

Trophic comparison among Triglidae (Pisces: Scorpaeniformes) off Baja California Sur, Mexico

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Abstract: Composition, intensity, diversity, ontogenetic and seasonal changes of feeding of *Prionotus stephanophrys*, *Bellator gymnostethus* and *P. albirostris* were studied in the Pacific coast of Baja California Sur, Mexico. A total of 547 individuals of the three species were sampled between 1988 and 1990. The euphausiid *Nyctiphanes simplex* was the main prey of *B. gymnostethus*, which caught it during the day, and of *P. stephanophrys*, which ate it at night and twilight; larger individuals of *P. stephanophrys* shifted to *Pleuroncodes planipes*, a change that coincided with the fish' shift from the pelagic to the benthic environment. Feeding intensity of this searobin was higher in summer, after reproduction. *P. albirostris* fed throughout the day; its diet, more diverse and equitable, was based on penaeids, pasiphaeids, and mysids. Differences in spatial distribution, diet and time of feeding suggested efficient habitat partitioning among these fishes.

Key words: Triglidae, *Prionotus stephanophrys*, *Bellator gymnostethus*, *Prionotus albirostris*, food habits, habitat partitioning, Eastern Pacific.

Searobins (Triglidae), known in Mexico as triglas or vaquitas and in South America as vocadores or cabrinhas, are benthic fishes inhabiting tropical and subtropical continental shelves worldwide, such as the outer (western) coast of Baja California Sur, Mexico. Six triglid species are found in this area: *Prionotus stephanophrys* Lockington (overwhelmingly dominant), *P. albirostris* Jordan & Bollman, *Bellator gymnostethus* (Gilbert), *P. ruscarius* Gilbert & Starks, *B. xenisma* (Jordan & Bollman) and *B. loxias* (Jordan), the last three being occasional. Their bathymetric distribution overlaps broadly. *P. stephanophrys* occurs throughout the explored latitudinal range; it was the only triglid collected as far north as the Bay of Sebastián Vizcaíno (Schmitter-Soto 1992).

Though abundances of the six species increase off the mouths of the Magdalena-Almejas Lagoon Complex (ca. 24°30'N), only *P. ruscarius* has been found inside the lagoons.

This, together with its much greater size (and, presumably, different diet), separates it from the other species. Sediment type distinguishes *B. xenisma* and *B. loxias*, which appear to be more frequent over sand, from the others, which occur more often over silt. As muddy bottoms are the rule in this area, it is not surprising that these *Bellator* species are scarce (Schmitter-Soto 1992).

Autoecological aspects of Triglidae in the Eastern Pacific have not received much attention. Samamé *et al.* (1983) and Meléndez (1987) offered some trophic data on *P. stephanophrys* from Peru and Chile, respectively; the Peruvian study discussed also distribution and reproduction. Schmitter-Soto & Castro-Aguirre (1991, 1994) examined age and growth of *P. stephanophrys*, *B. gymnostethus* and *P. albirostris*.

This work analyzes and compares diet composition, intensity and diversity, as well as ontogenetic, diel and seasonal trophic changes,

for *P. stephanophrys*, *B. gymnostethus* and *P. albirostris*. The results will aid in a discussion of habitat partitioning among these searobins.

MATERIAL AND METHODS

The analyzed fishes came from 50 diurnal and nocturnal samples, taken off the western coast of the southern half of the Baja California Peninsula, from the Bay of Sebastián Vizcaíno (29°N, 115°W) to the southern tip of the Magdalena-Almejas Lagoon Complex (24°N, 111°W), in depths from 20 to 240 m. We established the sampling stations on muddy or sandy bottoms, suitable for the operation of the fishing gear (trawl nets, 21 m wide at the opening, 24 m long, 3 cm mesh), during five cruises on board the R/V "El Puma", from 1988 to 1990 (Table 1); mean trawl duration was 20 min, at a speed of 3 knots.

We separated the triglids from the total catch, and took a stratified sample of *P. stephanophrys*; since *B. gymnostethus* and *P. albirostris* were scarce, we collected all available individuals, but still could not perform quantitative seasonal and ontogenetic analysis of these two species. Furthermore, length variation was very low in some seasons (Table 1), indicating bias towards the few size classes present in the habitat at that time. However, the samples were suitable for interspecific comparisons, as determined by plotting cumulative trophic diversity vs. cumulative number of stomachs examined (Pielou 1966): at approxi-

mately 30 stomachs the curve almost reached an asymptote.

When possible, we processed samples on board; if not, we injected 5% formaldehyde neutralized with seawater into stomach and coelom. We studied stomach contents on a Petri dish with 70% ethanol.

To cast light on feeding rhythms, we classified digestion stages as follows: 1, contents mostly intact, identifiable; 2, contents mostly not recognizable (fragments); 3, amorphous contents; 0, no contents. We included empty stomachs in this scale, considering vacuity a step that closes the cycle.

In stomachs in digestion stage 1 or 2, we identified prey items to the lowest possible taxon under a stereomicroscope, with the help of the pertinent literature. We counted the number of individuals, and measured the volume by displacement to the nearest 0.1 ml; excessive alcohol was previously blotted out.

The index of relative importance, IRI (Pinkas *et al.* 1971), has been criticized because of its supposedly questionable biological significance. Nevertheless, we chose it because it is a practical measure of trophic importance, which incorporates the relative number of organisms (N%), relevant in foraging theory, and the percent volume (V%), a probable reflection of caloric content (Wallace 1981, Moreno i Amich 1987).

We analyzed diet changes of *P. stephanophrys* by season, time of day and size. For that purpose, the winter sample consisted of the cruises of February 1989 and March 1990, and summer included July 1989 and

TABLE I

Collection data of Triglidae from the western coast of Baja California Sur

Cruise	<i>P. stephanophrys</i>		<i>B. gymnostethus</i>		<i>P. albirostris</i>			
	N	L (mm)	N	L (mm)	N	L (mm)	Depth (m)	Latitude (°N)
Oct 88	-	-	4	108±19	9	137±70	32-145	24.2-26.1
Feb 89	13	110±50	-	-	-	-	27-135	24.3-26.3
Jul 89	170	135±36	21	102±13	10	183±9	31-143	25.1-28.6
Mar 90	138	140±53	30	91±27	16	180±10	36-241	24.2-28.8
Sep 90	131	160±43	-	-	15	176±30	38-218	24.1-28.8
Total	452		55		50			

N, sample size (number of stomachs); L, mean standard length of fish (± 1 SD).

September 1990. The day was divided into dawn (0501-0700 h), day (0701-1700), sunset (1701-1900) and night (1901-0500). We did not *a priori* assign size categories of *P. stephanophrys*, but sought an abrupt change in consumption of the main prey. To do this, we examined curves of item frequency vs. standard length (SL) of the fish.

Non-parametric comparisons of feeding composition and intensity involved ranking food items according to their IRI values, to compare trophic spectra between seasons or sizes, and digestion stages according to their percent occurrence, to compare intensity by season or time of day.

To carry out a similarity analysis between specific diets we used Whittaker's PS_I on prey items whose IRI $\geq 0.1\%$. This measure of diet overlap is reputedly advantageous because of its independence from sample size (Kohn & Riggs 1982), and Wallace (1981) recommends it when data on prey availability are insufficient or absent; trophic spectra are considered significantly similar when $PS_I > 60\%$.

To further describe prey communities we obtained diversity, richness, and equitability indices (Pielou 1966, Margalef 1980); these indices, usually applied on N% or V%, were applied here on the feeding coefficient ($Q = N\% + V\%$, in Braga & Braga 1987). Thus, for example, diversity was determined as

$$H_Q = -\sum_{i=1}^S Q\%_i \ln Q\%_i$$

where S is the total number of food categories and $Q\%_i$ is the feeding coefficient of the i -th species, expressed as percentage of the sumatory of Q for all food categories. Braga & Braga (1987) used Q to classify prey items as "preferential" ($Q > 200$), "secondary" ($20 < Q < 200$) or "accidental" ($Q < 20$).

RESULTS

Trophic spectra: The sample of *P. stephanophrys* consisted of 452 stomachs (Table 1). The global trophic spectrum comprised 35 prey categories. The euphausiid *Nyctiphanes simplex* was clearly dominant ($Q \gg 200$), followed secondarily ($Q > 20$) by the red crab *Pleuroncodes planipes* (Fig. 1). All

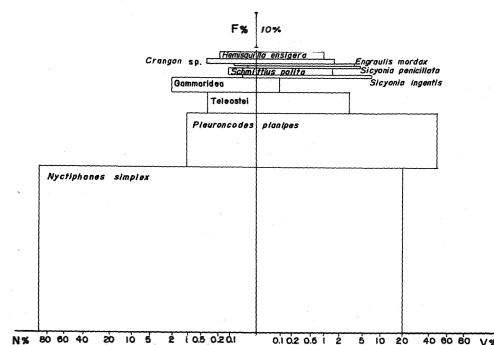


Fig. 1. Main prey of *Prionotus stephanophrys* off Baja California Sur. Rectangle area reflects prey importance as measured by percent volume (V%), percent abundance (N%) and percent occurrence (F%). Horizontal scales are logarithmic.

other items were occasional, including copepods, mysids, gammarideans, stomatopods, carideans, penaeids and fishes, among others (complete data are available from the first author).

The sample of *B. gymnothethus* consisted of 55 stomachs (Table 1). Among the 18 prey items, *N. simplex* was again dominant, followed by fish larvae and the penaeid shrimp *Sicyonia ingentis* (Fig. 2). Gammarideans, copepods, mysids, and carideans figured among the other items.

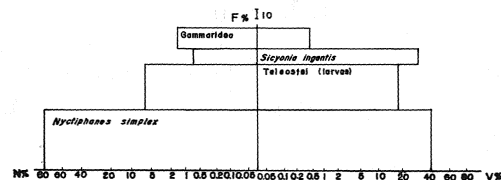


Fig. 2. Main prey of *Bellator gymnothethus* off Baja California Sur. See Fig. 1.

The sample of *P. albirostris* consisted of 50 stomachs (Table 1). The global trophic spectrum included 22 food items. The penaeid *Solenocera mutator* was preferred, followed by pasiphaeid *Leptochela serratorbita* and mysids (Fig. 3). Less important items included gammarideans, the stomatopod *Hemisquilla ensigera*, carideans other than *L. serratorbita*, *S. ingentis*, pinnotherids, portunids and fishes.

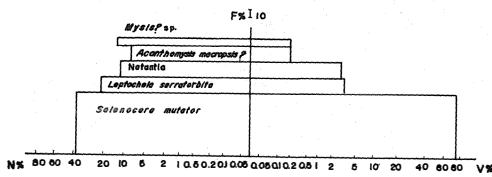


Fig. 3. Main prey of *Prionotus albirostris* off Baja California Sur. See Fig. 1.

Diet diversity: Though the diet of *P. stephanophrys* was the richest ($D_Q = 4.22$), it was the least diverse ($H_Q = 0.14$), due to the enormous numbers of *N. simplex*, which lowered equitability to 0.04. A partial reason for the richness of this trophic spectrum was the bathymetric and latitudinal ubiquity of the species, which enabled it to prey on organisms from different zones. Thus, for instance, *Mysis* sp., Palaemonidae and Copepoda appeared only off the mouths of the Magdalena-Almejas Lagoon Complex; Stomatopoda were found no deeper than 100 m, but *Hemisquilla ensigera* south and *Schmittius polita* north of parallel 26°N; the genus *Sicyonia* was circumscribed to the Bay of Sebastián Vizcaíno, but *S. penicillata* in shallower and *S. ingentis* in deeper waters.

B. gymnostethus had the least equitable ($J_Q = 0.01$) and poorest ($D_Q = 2.09$) trophic spectrum; yet, paradoxically, its diversity was comparatively high ($H_Q = 0.19$).

The relatively high diversity of the prey community of *P. albirostris* ($H_Q = 0.21$), was due more to equitability ($J_Q = 0.07$) than to richness ($D_Q = 2.37$).

Circadian variation of feeding intensity:

In winter, *P. stephanophrys* stomachs in digestion stages 2 and 1 were more abundant during the light hours and digestion stage 3 occurred more often after sunset. Vacuity had lower values as the hours passed, with most empty stomachs at dawn (Table 2). Thus, food was ingested mainly during the day, as happened in the other species, though the tendency was not clear enough to be statistically significant (Friedman's c^2).

A different pattern appeared in summer, when the maximum number of intact prey occurred at and after sunset, and stomachs in advanced digestion prevailed earlier in the day, while vacuity was higher towards sunset (Table 2). This circadian feeding rhythm change was significant in summer ($c^2 = 7.82$, $P < 0.05$). The seasonal change is discussed below.

Regardless of season, predation on the two main prey categories, *N. simplex* and *P. planipes*, had distinct patterns: the searobin ate the euphausiid almost exclusively at night, whereas the red crab was eaten mostly at sunset (Fig. 4).

The vacuity of *B. gymnostethus* stomachs decreased from dawn to night; the opposite happened with stomachs in digestion stage 3 (Table 3). This indicated that *B. gymnostethus* feeds during the day, like *P. stephanophrys* in winter. However, as most fish were captured only from 0800 to 1700 h, the tendency was not significant.

Although all *P. albirostris* empty stomachs appeared at sunset, and the greatest amounts of digested food concentrated towards midday,

TABLE 2

Circadian variation of feeding intensity in *Prionotus stephanophrys* by season off Baja California Sur. Figures are percent frequency by time of day; digestion stages are explained in text

Digestion state	Down 0501-0700		Day 0701-1700		Sunset 1701-1900		Night 1901-0500	
	Win	Summ	Win	Summ	Win	Summ	Win	Summ
0	36	3	26	11	17	10	10	0
1	9	22	21	15	0	45	17	41
2	50	31	47	41	8	23	17	18
3	5	44	6	33	75	23	57	41

Win, winter; Summ, summer.

TABLE 3

Circadian variation of feeding intensity in *Bellator gymnostethus* and *Prionotus albirostris* off Baja California Sur. Figures are percent frequency by time of day; digestion stages are explained in text. No specimens of *P. albirostris* were captured at night (1901-0500 h)

Digestion stage	Dawn 0501-0700	Day 0701-1700	Sunset 1701-1900	Night 1901-0500
<i>Bellator gymnostethus</i>				
0	100	14	10	0
1	0	23	10	0
2	0	49	30	50
3	0	14	50	50
<i>Prionotus albirostris</i>				
0	0	0	23	-
1	38	33	31	-
2	62	34	38	-
3	0	33	8	-

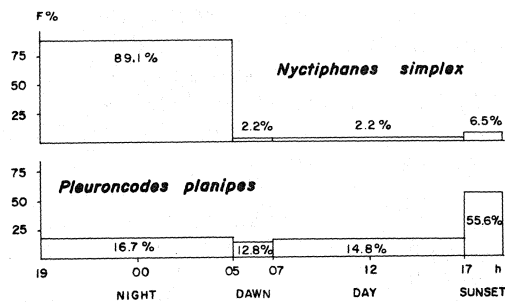


Fig. 4. Circadian variation of the consumption of *Nyctiphanes simplex* and *Pleuroncodes planipes* by *Prionotus stephanophrys* off Baja California Sur.

intact food could be found from dawn till sunset (Table 3). We did not capture the species at night.

Seasonal changes: Feeding intensity of *P. stephanophrys* increased in summer (Table 2; $c^2 = 61.8$, $P < 0.001$); so did diet diversity, richness and equitability. Diet composition was significantly different between seasons ($c^2 = 53.1$, $P < 0.001$). Nevertheless, the change was more quantitative than qualitative. *N. simplex* and the red crab predominated in both summer and winter. Fishes were more important in summer; in winter, gammarideans were in third place.

Sample size did not allow interseasonal analysis of *B. gymnostethus* or *P. albirostris*.

Ontogenetic changes: Two size categories of *P. stephanophrys* were established, below and above 133 mm SL, the median SL. This length coincided with a rather sharp shift in prey preference, from *N. simplex* to the red crab (Fig. 5). Similarly, other small prey, such as gammarideans, were more abundant in small searobins; the opposite happened with larger prey, such as fishes (Fig. 6).

Study of ontogenetic trophic changes in species other than *P. stephanophrys* was not possible, because of the small sample sizes.

Similarity analysis: The trophic spectra of *P. stephanophrys* and *B. gymnostethus* were significantly similar ($PS_T > 80\%$); *P. albirostris* diet was different from that of the other searobins.

DISCUSSION

Habitat partitioning: From the viewpoint of dietary diversity, *P. stephanophrys* and *B. gymnostethus* tend to stenophagy, with a high diet overlap. Competition is avoided, in the first place, by the difference in mouth size that allows *P. stephanophrys* to prey on items inaccessible to *B. gymnostethus*, mainly on the red crab *P. planipes*.

Competition for *N. simplex* between *B. gymnostethus* and small *P. stephanophrys* is diminished by the different time of predation: at

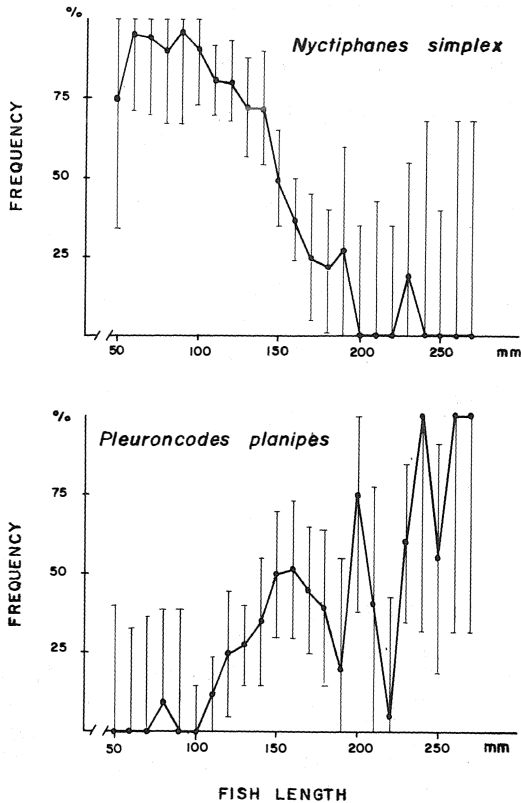


Fig. 5. Ontogenetic diet change in *Prionotus stephanophrys* off Baja California Sur. Bars are 95% confidence intervals.

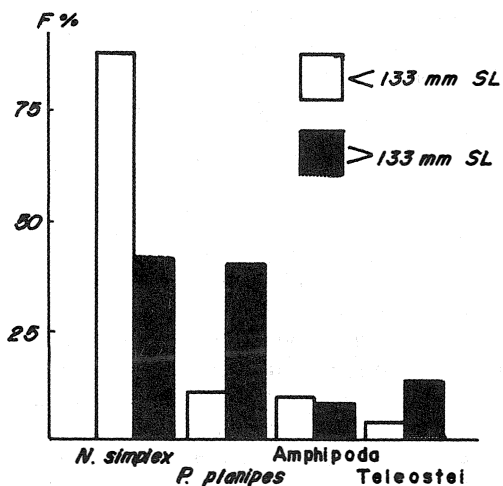


Fig. 6. Consumption of main prey by the two size classes of *Prionotus stephanophrys* off Baja California Sur.

night by the latter species, during the day by the former. Feeding time is a habitat partition factor as important as the trophic spectrum itself (Ross 1978, Teixeira & Haimovici 1989).

The fact that the euphausiid and the red crab are the most abundant and frequent non-infaunal invertebrates in the area (Brinton 1967a, Alvariño 1976) shows that *P. stephanophrys* and *B. gymnostethus* are opportunistic carnivores, feeding on the most readily available prey. Jardas & Zupanoviá (1983) reached the same conclusion regarding *Trigla lyra* in the Adriatic.

P. albirostris might also be labeled an opportunistic carnivore, though *S. mutator*, a crucial food item, is not among the most abundant members of the community. Its diet is less stenophagous, more diverse and equitable, and the fish seemingly feeds all day long. It does appear to avoid, however, competing with *P. stephanophrys* and *B. gymnostethus* for *N. simplex* and *P. planipes*, given the rarity of these organisms in its trophic spectrum.

The intensification of feeding that *P. stephanophrys* shows in summer takes place after the main reproductive pulse (Schmitter-Soto 1992). This seems to be a common phenomenon (Moreno & Matallanas 1983, Teixeira & Haimovici 1989), understandable in terms of higher energy needs.

A scheme of ecological partitioning among Triglidae in the western coast of Baja California Sur is proposed (Fig. 7): *P. ruscarius*, *B. xenisma* and *B. loxias* are separated mainly by spatial factors, such as distribution, sediment and temperature (Schmitter-Soto 1992) (the partitioning factor separating the latter two species, if there is one, remains to be found). The other three species avoid competition by trophic differences, reinforced between *P. stephanophrys* and *B. gymnostethus* by a temporal factor. This agrees with the findings by Ross (1977) and other authors, that the order of importance of resource partitioning factors is space > diet > time.

Are these observed patterns the effect of, or are they the cause that lessens, interspecific competition? Although quantitative data on resource availability are wanting, it seems clear that the main resources searched for (space on muddy bottoms, *P. planipes*, *N. simplex*) are not limited, but abundant. One might speculate that such partitioning patterns

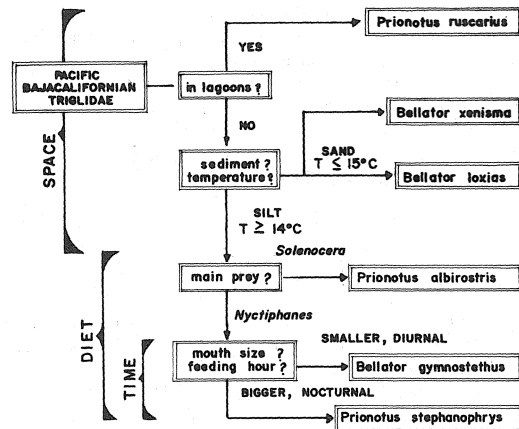


Fig. 7. Scheme of habitat partitioning among Triglidae in the western coast of Baja California Sur.

are relicts of a time when resources were indeed limited (the “ghost of competition past”). An alternative hypothesis is that differentiation in resource use is a by-product of the speciation process, as the selectivity differences between Peruvian and Mexican *P. stephanophrys* would illustrate (see below).

Geographical changes in selectivity: All studied Triglidae feed on epibenthos and benthopelagic zooplankton; infauna is very secondary. The most abundant organisms in the local infauna are polychaetes (de León González 1990), but this does not affect the diets of these fishes.

A similar situation exists in southern Brazil, where the “cabrinhas” seem to ignore the abundant annelids. *P. nudigula* and *P. punctatus* practically do not include infauna in their diets (Teixeira & Haimovici 1989).

In Chile, *P. stephanophrys* feeds on gammarideans, small shrimps and the galatheid *Pleuroncodes monodon* (Meléndez 1987), the ecological equivalent to its Californian diet.

The trophic spectrum of this searobin changes in Peru. Samamé *et al.* (1983) found 63% euphausiids (N%), but a much greater amount of Polychaeta. This difference in infaunal consumption between Peruvian and northern Mexican *Prionotus stephanophrys* seems comparable to the contrasting finds of Papaconstantinou (1982) and Moreno & Matallanas (1983) on *Lepidotrigla cavillone*:

the proportion of ophiuroids in its diet is much higher in Greek gulfs than at the other end of the Mediterranean.

These geographical changes in selectivity might be ethological side-effects of an evolutionary divergence. There are indeed morphological differences, proposed as subspecific, between South and North American *P. stephanophrys* (Neira *et al.* 1981).

Ontogenetic niche shift: The main prey of *P. stephanophrys*, the red crab and *N. simplex*, are diel vertical migrators. The euphausiid migrates upward at night; during the day it is found mostly at depths of 150 m (Brinton 1967b). *P. planipes* is pelagic when its carapace is less than 17 mm long (Longhurst 1967); after reaching 32 mm, it becomes strictly benthic (Alvariño 1976). The population between those sizes migrates upward at night, as does the euphausiid.

It can be hypothesized that the red crab becomes vulnerable at sunset, when migration starts and the crustaceans leave their refuges at the bottom. Most of the individuals eaten belong to the migrating part of the population, and predation is more intense at those hours.

On the other hand, predation on the euphausiid is more intense at night, when the greater part of the population is up in the water column. Moreover, some pelagic red crabs, shorter than 17 mm, were ingested. These facts can be explained by the ontogenetic habitat shift of *P. stephanophrys* and other triglids.

In Baja California Sur, older individuals of *P. stephanophrys* sporadically catch very mobile species and benthopelagic organisms, but they feed essentially on epibenthos. It is the younger fish that prey more on zooplankton. Schmitter-Soto (1989) found that immature searobins (mean standard length, 80 mm) swam in the water column at the same time and place as 140-mm-SL adults could be captured from the bottom. Hureau (1986) reported that European triglids descend to shallow bottoms after a pelagic pre-adult stage. It is thus quite probable that at least part of the euphausiid biomass was captured in the water column, as the smallest pelagic red crabs certainly were.

Moreno i Amich (1988) established that migrating prey tend to be less frequent as the predator grows, while benthic organisms

increase their occurrence. Ross (1978) detected a shift from epifauna in the diet of young *P. scitulus* to infauna in the adults, that is, a greater use of the substrate. The trophic separation corresponded to the transition size between immature and mature fishes, as happened here. However, the change was qualitative, while other authors (Moreno y Matallanas 1983, Braga & Braga 1987, this study) found that it was rather quantitative. An explanation can be found in the bathymetric spans covered. While the mentioned *P. scitulus* dwells in shallow bottoms no more than 10 m deep, other species occupy sizeable portions of the shelf; thus, *P. scitulus* would be forced to sharpen ontogenetic trophic changes in order to reduce intraspecific competition (Ross 1978).

According to Moreno i Amich (1988), major diet changes are due to recruitment and maturing. Ross (1978) found that the main diet change was preceded by an increase in mouth width and intestinal length, and followed by first reproduction. The descent of *P. stephanophrys* from the water column to the benthos and its concomitant trophic shift are probably related to these phenomena.

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RESUMEN

Se estudiaron los hábitos alimenticios (composición, intensidad, diversidad, cambios ontogénéticos y estacionales) de *Prionotus stephanophrys*, *Bellator gymnotethus* y *P. albirostris* en la costa del Pacífico de Baja California Sur, México. Se capturaron 547 individuos de las tres especies con red de arrastre entre 1988 y 1990. El eufáusido *Nyctiphanes simplex* fue la presa principal de *B. gymnotethus*, que lo consumió durante las horas diurnas, y de *P. stephanophrys*, que lo hizo en la noche y al atardecer; los individuos mayores de *P. stephanophrys*

cambiaron al galateido *Pleuroncodes planipes*, lo cual coincidió con el paso del pez del medio pelágico al béntico. La intensidad de alimentación de este trígido fue mayor en verano, después de la reproducción. *P. albirostris* se alimentó durante todo el día; su dieta, más diversa y equitativa, se basó en peneidos, pasifeidos y mísidos. Las diferencias en distribución, dieta y hora de alimentación indicaron un eficiente reparto de hábitat.

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