Gulf and Caribbean Research

Volume 17 | Issue 1

January 2005

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DOI: 10.18785/gcr.1701.16

Recommended Citation

Pelaez-Rodriguez, E., J. Franco-Lopez, W. A. Matamoros, R. Chavez-Lopez and N. J. Brown-Peterson. 2005. Trophic Relationships of Demersal Fishes in the Shrimping Zone Off Alvarado Lagoon, Veracruz, Mexico. Gulf and Caribbean Research 17 (1): 157-167.
Retrieved from http://aquila.usm.edu/gcr/vol17/iss1/16

Gulf and Caribbean Research Vol 17, 157–167, 2005

Manuscript received November 22, 2004; accepted February 4, 2005

TROPHIC RELATIONSHIPS OF DEMERSAL FISHES IN THE SHRIMPING ZONE OFF ALVARADO LAGOON, VERACRUZ, MEXICO

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ABSTRACT The diet of demersal piscivorous fishes captured as bycatch of the commercial shrimping fleet off the Alvarado lagoonal system, Veracruz, Mexico, was studied. Nine collections distributed throughout the nortes (windy), wet, and dry seasons were made from November 1993 to January 1995. Sampling yielded a total of 646 fishes representing 10 families and 14 species, of which 44.9% had empty digestive tracts and were excluded from analysis. *Trichiurus lepturus* and *Synodus foetens* were the most abundant demersal predators in the collections. Differences in food consumption of the 7 most abundant predators were observed among the 3 seasons, with the greatest variety of prey (20 species) taken during the nortes season and the lowest variety (9 species) during the dry season. Five distinct trophic guilds were determined based on an index of relative importance of prey. Prey type and location of prey within the water column helped determine guild classification. The occurrence of different trophic guilds may allow for decreased competition for food resources on the continental shelf off Alvarado, Mexico.

RESUMEN Se estudio la dieta de los peces piscívoros demersales capturados como fauna acompañante del camarón en la flota de barcos camaroneros del sistema de lagunas de Alvarado, Veracruz, México. Se obtuvieron nueve colectas que abarcaron las temporadas de nortes, lluvias y secas desde noviembre de 1993 hasta enero de 1995. Las muestras produjeron un total de 646 peces representados por 10 familias y 14 especies; 44.9% fueron encantrados con el tracto estomacal vacíos y no fueron analizados. *Trichiurus lepturus* y *Synodos foetens* fueron los depredadores demersales más abundantes en nuestras muestras. Se observaron diferencias en el consumo de alimento en las tres temporadas. La temporada de nortes mostró la mayor variación de presa (20 especies), y la menor variación se observó en la temporada de secas (9 especies). Cinco distintivos gremios tróficos fueron identificados basados en el índice de importancia relativa de la presa. El tipo de presa y la localización de las presas en la columna de agua permitieron determinar la clasificación de los gremios. La existencia de diferentes gremios tróficos permite una disminución en la competencia por recursos alimenticios en la plataforma continental del Alvarado, México.

INTRODUCTION

Shrimp trawling is one of the most important fishing industries in Mexico. In the southern Gulf of Mexico off Veracruz, a serious decline in the Mexican shrimping industry was observed from 1980 to 1991. In 1980, the shrimping industry reported a production of 5000 metric tons/year of penaeid shrimp (Grande and Díaz 1981), whereas in 1991 production using the same capture effort was only 1500 metric tons/year (SEMARNAP 1997). Currently, catches oscillate between 2000 and 3000 metric tons/year off Veracruz (Uribe-Marinez 2003). Worldwide, overfishing both by commercial and recreational fishers has reduced the abundance and biomass of apex predator species (Tegner and Dayton 1999, Jackson et al. 2001, Coleman et al. 2004) as well as non-targeted species (Burrage et al. 1993, Steele et al. 2001), leading to altered food webs in estuaries, coral reefs, and kelp forests (Jackson et al. 2001).

Data from several localities of the world show that in some types of fisheries more than 90% of the total catch (biomass) is discarded as waste bycatch (Alverson et al. 1994, Erzini et al. 2001, Kennelly and Broadhurst 2002). Studies have shown that the fish to shrimp ratio in temperate and subtropical areas of Mexico is 5:1 metric tons/yr, while the ratio in tropical areas is 10:1 metric tons/yr (Grande and Díaz 1981). Furthermore, shrimp trawling disturbs extensive areas of benthic habitat, affects the benthic macrofauna, and dramatically changes the diversity and abundance of demersal fish fauna (Alverson et al. 1994, Kaiser 1998, Rogers et al. 1999).

Little is known about the trophic structure and other ecological processes of the biotic community in the shrimping area off the Alvarado Lagoon, Veracruz, Mexico. This study was designed to examine the abundance and trophic interactions of demersal predatory fishes that are part of the bycatch in this area of high shrimp trawling effort. A common method of establishing trophic structure is by the determination of trophic guilds (Luczkovich et al. 2002). Trophic guilds, defined as the grouping of species that share similar resources in a competitive complex (Root 1973, Blondel 2003), were determined in this study through analysis of stomach contents of trawl-caught fishes.

METHODS

Study Area

The study area is located immediately offshore of the Alvarado Lagoon system in the central portion of the state of Veracruz, Mexico, between 18°45'N, 95°40'W and 19°00'N, 95°42'W. Three well defined seasons characterize the region: the wet season from June through September, the nortes (windy) season from October through January, and the dry season from February through May (Contreras 1985). Highest precipitation occurs during the rainy season and oscillates between 1100–2000 mm over the year (García 1973). The Alvarado area is characterized by extensive coastal vegetation including mangroves and seagrasses and a series of lagoons and rivers that brings considerable fresh water and organic matter to the continental shelf, particularly during the rainy season.

Sample collection and processing

We collected demersal fishes, known from the literature to be piscivores, from boats of the Alvarado shrimping fleet on 9 occasions from November 1993–January 1995, covering all 3 seasons. There were 4 collections during the nortes season, 3 collections during the wet season and 2 collections during the dry season. Boats in the fleet were equipped with a 20 m beam trawl with a 5.5 m mouth opening that was constructed with 3.85 cm mesh. Towing speed was 5–6 km/h, covering a distance of 1.8–18.5 km per sampling event. Fishing depths ranged from 30–90 m, with a mean depth of 50 m. A 30 l subsample of the bycatch (representing 25–27 kg of fish) was obtained using the methods described by Guzmán (1991) and Peláez-Rodríguez (1993) from trawls fished for 4 h between 0800–0730 local time (Central Time Zone).

Formaldehyde (10%) was injected into the oral and anal areas and then fish were immersed in the formaldehyde solution (Laevastu 1971). Fishes were labeled, bagged, and transported to the laboratory where samples were rinsed with tap water and preserved in 70% methanol within 48 to 72 hours. Species were identified with Hoese and Moore (1977), Fisher (1978), and Castro-Aguirre (1978). Fish were measured (standard length, SL, mm) and weighed to the nearest 0.1 g. Stomachs were extracted, and their contents were identified to the lowest possible taxon using hard parts such as otoliths, scales, jaw bones and cranial bones (Windell and Stephen 1978). Prey items were blotted with desiccant paper and weighed to the nearest 0.001 g; empty stomachs were noted but not included in the analysis. Stomach contents of the 7 most abundant predators captured were used for analysis. Prey items were classified as pelagic, benthic, or benthic-pelagic according to knowledge of their general occurrence within the water column (Carpenter 2002).

Data analysis

Abundance and biomass of the predator species were compared among seasons for each subsample with analysis of variance (ANOVA) and pairwise Sidak post-hoc tests to separate mean values if a significant F-test was determined. Species richness (S) was determined seasonally based on the abundance of the demersal, predatory fishes captured. Additionally, percent contribution of each species in terms of abundance and biomass were calculated by season.

The importance of each prey species for each of the 7 most abundant fishes was evaluated by pooling data for each season and then calculating the index of relative importance (IRI; Pinkas et al. 1971), defined as $IRI = \%F(\%N + \%W)$, where $\%F$ = frequency of occurrence of a food item, $\%N$ = numerical percentage of a food item in the stomachs, and $\%W$ = percentage by volume of the food item in the stomachs (Pinkas et al. 1971). IRI values were standardized to %IRI for comparison (Cortés 1997).

A Bray-Curtis dissimilarity matrix was calculated based on %IRI values, and this matrix was used to construct a dendrogram using the unpaired grouping mean average (UPGMA) method (Field et al. 1982). ANOVA was calculated using SPSS (SPSS Inc, ver 11.5, Chicago, IL). Values were considered significantly different if $P < 0.05$.

RESULTS

Predator abundance and seasonality

Fourteen species of demersal fishes belonging to 10 families were collected during the study, yielding a total of 646 individuals with a total biomass of 54 kg (Table 1). The families Synodontidae (4 species) and Sciaenidae (2 species) contributed almost half of the total species. Of the total catch, only 362 fishes or 56.1% contained prey in their stomachs. Three species have not been previously reported for the Alvarado area; they include *Rachycentron canadum*, collected only during the nortes season, and *Synodus poeyi* and *Trachinocephalus myops*, reported for both the nortes and wet seasons (Table 1). Overall,

TABLE 1

Composition of the demersal fish fauna collected from commercial shrimp nets off the Alvarado Lagoon system during the nortes, dry and wet seasons. Abbreviations are presented for the 7 most abundant species.

	Nortes		Dry		Wet		Total	
Species	**Abundance (ind)**	**Biomass (g)**	**Abundance (ind)**	**Biomass (g)**	**Abundance (ind)**	**Biomass (g)**	**Abundance (ind)**	**Biomass (g)**
Muraenidae								
Gymnothorax nigromarginatus	5	685.3	7	635.9	6	709.1	18	2030.3
Ophichthidae								
Myrophis punctatus	2	147.0	3	192.5	6	334.7	11	674.2
Synodontidae								
Synodus foetens (Syfo)	67	14811.7	32	3119.3	25	1761.0	124	19692.0
Synodus poeyi	25	868.4			32	717.2	57	1585.6
Trachinocephalus myops	8	369.4			15	849.8	23	1219.2
Saurida brasiliensis (Sabr)	15	75.7	5	47.9	66	291.5	86	415.1
Fistulariidae								
Fistularia tabacaria	2	84.1			2	42.1	4	126.2
Priacanthidae								
Priacanthus arenatus	15	1518.6	2	373.3	6	568.7	23	2460.6
Rachycentridae								
Rachycentron canadum	2	1208.0					2	1208.0
Sciaenidae								
Cynoscion arenarius (Cyar)	5	639.3	8	560.9	6	1100.6	19	2300.8
Cynoscion nothus (Cyno)	25	2316.5	13	619.5	22	1853.7	60	4789.7
Sphyraenidae								
Sphyraena guachancho (Spgu)	5	586.0	10	445.5	13	1612.7	28	2644.2
Trichiuridae								
Trichiurus lepturus (Trle)	43	4154.0	19	1514.9	87	6700.5	149	12369.4
Scombridae								
Scomberomorus cavalla (Scca)	31	540.0	6	1449.2	5	315.2	42	2304.4
Totals	250	28004.0	174	8958.9	291	16856.8	646	53819.7
Species collected	14		10		13		14	

Trichiurus lepturus was the most common predator species captured during the study, with a total of 149 individuals, and was the dominant species during the wet season. *Synodus foetens* and *Saurida brasiliensis* were the second and third most abundant predatory fishes captured, while *Cynoscion nothus*, *Scomberomous cavalla*, *Spyraena guachancho* and *C. arenarius* rounded out the top 7 species (Table 1).

The wet season showed the highest abundance of predatory fishes in the shrimp bycatch, but it ranked second in biomass, with 291 specimens and 17 kg. The nortes season accumulated the highest biomass of bycatch predators, 28 kg, but occupied the second place in predator fish abundance with 250 specimens. The lowest values of abundance and biomass were found during the dry season with a total of 174 specimens that yielded 9 kg (Table 1). However, there were no significant differences among seasons for either abundance (ANOVA, $F_{2,6} = 3.46$, $P = 0.100$) or biomass (ANOVA, $F_{2,6} = 0.95$, $P = 0.438$), suggesting a relatively stable and constant bycatch of predatory fishes in the shrimp trawl fishery in the area.

Seasonally, richness of predatory bycatch fishes was greater in the nortes season followed by wet and then dry seasons (Table 1); a similar pattern was seen in total abundance as well. *Synodus foetens*, *T. lepturus* and *S. brasiliensis* were important contributors numerically and/or in terms of biomass to the total species complement (Tables 1 and 2). *Synodus foetens* was first and *T. lepturus* second in the nortes and dry seasons in terms of abundance and biomass. In the wet season *T. lepturus* and *S. brasiliensis* were the first and 2nd most abundant species, whereas *T. lepturus* and *C. nothus* contributed more to biomass (Table 2).

TABLE 2

Percent contribution of abundant predatory fishes by season in terms of abundance and biomass in the shrimping zone off the Alvarado Lagoon, Veracruz, Mexico.

	Nortes		Dry		Wet	
Species	**Abundance**	**Biomass**	**Abundance**	**Biomass**	**Abundance**	**Biomass**
Synodus foetens	26.80	52.89	30.48	34.82	8.59	10.45
Trichiurus lepturus	17.20	14.83	18.09	16.91	29.90	39.75
Cynoscion nothus	10.00	8.27	12.38	6.91	7.56	10.99
Scomberomorus cavalla	12.40	1.93	5.71	16.18	1.72	1.87
Saurida brasiilensis	6.00	0.27	4.76	0.53	22.68	1.73
Sphyraena guachancho	2.00	2.09	9.52	4.97	4.47	9.57
Cynoscion arenarius	2.00	2.28	7.62	6.26	2.06	6.53
Synodus poeyi	10.00	3.10			10.99	4.25
Priancanthus arenatus	6.00	5.42	1.90	4.17	2.06	3.37
Gymnothorax nigromarginatus	2.00	2.45	6.67	7.10	2.06	4.21
Trachinocephalus myops	3.20	1.32			5.15	5.04
Myrophis punctatus	0.80	0.52	2.86	2.15	2.06	1.99
Fistularia tabacaria	0.80	0.30			0.69	0.25
Rachycentron canadum	0.80	4.31				

Predator size and diets

The modal SL for *S. foetens* was smaller in the nortes season than in the dry or wet seasons, whereas modal SL for *T. lepturus* was largest during the wet season (Table 3). However, the range in sizes for these 2 species overlapped for all 3 seasons. The modal SL for *S. guachancho* was larger in the nortes season compared to the dry or wet seasons, and the size range for the nortes season did not overlap with the other 2 seasons (Table 3). The remaining 4 predator size ranges and modal SL did not change much by season (Table 3). This suggests that potential ontogenetic diet shifts imbedded within seasons probably did not affect analyses of trophic spectrum.

Twenty-four prey species, including 20 fishes, three decapod crustaceans, and one cephalopod, were identified from the stomach contents of the top 7 predators. Among the fish prey, *Bregmaceros cantori* and *Microdesmus lanceolatus* have not been previously reported from the shelf off Alvarado Lagoon (Table 4). For the 7 predator species, the lowest number of prey types consumed (9) occurred during the dry season, while the highest number of prey types (20) was found during the nortes season. Prey types varied among predators and changed seasonally (Table 4).

Synodus foetens was the second most abundant predatory species overall and had the largest variety of prey, with a total of 17 taxa (Table 4). This species fed on the greatest diversity of prey during the nortes season, and its prey occurred throughout the water column (Figure 1). Fifty-one percent IRI of the prey was benthic and included

TABLE 3

Summary statistics on fish standard length (range and mode, cm) by season for the 7 predators used in the diet analysis.

	Nortes		Dry		Wet	
Species	**Range**	**Mode**	**Range**	**Mode**	**Range**	**Mode**
Sphyraena guachancho	29.3–34.2	30.0	16.5–19.1	18.0	18.0–20.8	19.0
Synodus foetens	12.3–21.7	18.0	20.6–35.7	29.0	17.6–43.5	32.0
Trichiurus lepturus	32.0–58.6	46.0	39.4–51.8	47.0	45.6–89.7	64.0
Cynoscion arenarius	18.5–23.4	20.0	17.5–19.40	18.0	18.5–24.6	21.0
Cynoscion nothus	15.6–19.0	17.0	14.2–18.0	16.0	16.2–21.6	19.0
Saurida brasiliensis	7.4–8.9	8.0	5.2–7.6	6.0	8.4–11.0	9.0
Scomberomorus cavalla	24.5–27.3	25.0	22.6–28.4	24.0	21.5–27.6	25.0

TABLE 4

Seasonal food composition and %IRI for 7 demersal fishes off Alvarado, Veracruz.

	Nortes		Dry		Wet	
Species	**Prey type**	**%IRI**	**Prey type**	**%IRI**	**Prey type**	**%IRI**
S. guachancho	*Anchoa hepsetus*	68.44	*Bregmaceros cantori*	66.15	*Anchoa hepsetus*	22.02
	Cynoscion nothus	1.82	*Saurida brasiliensis*	8.56	*Saurida brasiliensis*	57.6
	Bregmaceros cantori	8.94	*Loligo pealei*	25.29	*Loligo pealei*	20.38
	Saurida brasiliensis	15.34				
	Loligo pealei	5.46				
S. foetens	*Anchoa hepsetus*	21.17	*Anchoa hepsetus*	51.26	*Saurida brasiliensis*	19.36
	Saurida brasiliensis	2.03	*Upeneus parvus*	48.74	*Upeneus parvus*	8.29
	Upeneus parvus	12.92			*Loligo pealei*	19.33
	Loligo pealei	7.44			*Bregmaceros cantori*	17.70
	Harengula clupeola	14.55			*Pristipomoides aquilonaris*	1.76
	Trachurus lathami	2.64			*Diplectrum bivittatum*	23.17
	Micropogonias furnieri	2.99			*Syacium gunteri*	3.57
	Pristipomoides aquilonaris	9.16			*Trichiurus lepturus*	6.24
	Diplectrum bivittatum	8.57			*Engyophrys senta*	0.56
	Symphurus plagiusa	1.46				
	Haemulon aurolineatum	3.14				
	Serranus atrobranchus	13.01				
	Eucinostomus gula	0.90				
T. lepturus	*Anchoa hepsetus*	49.48	*Upeneus parvus*	33.28	*Anchoa hepsetus*	36.43
	Upeneus parvus	15.11	*Harengula clupeola*	24.01	*Upeneus parvus*	1.19
	Pristipomoides aquilonaris	13.72	*Loligo pealei*	42.71	*Pristipomoides aquilonaris*	1.49
	Harengula jaguana	12.2			*Diplectrum bivittatum*	0.55
	Harengula clupeola	5.85			*Synodus foetens*	0.23
	Loligo pealei	2.43			*Bregmaceros cantori*	2.54
	Farfantepenaeus sp.	1.21			*Saurida brasiliensis*	8.81
					Cynoscion nothus	0.38
					Myrophis punctatus	7.19
					Loligo pealei	8.27
					Farfantepenaeus sp.	32.89
C. arenarius	*Saurida brasiliensis*	27.05	*Upeneus parvus*	76.21	*Saurida brasiliensis*	33.96
	Upeneus parvus	35.47	*Diplectrum bivittatum*	23.79	*Upeneus parvus*	24.11
	Pristipomoides aquilonaris	15.21			*Loligo pealei*	41.93
	Loligo pealei	0.65				
	Farfantepenaeus sp.	21.62				
C. nothus	*Pristipomoides aquilonaris*	37.91	*Bregmaceros cantori*	95.49	*Bregmaceros cantori*	51.59
	Bregmaceros cantori	31.92	*Farfantepenaeus* sp.	4.51	*Saurida brasiliensis*	20.41
	Saurida brasiliensis	13.15			*Trichiurus lepturus*	6.05
	Trichiurus lepturus	4.16			*Farfantepenaeus* sp.	21.94
	Microdesmus lanceolatus	0.15				
	Loligo pealei	12.70				
S. brasiliensis	*Bregmaceros cantori*	78.42	*Bregmaceros cantori*	67.62	*Bregmaceros cantori*	75.16
	Loligo pealei	21.58	*Loligo pealei*	32.38	*Loligo pealei*	24.84
S. cavalla	*Anchoa hepsetus*	94.08	*Anchoa hepsetus*	69.67	*Anchoa hepsetus*	25.52
	Bregmaceros cantori	5.92	*Upeneus parvus*	30.33	*Diplectrum bivittatum*	53.52
					Loligo pealei	20.95

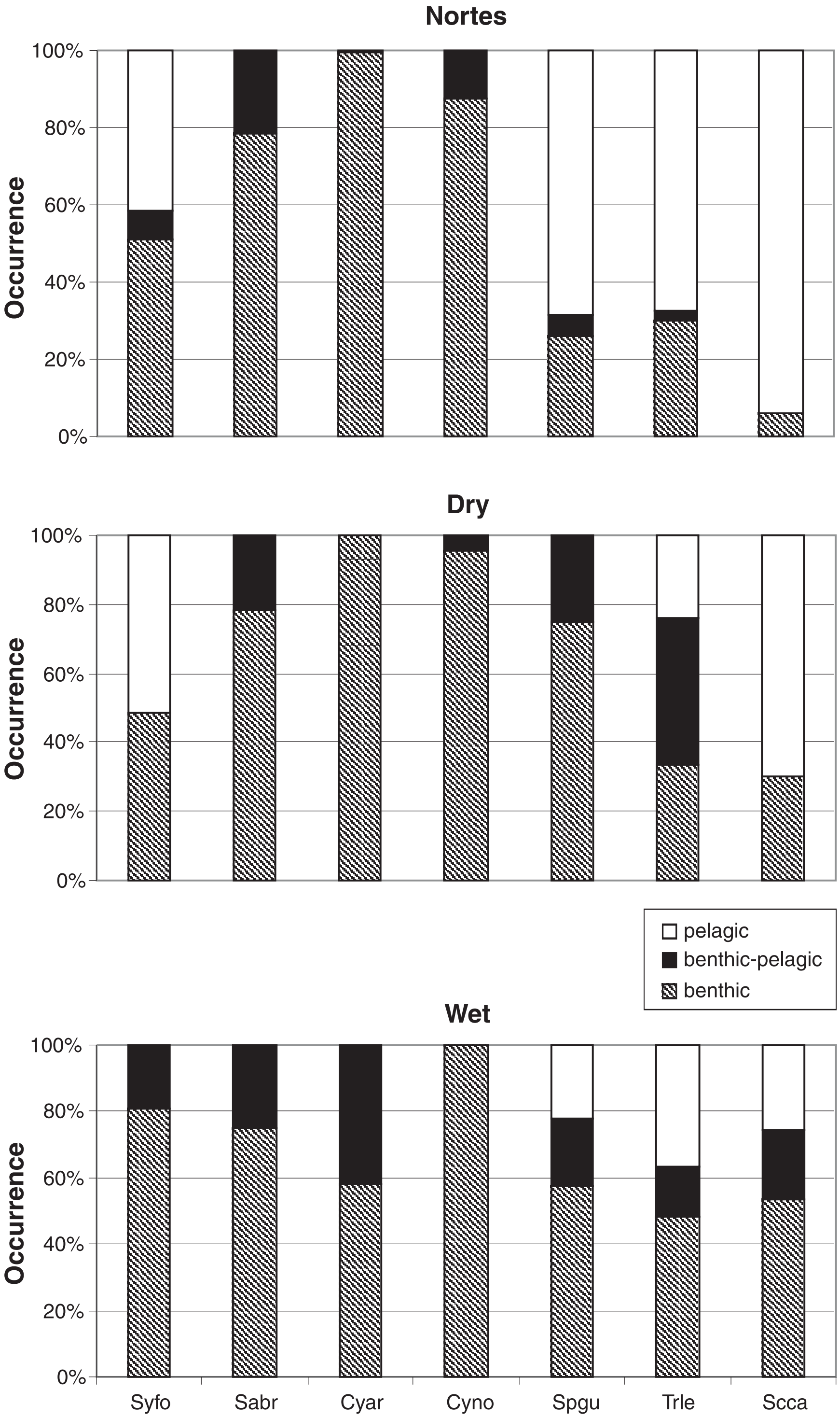

Figure 1. Percentage of prey occurring in the pelagic, benthic-pelagic, and benthic zones of the water column for 7 demersal fishes off the Alvarado Lagoon system, Veracruz, Mexico, during the nortes, dry, and wet seasons. *Synodus foetens* (Syfo), *Saurida brasiliensis* (Sabr), *Cynoscion arenarius* (Cyar), *Cynoscion nothus* (Cyno), *Sphyraena guachancbo* (Spgu), *Trichiurus lepturus* (Trle), *Scomberomorus cavalla* (Scca). Sample size for each species in the figure by season is found in Table 1.

Upeneus parvus, *Diplectrum bivittatum*, *Pristipomoides aquilonaris*, *Eucinostomus gula*, *Micropogonias furnieri*, *Symphurus plagiusa*, and *S. brasiliensis*. Species from the pelagic zone contributed 41.5 %IRI of stomach contents and included *Anchoa hepsetus*, *Harengula clupeola*, and *Trachurus lathami*. A smaller percentage of the diet, 10.5 %IRI, was composed of *Loligo pealei* and *Haemulon aurollineatum* from the benthic-pelagic zone. During the dry season, *S. foetens* fed about equally on *A. hepsetus* from the pelagic zone and on *U. parvus*, a bottom dweller. During the wet season, the diet of *S. foetens* was dominated by benthic prey (80.6 %IRI) which included *S. brasiliensis, D. bivittatum, T. lepturus. U. parvus, P. aquilonaris*, *Engyophrys senta*, *Syacium gunteri*, and *B. cantori*. The benthic-pelagic zone contributed 19.3 %IRI to the diet; the only prey was *L. pealei* (Table 4).

Saurida brasiliensis was the smallest piscivorous predator in the study and showed no differences in seasonal prey consumption (Table 4, Figure 1). This species also had the least diverse diet, with the benthic *B. cantori* accounting for 67–78 %IRI of the diet each season. A benthic-pelagic species, *L. pealei,* made up the rest of the diet (Table 4).

Neither *Cynoscion arenarius* nor *C. nothus* consumed any pelagic prey during the course of this study (Figure 1). Both species had the greatest diversity of prey items during the nortes season. During both the nortes and dry seasons, > 80 %IRI of the diet was composed of benthic species such as *U. parvus, Farfantepenaeus* sp., *P. aquilonaris*, *B. cantori*, and *S. brasiliensis*, whereas the remaining diet was composed of the benthic-pelagic *L. pealei* (Table 4). The diet of *C. arenarius* was dominated by benthic species during the wet season, as was the diet of the congener *C. nothus* (Figure 1). While the 2 *Cynoscion* species fed within the same areas of the water column, there were differences in the prey they captured. For instance, *B. cantori* was an important component of the diet of *C. nothus* throughout the year, yet this prey was never eaten by *C. arenarius* (Table 4). Similarily, *U. parvus* dominated the diet of *C. arenarius* but was never taken by *C. nothus* (Table 4).

Sphyraena guachancho consumed only 5 prey items, yet there was marked seasonal variation in the dominant prey items (Table 4). For instance, the pelagic *A. hepsetus* dominated the diet in the nortes season, while no pelagic species were consumed during the dry season when the benthic *B. cantori* dominated the diet (Table 4, Figure 1). During the wet season, benthic prey such as *S. brasiliensis* was dominant in the diet.

Trichiurus lepturus was the most abundant predator species captured during the study and the only species to feed throughout the water column year round (Figure 1). During the wet season, benthic (48 %IRI) and pelagic (36.4 %IRI) species constituted the majority of the diet (13 species) of *T. lepturus*; prominent taxa included *Farfantepenaeus* sp., *S. brasiliensis,* and *A. hepsetus* (Table 4). In contrast, the pelagic species *A. hepsetus, Harengula jaguana,* and *H. clupeola* dominated the diet during the nortes season (67.5 %IRI). During the dry season, *T. lepturus* fed on 3 prey species, one from each section of the water column. The benthic-pelagic *L. pealei* (42.7 %RI) dominated the diet (Table 4, Figure 1).

Scomberomorus cavalla consumed only 5 prey types during the course of the study. The pelagic *A. hepsetus* dominated the diet during both the nortes (94.1 %IRI) and dry (69.7 %IRI) seasons and also accounted for 25 %IRI of the diet during the rainy season (Table 4). While benthic prey were taken throughout the year and dominated the diet in the rainy season (Figure 1), *S. cavalla* fed on different benthic species during each season (Table 4).

Species/season dietary patterns

Five distinct trophic guilds were delimited (Figure 2). Fishes in feeding guild A consumed mainly pelagic prey like *A. hepsetus*, *H. jaguana*, and *H. clupeola*, whereas fish in guild B consumed not only pelagic species but transitioned to feeding on benthic-pelagic species like *L. pealei* (Figure 2). Fishes in guild C were characterized by feeding on a mixture of benthic-pelagic and benthic prey like *Farfantepenaeus* sp., *S. brasiliensis*, *U. parvus*, *Myrophis punctatus*, and *L. pealei* (Figure 2). Fishes in feeding guilds D and E tended to focus on more benthic prey like *S. brasiliensis*, *Farfantepenaeus* sp., *U. parvus*, and *B. cantori*.

In general, the species/season trophic patterns identified by guild analysis did not follow clear patterns, most likely due to body size-mouth gape differences and to seasonal prey availability. For example, *C. nothus*, *S. brasiliensis* and *C. arenarius* exhibited no seasonal differences in trophic guild, and *C. nothus* and *C. arenarius* were assigned to different guilds (Figure 2). This suggests minimal differences in prey across seasons for these species. In contrast, members of guilds A and B were comprised of different species and seasons with no clear patterns (Figure 2). Some species/season diets clustered together, and others did not. It was clear, however, that some species shifted from pelagic to benthic prey with season. For example, *S. guachancho* fed on pelagic species during the nortes and wet seasons but shifted to benthic prey during the dry season. However, the modal SL and size ranges for *S. guachancho* were virtually identical during the dry and wet seasons (Table 3), suggesting the seasonal shift in prey is not related to ontogenic feeding dif-

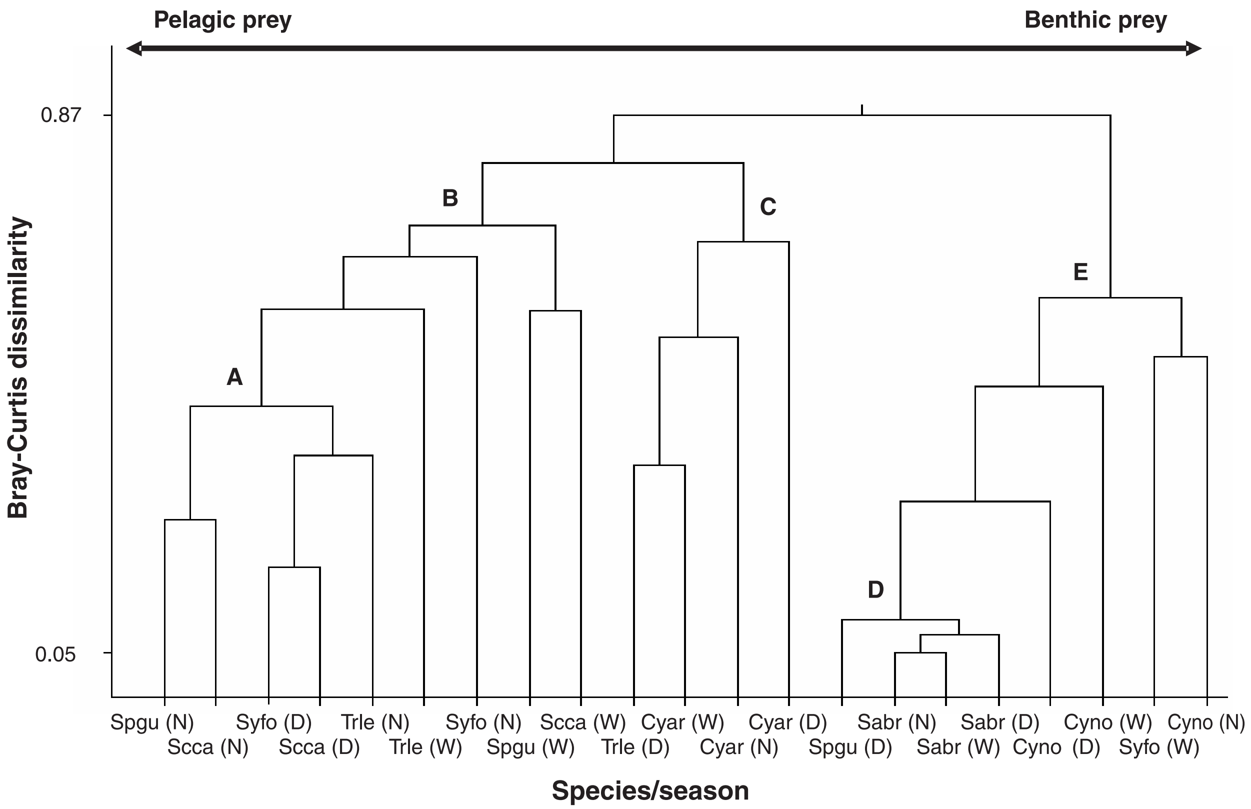

Figure 2. UPGMA cluster analysis of %IRI based on Bray Curtis dissimilarity index for 7 demersal fishes off Alvarado Lagoon Veracruz, Mexico. *Sphyraena guachancbo* (Spgu), *Synodus foetens* (Syfo), *Trichiurus lepturus* (Trle), *Scomberomorus cavalla* (Scca), *Cynoscion arenarius* (Cyar), *Cynoscion nothus* (Cyno), *Saurida brasiliensis* (Sabr). N = nortes season, W = wet season, and D = dry season. Letters indicate trophic guilds identified from the cluster analysis.

ferences. Similarily, *S. foetens* and *T. lepturus* were found in 3 different guilds based on season, suggesting differences in size may not be as important as other factors determining prey selection. *Synodus foetens* fed on pelagic, benthic-pelagic, and benthic prey during all seasons, and *T. lepturus* fed on pelagic and benthic-pelagic prey. These 2 species were the most abundant species examined during this study and contributed the highest portion of biomass.

DISCUSSION

Stomach content analysis is used widely to determine food composition, feeding strategies, trophic position, energy flow of predator and prey (Hyslop 1980), trophic structure (Luczkovich et al. 2002), and trophic partitioning (Ross 1986). Our analysis indicates the examination of stomach contents of top carnivores is an excellent way to evaluate the relationship between predators and food source in the shrimp grounds of Veracruz, Mexico.

The diets reported here for the 7 most abundant predators are generally similar to previous reports (Naughton and Saloman 1981, Mericas 1981, Divita et al. 1983, Sheridan et al. 1984, Cruz-Escalona et al. 2005), with some notable exceptions. While fish (in particular *Anchoa*) were important in the diet of *T. lepturus* in both this study and in the northern Gulf of Mexico (GOM) (Mericas 1981, Sheridan et al. 1984), the seasonal dominance of squid in the diet (42.7 %IRI during the dry season) has not been previously reported. The diets of both *C. arenarius* and *C. nothus* captured off Veracruz differed from previous reports for the species (Sheridan et al. 1984, Sutter and McIlwain 1987) in that no pelagic prey were noted in the present study, while *Anchoa* was a major component of the diet of both species in the northern GOM (Sheridan et al. 1984). Furthermore, *Bregmoceros*, common in the diets of other predators captured in the present study, was not found in either *Cynoscion* species, although this prey species was previously reported as an important component of the diet (Sheridan et. al 1984). While the diet of *S. brasiliensis* was dominated by fish as expected, squid was a more important component of the diet of (21.5–31.3 %IRI) than the 9% frequency of occurrence previously reported by Divita et al. (1983). The predominantly piscivorous diet of *S. foetens* agrees with previous reports from the northern GOM (Divita et al. 1983) and the Veracruz, Mexico, area (Cruz-Escalona et al. 2005), although the complete absence of penaeid shrimp in the diet is in contrast to reports from the northern GOM (Divita et al. 1983).

Our results showed patterns of resource partitioning and indicated that the 7 most abundant species examined in our study had proportioned diets based on where in the water column their prey was found. This tendency towards resource partitioning coincides with findings by Abarca-Arenas et al. (2004), who found similar evidence of resource partitioning in the Alvarado area based on the entire fish community. Macpherson (1981) and Livingston (1982) stated that in a trophic system, resource partitioning always will be observed; the pattern can be observed at the temporal level or in some cases at the diel level, even when competition among species exists

Five trophic guilds were clearly identified in our study based on the level of the water column in which the prey was obtained. Two guilds fed mainly on pelagic prey, 2 fed more on benthic prey, and one fed more on benthic-pelagic prey. Noteworthy is the large number of prey items consumed by the latter guild, demonstrating capacity to feed throughout the water column and to maintain generalist prey consumption habits.

Formation of the guilds did not appear related to body size, but rather to prey availability. Based on stomach contents, prey selection varied among the 3 seasons. Sedberry (1983) studied a community of demersal fishes on the continental shelf of the middle Atlantic Bight and also documented seasonal prey-shifting that appeared to be independent of predator size. The dry season showed the fewest taxa of prey taken, and the nortes season showed the most. With predator abundance remaining constant year-round and prey sources varying, guild structure was most likely affected. Although measurements were not made of abundance and diversity of prey beyond those obtained via stomach contents, our results suggest that prey in the nortes and wet seasons are more diverse than prey in the dry season, thus affecting the trophic guilds (sensu Darnell 1961).

Seasonal nutrient flux may influence prey availability in the study area and thus the structure of trophic guilds. Nutrients in the Alvarado Lagoon system are largely dependent upon influx from the Papaloapan River. The river deposits the largest amount of nutrients into the system during the wet and nortes seasons (Moran-Silva et al. 2005), resulting in higher productivity levels (Abarca-Arenas et al. 2004) and a general increase in the amount of exploitable resources in the system (Contreras 1985, Soberón and Yañez-Arancibia 1985). Thus, it was not a surprise that our study found the largest variety of prey and the highest abundance of predators during these 2 seasons.

Anthropogenic factors can affect the guild structure as well. Shrimp trawling is an important commercial activity off Alvarado (Grande and Díaz 1981). The effects of bycatch removal on the local demersal fish community have not been measured; however, evidence suggests that large-scale fishing affects the structure of fish communities by reducing the abundance of prey and predators and by reducing the size of predators (Pope and Knights 1982, Rice and Gislason 1996, Jennings et al. 1998, Rogers et al. 1999). In the Alvarado area, information is lacking regarding fishing activities and the life history and ecology of piscivorous fishes and their prey; thus, it is difficult to estimate the effect of the shrimp fishery and its bycatch on the trophic dynamics of the area. However, intense fishing activity in tropical waters can cause reduction in species richness and dominance of the smaller targeted and non-targeted fishes in the assemblage (Rogers et al. 1999). Our data suggest that a similar reduction in larger species may have occurred near Alvarado. For instance, large, potentially commercially important species such as *R. canadum*, *F. tabacaria*, *S. guachancho,* and *S. cavalla* composed only 11% of the total bycatch. Dominance of *S. foetens* and *T. lepturus*, 2 non-target species with the greatest variety of prey, suggests trophic adaptability and generalization may be important in this heavily fished system.

ACKNOWLEDGMENTS

This manuscript is based on the senior thesis of the lead author submitted in 1996 in pursuit of the biologist degree to the Facultdad de Estudios Superiors at the Iztacala campus of the Universidad Naciónal Autónoma de México. We thank personnel from the Cet-Mar Academy in Alvarado, Mexico, for assistance with field collections, particularly Tomas Corro-Ferreiro. In particular, we thank M.S. Peterson for assistance and advice during the preparation of this manuscript.

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