Feeding habits of the dwarf weakfish (*Cynoscion nannus*) off the coasts of Jalisco and Colima, Mexico

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Sciaenids from the Pacific coast of Mexico are used as a second-class fish species for human consumption (Aguilar-Palomino et al., 1996). The dwarf weakfish (*Cynoscion nannus*) (Castro-Aguirre and Arvizu-Martínez, 1976) is often caught as bycatch in the shrimp fishery but, because of its small size (<27 cm TL, total length), it is not considered a valuable resource. This species can be found in great numbers in waters between 100 and 812 m (Allen and Robertson, 1994; Fischer et al., 1995) associated with the soft-bottom regions off the coast of Jalisco and Colima (González-Sansón et al., 1997).

Previous studies of the trophic biology of the Sciaenidae (Chao and Musik, 1977; Campos and Corrales, 1986; Chao, 1995; Peláez-Rodríguez, 1996; Cruz-Escalona, 1998; Lucena et al., 2000) have shown that they feed on a variety of small fish and benthic invertebrates (Allen and Robertson, 1994). However, there are few studies concerning the feeding habits of *C. nannus*, and its dietary preferences are not known. Considering its abundance, *C. nannus* must play an important role in the trophic relationships of soft-bottom ecosystems in this region.

Most studies describing the feeding habits of fish have used the normalized version of the breadth niche index proposed by Levins (1968). This index is based both on the number of food resources and on the proportion of prey used by a species. The appropriate distribution function for this index ensures sample independence among prey found in any particular stomach. Distribution functions based either on the number or the relative biomass or volume of dietary items do not ensure such independence, given that all items found in any particular stomach are statistically associated (Hurlbert, 1984). Therefore, neither the number nor the relative biomass or volume of dietary items should be used to calculate the Levins index. The only distribution function that ensures statistical independence is that which is based on the proportion of stomachs in which a certain food resource is found (Krebs, 1999).

Considering the ecological importance of studying the feeding habits of this abundant fish species, we examined trophic breadth variations (temporally and ontogenetically) of *C. nannus*. When attempting to correctly apply the Levins index, we used the distribution function of prey that ensures statistical independence among sampling units.

Materials and methods

The sampling area was located in the central region of the continental shelf off the Pacific coast of Mexico, where the mouth of the river Cuitzmala, in Punta Farallón, Jalisco (19°22′N, 105°01′W), is the northern limit, and Cuyutlán, Colima (18°55′N, 104°08′W), is the southern limit. Samples of *C. nannus* were collected on a monthly basis from January to December 1996 (except February, August, and September) on the research vessel *BIP V*, equipped with a trawl net with a pair of codends. Sampling was carried out over seven transects perpendicular to the coast, each comprising four bathymetric strata: 20, 40, 60, and 80 m mean depth.

Fish were individually identified, measured (TL, ±1 mm), and the total weight of each fish was recorded to the nearest 0.1 g. The stomachs of individual fish were dissected and preserved in 10% neutralized formalin. Stomach contents were analyzed

with a stereoscopic microscope and dietary items were identified to the lowest taxonomic level possible by using specialized keys. Garth (1958), Rodríguez de la Cruz (1987), Hendrickx and Salgado-Barragán (1991), and Hendrickx (1996), were consulted for crustacean identification, whereas Jordan and Evermann (1896–1900), Castro-Aguirre (1978), Allen and Robertson (1994), Thomson et al. (2000), and FAO guides were used for fish identification (Fischer et al., 1995).

Both the number of individuals and weight of each dietary category were quantified, and mean proportions in terms of number ($\%N_{\bar{x}}$) and biomass ($\%W_{\bar{x}}$) were calculated according to Tirasin and Jørgensen (1999):

$$\%\bar{X}_i = \frac{\sum_{j=1}^{n_j} X_{ij}}{\sum_{i=1}^{k} \sum_{j=1}^{n_j} X_{ij}} \times 100,$$

where X_{ij} = the number or weight of each taxa i in the jth stomach; and
k = the number of dietary components found in all stomachs analyzed, n_j.

The percent frequency of occurrence of each component was also obtained (%F). Finally, the index of relative importance for each dietary category was calculated (IRI, Pinkas et al., 1971; Rosecchi and Nouaze, 1987):

$$IRI_i = (\%N_i + \%P_i) \times \%F_i.$$

Relative importance index values were expressed as a percentage of the total items analyzed (Cortés, 1997) and results were graphically represented as a rectangle of base %F and height %N + %W.

Variance analysis was applied on transformed W′= $\sin^{-1}(\sqrt{W})$] gravimetric proportions of the dietary components (Zar, 1999) to evaluate both monthly and ontogenetic variations in the feeding habits of C. nannus. The number [$q=1+3.322(\text{Log}_{10}n)$] and width of size classes ($w=R_{TL}/q$) were considered for analysis, where n is the sample size and $R_{TL}=TL_{\max}-TL_{\min}$.

For the analysis of trophic niche breadth, the normalized version of the index proposed by Levins (1968) was used. This index combines both the number of prey resources used (k) (i.e., the trophic spectrum) and the relative frequency with which each prey resource is consumed (j). This represents the distribution function of prey proportions in diet (Hespenheide 1975; Hurlbert, 1978):

$$Ba = \frac{\left(\sum_{j=1}^{n_j} p_j^2\right)^{-1} - 1}{k - 1}.$$

Because the ensemble of prey found in any given stomach does not constitute independent samples (Hurlbert, 1984), p_j was calculated as the proportion of individual fish (N^*) that consumed a certain food resource in relation to the number of resources used by the total number of fish:

$$P_j = \frac{N_j^*}{\sum_i \sum_j N_j^*} \text{ so that } \sum p_j = 1.$$

Ba values range between 0 and 1. Zero values indicate that fish feed on only one prey type, representing the minimum diet breadth and high feeding specialization. Unity values, on the other hand, indicate that the species consumed all k food resources in the same proportion ($p_j=1/k$), representing no selection among prey types and the widest possible trophic niche (Gibson and Ezzi, 1987; Labropoulou and Eleftheriou, 1997). Ba values were calculated on the basis of matrix resources (Colwell and Futuyma, 1971) both for each month and for each size class. The percentage similarity measure (R) between size classes q' and q'' (Renkonen, 1938; Schoener, 1970; Hurlbert, 1978) was calculated as

$$R_{q'q''} = 1 - \frac{1}{2}\left[\sum_{j=1}^{k} |p_{jq'} - p_{jq''}|\right],$$

where p_{jq} is the proportion of individual fish in each size class that consumed a certain food resource, calculated over the total number of stomachs per size class.

Confidence intervals (CI$_{95\%}$) of Ba were obtained by means of the bootstrap method (Mueller and Altenberg, 1985; Efron and Tibshirani, 1986) by considering two thousand resamplings of the data (Hamilton, 1991).

Results

The 311 Cynoscion nannus examined ranged from 7.5 to 20.6 cm TL. Food was found in 287 (92%, ranging from 85% to 98% among size classes) stomachs. The trophic spectrum of C. nannus is composed of 29 dietary items (Table 1), which were classified into four general categories: penaeid shrimp, fish, stomatopods, and cephalopods.

Penaeid shrimp constituted the principal dietary category of C. nannus ($N_{\bar{x}}=82.5\%$, $W_{\bar{x}}=35.4\%$; $F_{\bar{x}}=43.9\%$, $IRI_{\bar{x}}=74.6\%$; Fig. 1), of which juvenile stages were the most frequent ($F_{\bar{x}}=23.4\%$). Fish were the second most important category ($N_{\bar{x}}=6.5\%$, $W_{\bar{x}}=36.5\%$, $F_{\bar{x}}=37.7\%$, $IRI_{\bar{x}}=14.5\%$), followed by stomatopods of the Squilla genus ($N_{\bar{x}}=5.8\%$, $W_{\bar{x}}=8.6\%$, $F_{\bar{x}}=25.5\%$, $IRI_{\bar{x}}=6.6\%$). The cephalopod Loliopsis diomedae was the last category in order of importance ($N_{\bar{x}}=1.0\%$, $W_{\bar{x}}=12.4\%$, $F_{\bar{x}}=4.2\%$, $IRI_{\bar{x}}=1.8\%$).

Overall, significant differences in diet were found between individuals of different size classes ($F=1.03$; $P<0.05$). Values of the percentage similarity of diet (R) between size classes were, in general, <50% (Table 2). R-values were relatively high only among size classes 2

Table 1

Composition of the trophic spectrum of *Cynoscion nannus* (7.5 cm ≤TL ≤20.6 cm; *n*=287) from the coast of Jalisco and Colima (mean percentage by weight [g; %W], frequency of occurrence [%F], number [%N], and index of relative importance [%IRI] of prey).

Dietary categories		%W	%F	%N	%IRI
Cephalopods	*Loliopsis diomedae*	12.4	4.2	1.0	1.8
	Remains	0.1	0.4	0.1	0.0
Stomatopods	*Squilla* sp.	5.9	19.7	4.0	6.4
	S. panamensis	1.5	1.7	0.8	0.1
	S. hancocki	0.5	1.7	0.4	0.0
	S. mantoidea	0.7	2.5	0.7	0.1
Penaeid shrimps	*Solenocera* sp.	7.6	10.9	4.3	4.2
	S. florea	2.2	1.3	0.6	0.1
	S. mutator	3.8	2.9	4.6	0.8
	Trachypenaeus brevisuturae	3.5	5.4	2.3	1.0
	Juvenile shrimps	18.2	23.4	70.8	68.4
Other crustaceans	Carideans	1.3	4.2	0.9	0.3
	Panulirus sp. larvae	0.1	0.4	0.1	0.0
	Other crustacean larvae	0.1	0.4	0.3	0.0
	Euphausiids	0.5	1.3	2.3	0.1
	Microcrustaceans	0.2	0.4	0.1	0.0
	Unidentified remains	4.2	13.8	—	1.9
Fish	*Cynoscion nannus*	2.1	0.8	0.4	0.1
	Cherublemma emmelas	1.3	1.7	1.0	0.1
	Polydactylus opercularis	1.6	1.3	0.4	0.1
	Ophidium sp.	0.7	0.4	0.8	0.0
	Monolene sp.	0.9	0.4	0.1	0.0
	Symphurus sp.	0.1	0.4	0.1	0.0
	Bregmaceros bathymaster	1.6	2.5	0.7	0.2
	Anguilliformes	1.2	2.1	0.5	0.1
	Leptocephalus larvae	8.9	4.2	1.1	1.4
	Other fish larvae	1.4	1.7	1.0	0.1
	Unidentified remains	16.6	22.2	0.3	12.3
Anelids	Polychaeta	0.62	1.26	0.38	0.0

Table 2

Percentage similarity values (*R*) of the diet between size classes (cm, TL) of *Cynoscion nannus* (*n*=287) from the coast of Jalisco and Colima.

	Size class (cm)					
	7.0–8.9	9.0–10.9	11.0–12.9	13.0–14.9	15.0–16.9	17.0–18.9
Size class (cm)						
9.0–10.9	37.0					
11.0–12.9	44.2	54.2				
13.0–14.9	33.5	65.1	51.1			
15.0–16.9	31.0	47.6	51.4	64.1		
17.0–18.9	12.5	31.6	39.6	38.0	40.4	
19.0–20.9	29.3	45.8	44.3	47.9	40.1	21.6
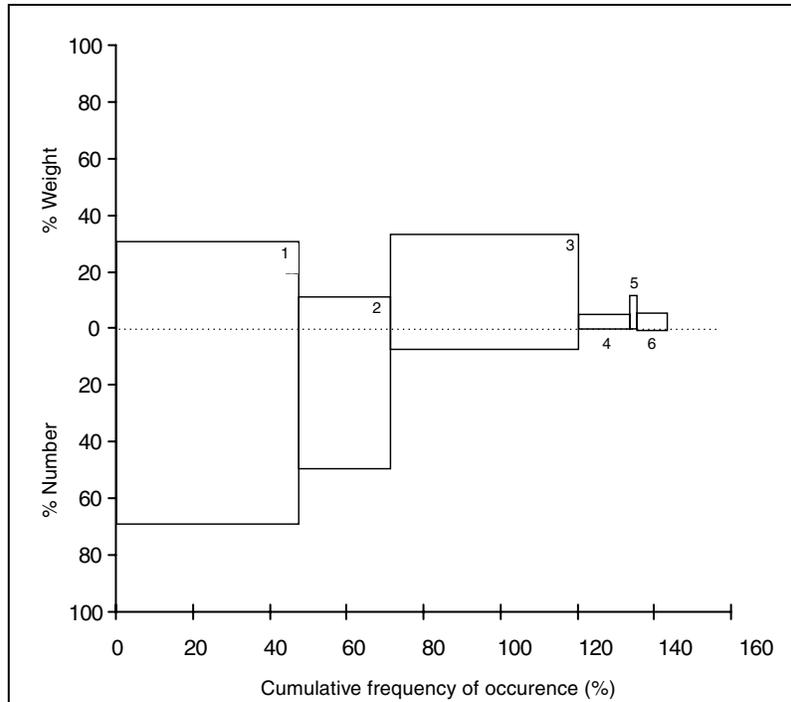
Figure 1

Graphical representation of the percentage values of the index of relative importance (*IRI*) of the main dietary components found in the stomachs of *Cynoscion nannus* (*n*=287). 1: penaeid shrimps; 2: stomatopods; 3: fish; 4: crustacean remains; 5: cephalopods; 6: other crustaceans.
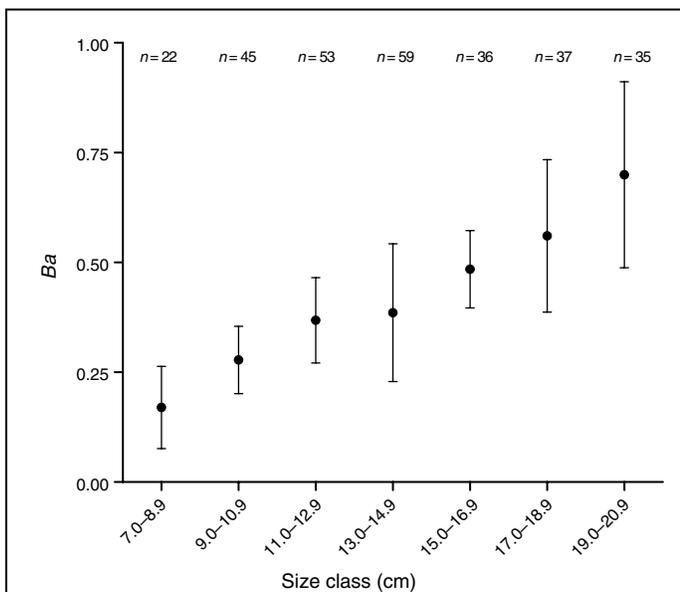
Figure 2

Ontogenetic variations of the diet diversity index ($Ba \pm CI_{95\%}$) of *Cynoscion nannus* (*n* is the number of stomachs containing food).

through 5 (51.1%–65.1%). The trophic spectrum of the smallest *C. nannus* (7 cm ≤TL ≤10.9 cm, *n*=67) was composed by crustaceans ($W_{\bar{x}}=68\%$), mostly carideans and stomatopods ($W_{\bar{x}}=20\%$). The diet of intermediate individuals (11 cm ≤TL ≤16.9 cm; *n*=148) was composed by penaeid shrimp, fish, and stomatopods. Only fish of the size classes grouped in this range showed percentages of diet similarity >50%. Among *C. nannus* between 17 and 18.9 cm TL (*n*=37), the value of consumed fish biomass attained 69%, whereas that of penaeid shrimp reached 20%. Only among the larger individuals (19 cm ≤TL ≤20.9 cm; *n*=35) did cephalopods attain high gravimetric values ($W_{\bar{x}}=45\%$) followed by penaeid shrimp ($W_{\bar{x}}=38\%$).

Values of trophic niche breadth for each size class indicated ontogenetic variation in the diet (Fig. 2). The smallest individuals fed on a smaller number of prey species and showed a trend towards higher trophic specialization. Larger individuals, however, had a wider trophic spectrum and fed on a greater number of different prey species.

Temporal variations in the dietary composition of *C. nannus* were significant (*F*=3.58; *P*<0.05). During the first months of the year, *C. nannus* consumed a higher percentage of fish ($W_{\bar{x}}=37.2\%$),

Figure 3

Monthly mean values of the diet diversity index ($Ba \pm CI_{95\%}$) of *Cynoscion nannus*. The overall mean value of the index (Ba; - - -) and its confidence intervals ($CI_{95\%}$; ....) are shown (n is the number of stomachs containing food).
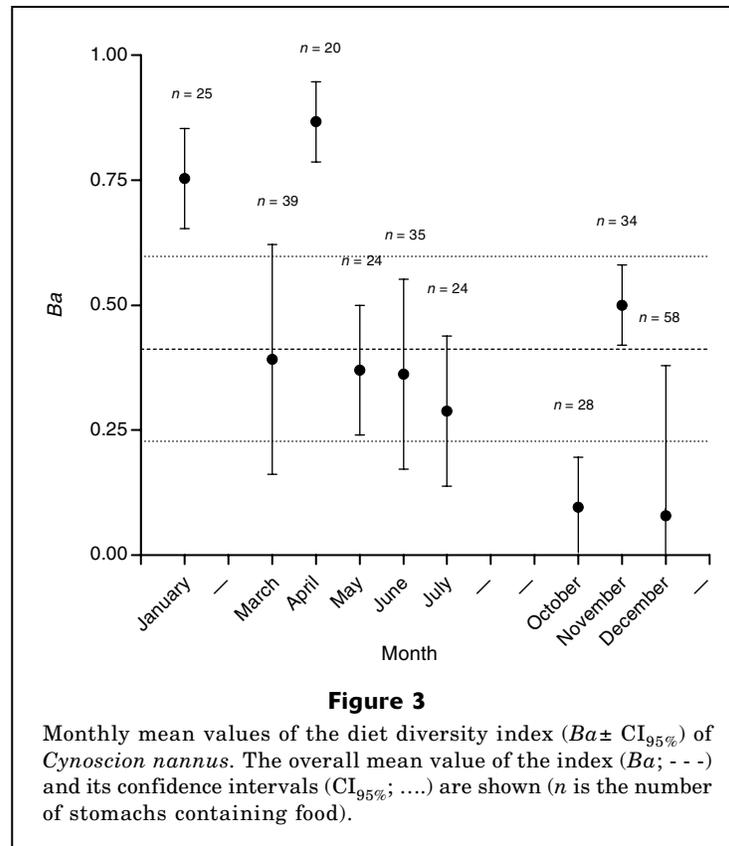
whereas towards the end of the year, penaeid shrimp were eaten in higher proportions ($W_{\bar{x}}$=50.6%). During May, stomatopods and carideans were found with higher biomass values than during the rest of the year ($W_{\bar{x}}$ =68.2% and 20%, respectively). Cephalopods were found in most months with biomass values ranging from 4% to 34% of consumed biomass.

The mean value of diet diversity was 0.41 ($\pm$0.18 $CI_{95\%}$). Although the number of dietary categories for *C. nannus* that were identified was high (29 prey types), there were a few items with significant importance. Monthly variations in *Ba* ranged from 0.1 to 0.8 (Fig. 3). During most of the period analyzed, *Ba* values were not significantly different from each other as shown by the lack of overlap between $CI_{95\%}$. The only exceptions were January and April, when $CI_{95\%}$ was above the mean *Ba* $\pm CI_{95\%}$ value, and October when $CI_{95\%}$ was below the mean *Ba*.

Discussion

Cynoscion nannus is a carnivorous fish that feeds on at least 29 different prey types. Although cannibalistic behavior has been reported for several fish species in a variety of habitats and life-history strategies (Smith and Reay, 1991), *C. nannus* as a prey type was

found in only 0.8% (two individuals >15.0 cm TL) of all stomachs analyzed. According to the IRI values, crustaceans—specifically juvenile shrimp and stomatopods of the genus *Squilla*—appear to be the most important items in the diet. The type of substrate can influence the feeding habits of these fish. For example, Minello and Zimmerman (1984) observed that under experimental conditions, the feeding preferences of *C. nebulosus* (16 cm≤TL≤21 cm) for *Farfantepenaeus aztecus* varied depending on the substrate. These authors suggested that substrate characteristics determine the burrowing capacity of *F. aztecus* and thus predator avoidance. In the study area, juvenile shrimp and stomatopods of the genus *Squilla* can be abundantly found in soft-bottom habitats (González-Sansón et al., 1997). Both the cephalopod (*Loliopsis diomedae*) and the fish species found in the stomach contents of *C. nannus* are pelagic or demersal species, indicating that the feeding activities of *C. nannus* are not exclusively limited to the benthos, and that this species can forage throughout the water column. Results in the present study provide evidence that fish feeding at different water depths have access to a broader variety of prey types. This has been shown both for other Sciaenidae (Chao and Musik, 1977; Campos and Corrales, 1986; Chao, 1995; Peláez-Rodrí-guez, 1996; Cruz-Escalona, 1998), and other species of demersal fish (Lucena et al., 2000).

It should be noted that graphic representations of the IRI values are more accurate in describing the diet of fish species (Cortés, 1997). Our results (Fig. 1) demonstrate that the three indices representing the relative importance of each food item highlight the influence that the percentages of occurrence, by number and by weight, have on the overall IRI values.

The temporal analysis of the tropic spectrum of *C. nannus* showed that during October, November, and December this species fed mainly on penaeid shrimps. Fish prey were abundant in stomachs collected only during March, April, June, and November. Stomatopods were present all year round, but only abundant during May. Low *Ba* values in October were due to the prevailing consumption of *Solenocera* spp. Monthly differences in the diet of *C. nannus* were most probably in accordance with the seasonal variations in prey species abundance, which in turn determined their availability. Lucena et al. (2000) found that temporal variations in the diet of *C. guatucupa* from southern Brazil are related to seasonal production cycles of prey, mainly fish and crustaceans, thus supporting the view that sciaenids can generally be considered opportunistic species.

Results of this study showed ontogenetic variations in the trophic spectrum of *C. nannus*. The smallest individuals (7 cm ≤TL ≤10.9 cm) feed mainly on stomatopods, whereas larger individuals (≥11 cm TL), consume less stomatopods and more penaeid shrimp and fish. Merriner (1975) also found ontogenetic variations in the diet of *C. regalis*, where the smallest individuals (age group "0") fed on crustaceans and small fish. The relative importance of shrimp, however, decreased as *C. regalis* increased in size, and individuals of age group "2" generally consumed different species of clupeids, depending on the local abundance of each prey species. The measure of percentage similarity among size classes (Table 2) shows that *C. nannus* share a limited number of resources. Only fish belonging to intermediate lengths feed on the same prey types in percentages greater than 50% for the total number of food resources used.

Ontogenetic changes in the diet of *C. nannus* observed in the present study are due to differences in diet composition and proportions of consumed prey. These results suggest that food types are ingested unequally as fish grow and that morphological and physiological changes take place. As fish grow, the size of their mouth increases proportionally, their swimming capacity is modified, and their energetic requirements vary. Thus, larger fish have different feeding requirements than smaller ones and will attempt to satisfy them by consuming a larger variety of prey types. As *C. nannus* grow, *Ba* values increase and the trophic spectrum of the species grows wider (Fig. 2). Our results indicate that there is a pattern of differential use of food resources throughout the different size classes of *C. nannus*, and suggest a possible ecological strategy to reduce intraspecific competition for food in the population (Schoener, 1974; Werner, 1979).

The increasing variety of food resources used as predators increase in size is a common pattern among marine organisms, including invertebrates (Rangeley and Thomas, 1987; Mascaró and Seed, 2001). These ontogenetic variations in food preferences can be explained by changes in foraging behavior where predators of certain size classes actively select their prey (Jubb et al., 1983; Allan et al., 1987). Alternatively, they can be the result of passive mechanisms that do not involve individual decisions associated with age or life stages, such as differences in the predator's mouth structures, changes in movement velocity of both prey and predator, and spatial or temporal variations in habitat as predators increase in size (Hughes, 1979; Rodrigues et al., 1987).

To show that *Ba* values are affected by the type of prey distribution function used, we calculated the mean diet diversity index using 1) the proportion of the number of prey (*N*; *Ba*=0.03), 2) the percent frequency of occurrence of prey (*F*; *Ba*=0.16), and 3) the proportion of prey biomass (*W*; *Ba*=0.32). The values obtained were then compared to those calculated by considering the proportion of individuals (*N**; *Ba*=0.41) that use a certain food resource for the total number of stomachs analyzed. *Ba* values calculated by using *N*, *F*, and *W* are markedly lower than the *Ba* value obtained by using *N**. These differences serve to underline the importance of complying strictly with the property of statistic independence of sampling units when the feeding habits of a species are being studied.

Given the numerical importance of *C. nannus* as part of demersal assemblages, observations on the trophic spectrum of this and other species can help to generate a conceptual model of the trophic webs and dynamics of the feeding relations among communities found on the continental shelf of Jalisco and Colima, an area that has received little attention in the past.

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