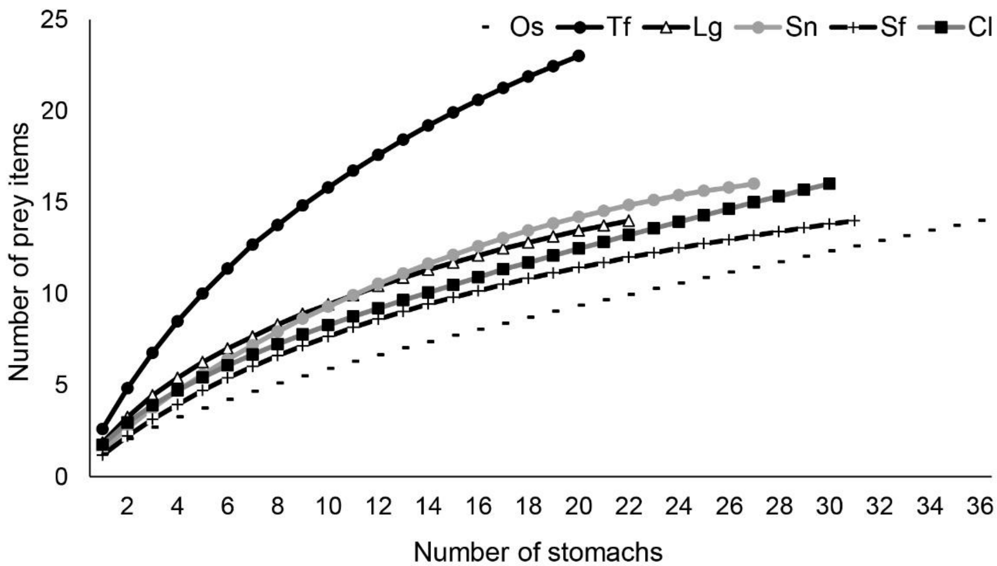

Figure 3. Prey type accumulation curve (scaled by the number of stomachs) of each of the six marine fish species in the La Carbonera Lagoon (Os: *Oligoplites saurus*, Tf: *Trachinotus falcatus*, Lg: *Lutjanus griseus*, Sn: *Strongylura notate*, Sf: *Synodus foetens*, Cl: *Caranx latus*).

Feeding strategy and trophic overlap

Values of the Shoener's index of trophic overlap were greater than 0.6, indicating that the piscivorous species display a significant diet overlap (Table 4).

The feeding strategy displayed by the specialist fish analyzed was confirmed by the Costello method (Fig. 5). *O. saurus*, *S. notate*, *S. foetens*, and *C. latus* were classed as piscivorous. *L. griseus* specializes in the consumption of penaeid crustaceans, and *T. falcatus* feeds mainly on mollusks.

DISCUSSION

Shallow soft-bottom habitats are recognized worldwide as important nurseries for many marine fish species. Several factors, including high structural complexity, low predation risk, and high foraging efficiency, may explain why juvenile of many marine species use these shallow habitats (Tse *et al*., 2008).

The six species of fish examined are considered to be marine migrants (Castro-Aguirre *et al*., 1999; Elliott *et al*., 2007) that use shallow waters as nurseries, refuge, and feeding grounds. They are carnivorous species, mainly piscivores with stenophagy and trophic specialization (Carr & Adams, 1973; Arceo-Carranza *et al*., 2004; Cocheret de la Morinière *et al*., 2004; Cruz-Escalona *et al*., 2005; Guevara *et al*., 2007). Even if many marine fish species exhibit marked changes in their diet according to the temporal availability of prey and life stage of individuals (Blaber, 1997; Platell *et al*., 1997; Hajisamae, 2009), our observations allow to say that five of them show a relatively homogeneous diet over time since the overall occurrence of these species within the study area is low (Gallardo-Torres *et al*., 2012). The species accumulation curves did not reach the asymptote, but values of $r^2 > 0.9$ indicate a good fit of the Clench model. Although one or two prey types dominate the diets of the majority of the analyzed species, representativeness of prey types was not achieved indicating that a greater number of stomachs ought to be analyzed. Anyhow, this is the first report on the diet of these migratory fish species in the study area.

In general, carangid are pelagic species considered to be piscivorous. Silvano (2001) reported that *C. latus* feeds on crustaceans and fish, and Carr & Adams (1973) place *O. saurus* as a piscivorous species; indeed, juvenile *O. saurus* analyzed in the present study fed almost exclusively on small fishes, principally Engraulidae.

Qualitative studies (Carr & Adams, 1973) on the feeding habits of *T. falcatus*, in the Cristal River, Florida, indicate that juvenile fish feed primarily on fish and benthic invertebrates, including worms, mollusks, and crustaceans, mainly shrimps. In La Carbonera Lagoon, juvenile fish consumed mainly mollusks, gastropods, and bivalves. Differences in the diet composition among geographical zones demonstrate the flexibility of this tropical marine fish, whose juveniles take advantage of the available resources in

Table 2. IRI values for each prey type of six carnivorous fish species in La Carbonera Lagoon, Yucatán.

	C. latus	*O. saurus*	*T. falcatus*	*L. griseus*	*S. foetens*	*S. notata*
Size class	4.7-23.5	5.09-8.82	4.7-14.2	3.13-22.5	4.02-15.1	9.24-41.5
N	42	36	35	39	34	37
Fish						
Unidentified fishes	77.6111	86.9352	0.7997	32.7878	68.1451	78.5323
Clupeidae		0.8013		0.2086	1.8587	1.9298
Opisthonema oglinum					1.3828	
Belonidae						0.6713
Strongylura notata						0.1930
Poecilidae						0.6713
Cyprinodontidae						4.1490
Floridichthys polyommus	0.5665			2.0174	1.9498	
Fundulus spp.					0.4874	
Gerreidae		0.2050			1.9498	2.3234
Eucinostomus spp.	0.0221				0.4874	
Ariopsis spp.				0.4246		
Engraulidae		9.4364			0.4874	
Menidia spp.	0.0055					2.6852
Mugilidae		0.0277				
Sciaenidae	0.2772	0.2050				
Synodontidae	0.0118				9.9735	
Crustacea						
Unidentified crustaceans	15.5034		1.6876	41.0167	0.1707	1.9139
Decapoda				3.4835		0.6713
Brachyura				0.2212		2.6852
Penaeidae	2.5369	1.2297	0.2349	4.3734	8.7165	1.3182
Farfantepenaeus				1.3034		
Caridea		0.0094		0.7781		
Portunidae	0.1604			0.6336		0.6453
Amphipoda				4.2152		0.9457
Gammaridae			0.7997	0.5106		
Corophiidae			1.5586	0.4584		0.1483
Isopoda				0.2893		
Cassidinidae				2.0424		
Tanaidacea			0.0399			0.0510
Mysidacea	2.1676	0.8203	0.0075	0.0556		
Ostracoda			2.5901	0.5106		
Copepoda					0.0032	
Mollusca						
Unidentified gastropods	0.0116	0.0811	3.3713			
Odostomia			0.4139	0.0409		
Truncatella	0.0008		0.7634			
Caecum			6.4368			
Bittium			0.0799			
Cerithium			22.8660			
Bulla			0.0399			
Neritina			0.0316			
Olivella			0.3743			
Unidentified bivalves		0.0328	16.3846			
Musculus			0.2079			
Anomalocardia			3.0710			
Tellina			34.6154			
Veneridae			1.2497			
Brachidontes			1.9249			

Continuation

	C. latus	*O. saurus*	*T. falcatus*	*L. griseus*	*S. foetens*	*S. notata*
Annelida						
Polychaeta			0.0777			
Insecta						
Diptera						0.4389
Hymenoptera		0.1989				
Foraminiferida						
Quinqueloculina			0.1758			
Plant remains						
Seagrass	0.3481	0.0166	0.0062			0.0259
Organic matter no identified	0.7764		0.1901	4.6276	4.3871	

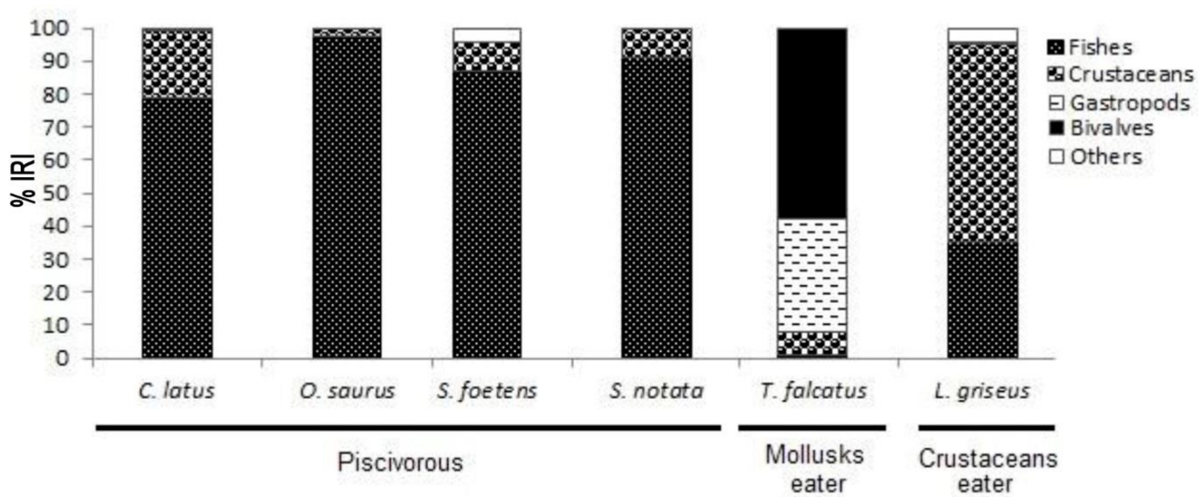

Figure 4. Diet composition and trophic guilds of six marine fish species, based on the Bray-Curtis similarity index.

the environment. It has been reported that adults feed almost exclusively on mollusks and crabs (Carr & Adams, 1973).

On the other hand, the snapper *L. griseus*, is an euryhaline marine species that uses coastal lagoons bordered by mangroves for feeding. In the present study the trophic groups found in the stomachs of young individuals were benthic organisms (caridean shrimp and other crustaceans), which are usually considered as evasive species (Nagelkerken *et al*., 2000; Cocheret de la Morinière *et al*., 2004; Guevara *et al*., 2007). In coastal systems of the southern Gulf of Mexico, Guevara *et al*. (2007) found that juvenile *L. griseus* feed on penaeid and caridean shrimp species during the night. This probably explains the fact that few individuals were collected since samplings for the present study were during the day.

The inshore lizardfish, *Synodus foetens*, is one of the most common coastal demersal predators on the Gulf of Mexico´s continental shelf (Cruz-Escalona *et al*., 2005). This is a piscivorous species that feeds mainly on juvenile of other marine fishes known to be carnivorous, so it can be considered an apex predator on sandy bottoms of the continental shelf, which uses different habitats during its feeding activity and hunts various prey types, depending on resource availability and the size of prey (Esposito *et al*., 2009). There are no reports on the feeding habits of this species in the Gulf of Mexico but, off the coast of Italy, *Synodus saurus* is also a piscivorous species that feeds on small fish like sardines and anchovies (Esposito *et al*., 2009).

The needlefish, *S. notata*, is considered a piscivore (Carr & Adams, 1973; Arceo-Carranza *et al*., 2004) that obtains prey throughout the water column, as demonstrated by the presence of both demersal and pelagic components in the diet (Arceo-Carranza *et al*., 2004). Even if in this study juvenile and adult fish were analyzed, the low number of fish collected prevented to formally compare between size classes but it has been shown that this species displays ontogenetic changes in

Table 3. Similarity, R statistic and *P*-values of ANOSIM test of prey types that contribute to differences of diets among fish species. Only significant combinations are show.

Predators	% similarity	R value	*P*
O. saurus & *C. latus*	71.33	0.051	0.019
O. saurus & *S. notata*	78.23	0.081	0.014
O. saurus & *S. foetens*	82.26	0.088	0.005
O. saurus & *L. griseus*	84.83	0.171	0.001
O. saurus & *T. falcatus*	95.95	0.344	0.001
C. latus & *S. notata*	81.09	0.035	0.05
C. latus & *S. foetens*	85.39	0.056	0.01
C. latus & *L. griseus*	80.40	0.062	0.031
C. latus & *T. falcatus*	96.76	0.359	0.001
S. notata & *L. griseus*	88.66	0.046	0.041
S. notata & *T. falcatus*	97.68	0.199	0.001
S. foetens & *L. griseus*	92.04	0.060	0.016
S. foetens & *T. falcatus*	97.83	0.149	0.001
L. griseus & *T. falcatus*	97.10	0.254	0.001

Table 4. Trophic overlap (Schoener index) values for the six species of juvenile marine fish (significant values in bold).

	C. latus	*O. saurus*	*T. falcatus*	*S. foetens*	*L. griseus*	*S. notata*
C. latus		-	-	-	-	-
O. saurus	**0.8078**		-	-	-	-
T. falcatus	0.0240	0.0212		-	-	-
S. foetens	0.5050	**0.8325**	0.0239		-	-
L. griseus	**0.6413**	0.4587	0.0192	0.5648		-
S. notata	**0.8733**	**0.9343**	0.0225	**0.8982**	0.5212	

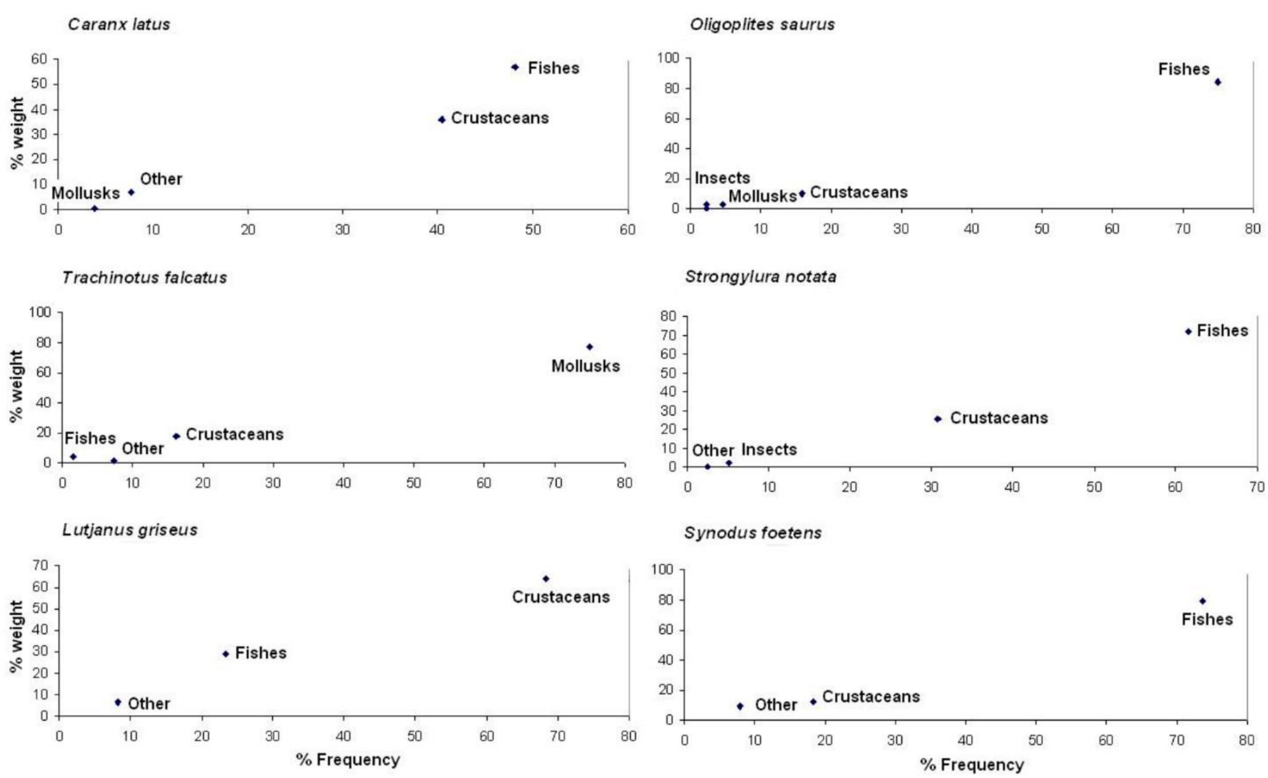

Figure 5. Graphic representation of the dominant prey types (frequency of occurrence % and weight %) of six marine fish species.

its diet (Arceo-Carranza, 2002; Hajisamae, 2009). Arceo-Carranza *et al*. (2004) found that *S. notata* from the Alvarado Lagoon, Mexico, is an active predator with great trophic plasticity to exploit the available resources in the environment (fish, shrimp, and insects among other prey types) while in the clearer waters of the northwestern coast of the Yucatán Peninsula it behaves as a piscivorous species.

Diet breadth of predators tends to increase when food availability is low, and decreases when food availability is high (Tse *et al*., 2008). The behavior of large predators feeding on larger prey usually follows the traditional optimal foraging theory which states that animals should maximize their net rate of energy return when selecting prey (Shoener, 1971; Bacha & Amara, 2009). The high diversity of prey found in the stomach contents of the six species analyzed in this work indicates that numerous food resources are exploited.

Piscivory is a common phenomenon in aquatic and marine ecosystems, and is the largest cause of fish removal in most marine ecosystems, usually larger than fishery catches (Link & Garrison, 2002) but, within this fish assemblage, it is difficult to determine the relative impacts of the different piscivores on other fish populations when considered as prey. For instance, some carangids can consume large numbers of demersal juveniles that use shallow nurseries, but these predators may feed only sporadically in shallow waters, in a manner similar to their transient feeding on coral reefs (Hixon & Carr, 1997). The coexistence of pelagic and demersal prey adds further complexity to the structuring of predation pressure by carangids on individual cohorts of recruits in shallow systems (Baker & Sheaves, 2005).

This study provides important information about shallow soft bottoms, including mudflats as important feeding grounds for fish. The species studied in La Carbonera Lagoon are marine fish that use turbid and shallow waters that provide shelter and food for juvenile stages. Furthermore, these results on the diet composition of juvenile fish provide evidence on the protection value of the mudflats adjacent to mangroves.

ACKNOWLEDGEMENTS

The authors wish to thank Maribel Badillo Alemán for the administrative and operational support during sampling; Juani Tzeek and Alfredo Gallardo for technical assistance during sampling, and help in fish identification; the POSDOC program from DGAPA-UNAM for a postdoctoral scholarship to D.A.C. This project was funded by PAPIIT (IN213012, IN219515) and FOMIX-Yucatán (103229) research grants. Fish were captured under the permit for collection awarded by the National Commission of Aquaculture and Fisheries number DGOPA/04031/310510.1940

REFERENCES

Amundsen, P.A., H.M. Gabler & F.J. Staldvik. 1996. A new approach to graphical analysis of feeding strategy from stomach contents data-modification of the Costello (1990) method. J. Fish. Biol., 48: 607-614.

Arceo-Carranza, D. 2002. Comparación trófica de la familia Belonidae en el Sistema Lagunar de Alvarado, Veracruz, México. Tesis de Licenciatura, Universidad Nacional Autónoma de México, México D.F., 64 pp.

Arceo-Carranza, D. & M.E. Vega-Cendejas. 2009. Spatial and temporal characterization of fish assemblages in a tropical coastal system influenced by freshwater inputs: northwestern Yucatan Peninsula. Rev. Biol. Trop., 57: 89-103.

Arceo-Carranza, D., J. Franco-López, G.L. Waggy & R. Chavez-López. 2004. Trophic comparison of two species of needlefish (Belonidae) in the Alvarado Lagoonal System, Veracruz, México. Gulf Caribb. Res., 16: 81-88.

Bacha, M. & R. Amara. 2009. Spatial, temporal and ontogenetic variation in diet of anchovy (*Engraulis encrasicolus*) on the Algerian coast (SW Mediterranean). Estuar. Coast. Shelf Sci., 85: 257-264.

Baker, R. & M. Sheaves. 2005. Redefining the piscivore assemblage of shallow estuarine nursery habitats. Mar. Ecol. Prog. Ser., 291: 197-213.

Blaber, J.S.M. 1997. Fish and fisheries of tropical estuaries. Chapman & Hall, London, 367 pp.

Blay, J. Jr, W.K. Awittor & D. Agbeko. 2006. Seasonal variation in food preference and feeding ecology of two juvenile marine fishes, *Pseudotolithus senegalensis* (Sciaenidae) and *Brachydeuterus auritus* (Haemulidae) off Cape coast, Ghana. WAJAE, 9: 1-6.

Carr, W. & C.A. Adams. 1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. Trans. Am. Fish. Soc., 102: 511-540.

Castro-Aguirre, J.L., H.S. Espinoza-Pérez & J.J. Schmitter-Soto. 1999. Ictiofauna estuarina lagunar y vicaria de México. Colección Textos Politécnicos, Serie Biotecnologías, Editorial Limusa, México, 711 pp.

Clarke, K.R. & R.M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council, Plymouth Marine Laboratory, Plymouth, 176 pp.

Clench, H. 1979. How to make regional list of butterflies: some thoughts. J. Lepid. Soc., 33: 216-31.

Cocheret de la Morinière, E., I. Nagelkerken, H. Van Der Meij & G. Van Der Velde. 2004. What attracts coral reef fish to mangroves: habitat complexity or shade? Mar. Biol., 144: 139-144.

Colwell, R. 2006. Statistical estimation of species richness and share species from samples. University of Connectticut, USA. URL. Purl.oclc.org/estimates.

Cortés, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: applications to elasmobranch fishes. Can. J. Fish. Aquat. Sci., 54: 726-738.

Costello, M.J. 1990. Predator feeding strategy and prey importance: a new graphical analysis. J. Fish Biol., 36: 261-263.

Cruz-Escalona, V.H., M.S. Peterson, L. Campos-Dávila & M. Zetina-Rejón. 2005. Feeding habits and trophic morphology of inshore lizardfish (*Synodus foetens*) on the central continental shelf off Veracruz, Gulf of Mexico. J. Appl. Ichthyol., 21: 525-530.

Elliott, M., A.K. Whitfield, I.C. Potter, S.J.M. Blaber, D.P. Cyrus, F.G. Nordlie & T.D. Harrison. 2007. The guild approach to categorizing estuarine fish assemblages: a global review. Fish Fish., 8: 241-268.

Esposito, V., P. Battaglia, L. Castriota, M.G. Finoia, G. Scotti & F. Andaloro. 2009. Diet of Atlantic lizardfish, *Synodus saurus* (Linnaeus, 1758) (Pisces: Synodontidae) in the central Mediterranean Sea. Sci. Mar., 73(2): 369-376.

Froese, R. & D. Pauly. 2014. FishBase. [www.fishbase. org]. Reviewed: 8 January 2015.

Gallardo-Torres, A., M. Badillo-Alemán, C. Galindo de Santiago, J. Loera-Pérez, R. Rioja-Nieto & X. Chiappa-Carrara. 2012. Listado taxonómico de los peces de la Laguna Boca de la Carbonera, Yucatán: un primer paso para el manejo y evaluación de los recursos costeros del norte de Yucatán. In: A.J. Sánchez, X. Chiappa-Carrara & R. Brito-Pérez (eds.). Recursos acuáticos costeros del sureste. CONCIYTEY-UNAM, ISBN 978-607-9060-08-4, 1106 pp.

Guevara, E., H. Alvarez, M. Mascaró, C. Rosas & A. Sánchez. 2007. Hábitos alimenticios y ecología trófica del pez *Lutjanus griseus* (Pisces: Lutjanidae) asociado a la vegetación sumergida en la Laguna de Términos, Campeche, México. Rev. Biol. Trop., 55(3-4): 989-1004.

Hajisamaea, S. 2009. Trophic ecology of bottom fishes assemblage along coastal areas of Thailand. Estuar. Coast. Shelf Sci., 82: 503-514.

Hajisamaea, S., L.M. Choua & S. Ibrahim. 2003. Feeding habits and trophic organization of the fish community in shallow waters of an impacted tropical habitat. Estuar. Coast. Shelf Sci., 58: 89-98.

Hixon, M.A. 1980. Competitive interactions between California reef fishes of the genus *Embiotoca*. Ecology, 61(4): 918-931.

Hixon, M.A. & M.H. Carr. 1997. Synergistic predation, density dependence, and population regulation in marine fish. Science, 277: 946-949.

Hyslop, E.J. 1980. Stomach contents analysis-a review of methods and their application. J. Fish Biol., 17: 411-429.

Jansen, P.A., H. Slettvold, A.G. Finstad & A. Langeland. 2002. Niche segregation between Arctic char *(Salvelinus alpinus)* and brown trout *(Salmo trutta)*: an experimental study of mechanisms. Can. J. Fish. Aquat. Sci., 59: 6-11.

Jiménez-Valverde, A. & J. Hortal. 2003. Las curvas de acumulación de especies y la necesidad de evaluar la calidad de los inventarios biológicos. Rev. Ibérica Aracnol., 8: 151-161.

Krebs, J.C. 1999. Ecological methodology. Addison Welsey, Menlo Park CA, 620 pp.

Laegdsgaard, P. & C.R. Johnson. 1995. Mangrove habitats as nurseries: unique assemblages of juvenile fish in subtropical mangroves in eastern Australia. Mar. Ecol. Prog. Ser., 126: 67-81.

Laegdsgaard, P. & C.R. Johnson. 2001. Why do juvenile fish utilize mangrove habitats? J. Exp. Mar. Biol. Ecol., 257: 229-253.

Link, J.S. & L.P. Garrison. 2002. Changes in piscivory associated with fishing induced changes to the finfish community on Georges Bank. Fish Res., 55: 71-86.

Nagelkerken, I. & G. Van der Velde. 2002. Do non-estuarine mangroves harbor higher densities of juvenile fish than adjacent shallow-water and coral reef habitats in Curaçao (Netherlands Antilles)? Mar. Ecol. Prog. Ser., 245: 191-204.

Nagelkerken, I., M. Dorenbosch, W.C.E.P. Verberk, E. Cocheret de la Morinière & G. Van Der Velde. 2000. Day-night shifts of fishes between shallow-water biotopes of a Caribbean Bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. Mar. Ecol. Prog. Ser., 194: 55-64.

Pinkas, L., M.S. Oliphant & I.L.K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Fish Game. Fish. Bull., 152: 1-105.

Platell, M.E., G.A. Sarre & I.C. Potter. 1997. The diets of two co-occurring marine teleosts, *Parequula melbournensis* and *Pseudocaranx wrighti*, and their relationships to body size and mouth morphology, and the season and location of capture. Env. Biol. Fish, 49: 361-367.

Ramírez-Luna, V., A.F. Navia & E.A. Rubio. 2008. Food habits and feeding ecology of estuarine fish assemblage of northern Pacific coast of Ecuador. PANAMJAS, 3(3): 361-372.

Root, R.B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. Ecol. Monogr., 37: 317-350.

Ross, S.T. 1986. Resource partitioning in fish assemblages: a review of field studies. Copeia, 1986(2): 352-388.

Ruiz, G.M., A.H. Hines & M.H. Posey. 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. Mar. Ecol. Prog. Ser., 99: 1-16.

Shoener, T.W. 1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst., 2: 369-404.

Silvano, R.A.M. 2001. Feeding habits and interspecific feeding associations of *Caranx latus* (Carangidae) in a subtropical reef. Env. Biol. Fish., 60(4): 465-470.

Received: 26 September 2014; Accepted: 2 February 2015

Tse, P., T.H.M. Nip & C.K. Wong. 2008. Nursery function of mangrove: a comparison with mudflat in terms of fish species composition and fish diet. Estuar. Coast. Shelf Sci., 80: 235-242.

Tzeek-Tuz, J.G. 2013. Biología de la reproducción de *Strongylura notata* y *Sphoeroides testudineus*, de la laguna “La Carbonera” en Sisal, Yucatán. Tesis de Maestría, Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, México D.F., 125 pp.

Verweij, M.C., I. Nagelkerken, S. Wartenbergh, I.R. Pen & G. Van Der Velde. 2006. Caribbean mangroves and seagrass beds as daytime feeding habitats for juvenile French grunts, *Haemulon flavolineatum*. Mar Biol., 149: 1291-1299.

Wallace, Jr., R.K. 1981. An assessment of diet-overlap indexes. Trans. Am. Fish. Soc., 110: 72-76.

Yáñez-Arancibia, A. & R.S. Nugent. 1977. El papel ecológico de los peces en estuarios y lagunas costeras. An. Inst. Cienc. Mar Limnol., 4(1): 107-114.