SEASONAL AND BATHYMETRIC CHANGES IN FEEDING HABITS OF THE BENTHIC RED CRAB *PLEURONCODES PLANIPES* (DECAPODA, ANOMURA, GALATHEIDAE) OFF THE PACIFIC COAST OF BAJA CALIFORNIA SUR, MEXICO

ΒY

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ABSTRACT

Stomach contents of benthic red crabs (Pleuroncodes planipes) were analyzed to document number of items and composition. The crabs were captured along a series of latitudinal transects covering depths from 50 to 250 m, during March (12 stations) and September 1990 (8 stations). The number of food items decreased significantly from March to September at 150 and 200 m depth, the only strata compared since red crabs are usually absent from the coast above 100 m in summer. The particulate organic matter (POM) varied from 60 to 70% of total food items. The zooplankton fraction, mainly crustaceans, foraminiferans, and radiolarians, was second in importance. Phytoplankton was the next most important group, and was represented by 17 genera in March and 11 in September. The mean number of diatoms in stomachs per station decreased significantly (73.5 versus 7) from March to September. The number of genera/station showed the same pattern (5.36 versus 3.6). The most abundant (number of cells) and frequent (presence over number of stations) diatom genera in March were Nitzschia, Melosira and Cocconeis in that order, accounting for 74% of the relative importance index. In September, Cyclotella, Nitzschia and Melosira accounted for 42% of the importance index. The stomach contents in benthic red crabs indicate a decreasing availability of food in the area from winter-spring through the summer. This pattern correlates well with the diminishing intensity of the coastal upwelling system and weakening of the California Current. The amount of stomach contents in red crabs decreased as the density of the crustacean species increased.

RÉSUMÉ

Des contenus stomacaux des crabes benthiques *Pleuroncodes planipes* ont été analysés afin de déterminer les nombres et la composition des éléments alimentaires. Les crabes ont été capturés le long d'une série de sections latitudinales couvrant des profondeurs de 50 à 250 m, en mars (12 stations) et septembre 1990 (8 stations). Le nombre des éléments de nourriture a décru

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de facon significative de mars à septembre à 150 et 200 m de profondeur, les seules strates comparées puisque les crabes sont habituellements absents de la côte au-dessus de 100 m en été. La matière organique particulaire variait entre 60 et 70% des éléments alimentaires totaux. La fraction zooplancton, surtout des crustacés, des foraminifères et des radiolaires, venait en second par l'importance. Le phytoplancton était ensuite le groupe le plus important et était représenté par 17 genres en mars et par 11 en septembre. Le nombre de diatomées dans l'estomac par station a décru de façon significative de mars à septembre (73,5 contre 7) et il en a été de même pour le nombre de genres (5,36 contre 3,6). En mars, les genres de diatomées les plus abondants (en nombre de cellules) et les plus fréquents (présence par rapport au nombre des stations) ont été, dans l'ordre, Nitzschia, Melosira, et Cocconeis, comptant pour 74% dans l'index d'importance relative. En septembre, Cyclotella, Nitzschia et Melosira ont compté pour 42% dans cet index. Les contenus stomacaux de ces crabes bentiques indiquent une disponibilité décroissante de la nourriture dans cette zone du début du printemps à l'été. Ceci correspond bien à la diminution d'intensité du système d'upwelling côtier et à l'affaiblissement du Courant de Californie. Les contenus stomacaux des crabes ont aussi décru alors que la densité des espèces de crustacés augmentait.

INTRODUCTION

The pelagic red crab (*Pleuroncodes planipes* Stimpson, 1860), known as langostilla in Mexico, spends its first year (larvae, juvenile and young adults) as part of the micronekton.

This species then alternates between pelagic and benthic environments until the 3rd year of life. Upon reaching a cephalothorax length of 32 mm, the langostilla becomes strictly benthic, and inhabits depths between 200 and 500 m (Boyd, 1967; Aurioles-Gamboa, 1992).

The standing stock of the benthic-phase population on the continental shelf off Baja California is estimated to be from 300 to 500 thousand metric tons (Erhardt et al., 1982; Aurioles-Gamboa, 1995). Maximum densities reach 40 crabs/m² (Aurioles-Gamboa, 1995), but may even be higher. Arana & Ziller (1990) reported densities around 100 individuals/m² for *Pleuroncodes monodon* (H. Milne-Edwards, 1837) off the Chilean coast.

The major ecological importance of langostilla in the food web off the west coast of Baja California was noted by Blackburn (1969) and Longhurst et al. (1967). The red crab is known to graze heavily on phytoplankton in the upwelling ecosystem of Baja California (Longhurst et al., 1967; Smith et al., 1975).

The langostilla is food for many predators including cetaceans (Mathews, 1932; Boyd, 1962), pinnipeds (Boyd, 1962; Lowry et al., 1990), birds (Glynn, 1961; Boyd, 1962; Longhurst, 1967), turtles (Villanueva, 1991), and fish (McHugh, 1952; Quast, 1968; Glynn, 1961; Boyd, 1962; Alverson, 1963; Balart & Castro-Aguirre, 1995).

The feeding habits of the langostilla are poorly known. Longhurst et al. (1967) reported that the pelagic red crab feeds mainly on phytoplankton cells such as *Coscinodiscus* and *Ceratium*. Boyd (1962) showed that *Pleuroncodes* can filter cells as small as 30-80 μ m and Beklemishev (1960) observed that radiolarians constitute a large part of their diet.

Pérez & Aurioles-Gamboa (1995) observed that breeding benthic red crab fed mainly on organic matter (approximately 60%), and that food composition varied with depth.

We suspect important seasonal changes in the feeding habits of the langostilla because of their mass bathymetric migration. During winter-spring (breeding season), the crabs occupy the whole continental shelf. In summer, they move into zones deeper than 100 m and cooler than 16°C (Aurioles-Gamboa, 1992; Aurioles-Gamboa et al., 1994).

In this work, we report seasonal and spatial changes of the stomach contents of benthic red crabs inhabiting the continental shelf off Baja California.

MATERIALS AND METHODS

Benthic red crabs were sampled in winter-spring between 9 and 13 March 1990 and in summer-fall from 2 through 12 September 1990. Benthic samples were collected with a 20 m shrimp bottom trawl (3 cm mesh size) from aboard the R/V "El Puma" (Universidad Nacional Autónoma de México). We followed a plan of seven transects perpendicular to the coast, trawling at 50, 100, 150 and 200 m depths. Bottom temperatures were taken directly from sediment collected by a Smith-McIntyre dredge at each station (table I).

Thirty specimens were randomly selected from each station and fixed in a solution of 4% formalin (Knudsen, 1972; Sumich & Dudley, 1980). In the laboratory, all specimens were sexed, weighed and measured for cephalothorax length. The stomachs (cardiac and pyloric sections) were excised and the total contents place on a slide preparation. From preliminary observations, this part of the digestive system offered the best possibility of identifying the food contents (e.g., diatoms or foraminiferans) (Pérez & Aurioles-Gamboa, 1995). Even though the whole stomach content was analyzed, it is likely that very delicate structures may have been destroyed by the crustacean before identification.

Food contents were identified with the help of several keys (Sumich & Dudley, 1980; Heurck, 1962; Cupp, 1943; Newell & Newell, 1963; Wickstead, 1965; Licea-Durán, 1974; Casimiro, 1988; Garate, 1988). Only diatoms were identified to genus level, some zooplankton organisms were identified to class level and both groups counted individually because they appeared as whole organisms.

TABLE I

Transects	Location	Depth m	Red Crab density individual/m ²	Bottom temperature °C	
	Ν	Aarch 1990			
TI	26°09′N, 113°10′W.	105	4.6	12	
TI	26°05′N, 113°17′W.	150	а	13	
T2	25° 39' N, 113° 00' W.	219	0.5	15.5	
Т2	25°42′N, 112°55′W.	150	0.1	15.6	
Т2	25°46′N, 112°49′W.	108	16.3	12	
ТЗ	25°18′N, 112°36′W.	207	0.1	12	
Т4	24° 20' N, 112° 09' W.	237	0.8	14	
74	24°21'N, 112°03'W.	154	0.9	13	
Т4	24°24′N, 111°59′W.	104	10.3	13.5	
Т5	24°11′N, 111°38′W.	149	2.1	13	
Т5	24°12'N, 111°29'W.	100	2.0	13	
Т5	24°15′N, 111°26′W.	52	16.2	13.5	
	Se	ptember 1990			
ТІ	26°01'N, 113°19'W.	218	5.7	11.5	
Т2	25° 38'N, 112° 59' W.	217	5.6	11.5	
T 3	25° 18'N, 112° 37' W.	209	0.1	12.5	
Т3	24°42′N, 112°31′W.	204	10.8	11.8	
T'4	24°22'N, 112°08'W.	194	5.6	12.5	
T4	24°20'N, 112°02'W.	147	25.4	13.5	
Т5	24°04′N, 111°53′W.	187	4.8	13	
T5	24° H′N, H1° 38′W.	149	7.0	13	

Location and depth of stations for positive benthic red crab captures during March and September 1990, off the west coast of Baja California Sur, Mexico

a. Not estimated.

Crustaceans, however, were found in fragments, so we counted them as pieces because it was not possible to reconstruct the organisms. The organic matter usually formed compact units of lengths varying in size from 60 to 600 μ m (maximum length). Thus, the organization of food items fell into one of the following groups; phytoplankton, zooplankton (crustaceans, foraminiferans, radiolarians, etc.), particulate organic matter (POM) and inorganic matter (sand, mud, etc.).

To establish the minimum sample size for determining the food composition in the red crab stomachs, we compared the mean values of different groups from samples of 3, 6, 9, and 12 organisms per station. Having found no statistical differences (*t*-test, P > 0.05) from five stations, we decided that nine individuals were sufficient to determine the feeding habits at each station.

RESULTS

At the stations where benthic red crabs were collected (table 1), the bottom temperatures were consistent with previous reports. In March, the sediment temperature varied from 12 to 15.6° C at stations where langostilla was present. In September, however, the range was between 11.5 and 13.5°C (table I).



Fig. 1. Amount of stomach contents from benthic red crab (*Pleuroncodes planipes* Stimpson, 1860) in stations arranged by depth and latitude (T = transects) during March (A) and September (B). Note that variation in number of items is greater by depth than by latitude. During September red crabs were only found on the outer continental shelf.

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Fig. 2. Relationship between stomach content and red crab density on the continental shelf off Baja California. Data come from table I and include both cruises.

Total stomach contents

In March the mean number of items in the langostilla stomachs varied from 100 to around 1150. The highest variation was found according to depth, while a moderate variation existed between transects or latitude (table I; fig. 1A). The stomachs surveyed at 150 m, had the largest number of items (between 450 and 1150), decreasing in stations at 100 and 200 m (fig. 1A).

In September the mean number of items in langostilla stomachs decreased considerably (fig. 1B) to a maximum of around 600 items which was half the March value. The comparison of the mean number of items at 150 and 200 m between both seasons showed clear differences (fig. 1A, B).

By relating total food content to red crab density (fig. 2), a rough diminishing trend was apparent. Stomachs from sites with higher red crab density on the benthos, yielded a lower number of food items. Red crab mean density for March was 4.9 crabs/m^2 in contrast to 8.1 crabs/m^2 during September (table I).

Major group composition

In March the group composition in langostilla stomachs varied according to depth (fig. 3A). The proportion of POM (particulate organic matter) was between 60% to 74%, decreasing from shallow to deep stations. The inorganic matter



Fig. 3. Gross composition of benthic red crab stomach contents ordered by depth strata during March (A) and September (B) 1990 off Baja California.

(grains of sand or mud) was the next most abundant item, with a larger percentage in the two deeper strata (150-200 m). Phytoplankton was very abundant at the 100 m stations, while the zooplankton component was most numerous at 150 m (fig. 3A).

In September the POM continued to be the most important fraction in the langostilla food (fig. 3B). The zooplankton fraction presented similar values to those found in March (around 10-15%) in the two only strata where the langostilla

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were found. The phytoplankton fraction diminished in both strata while the inorganic matter was very similar during both periods (fig. 3A, B).

Phytoplankton composition

In March seventeen genera of diatoms were identified in the red crab stomachs. *Nitzschia* cells were most abundant, representing about 49% of 883 diatoms

TABLE II

Genera of diatoms identified in benthic red crab stomachs on the west coast of Baja California Sur, Mexico (frequency = number of stations where the genus appeared over all stations sampled)

					М	arch	statie	ons							
Genera	No.	%	17	18	22	23	24	29	39	41	42	48	49	50	Frequency
Nitzschia	355	49.1	*	*	*	*	_	*	*	*	*	*	*	*	0.92
Melosira	168	23.2	*		*			*	*	*		*	*	*	0.66
Cocconeis	120	16.5	*	*	*	*			*	*	*	*	*	*	0.83
Coscinodiscus	28	3.8		*		*			*		*	*	*		0.5
Amphora	15	2.0		*		*				*	*	*	*	*	0.58
Actinoptychus –	17	2.3		*		*						*	*	*	0.41
Diploneis	3	0.4												*	0.08
Navicula	3	0.4										*			0.08
Rhizosolenia	2	0.2										*	*		0.16
Actinocyclus	2	0.2											×		0.08
Cyclotella	2	0.2	*												0.08
Chaetoceros	2	0.2											*		0.08
Pleurosigma	2	0.2	*												0.08
Surirella	1	0.1									*				0.08
Thalassiothrix	1	0.1	*												0.08
Triceratium	1	0.1										*			0,08
Tropidoneis	1	0.1											*		0.08
					Sept	lemb	er sta	ations	;						
			19	22	29	33	40	41	47	48					
Cyclotella	21	36.8	*		*	*	*		*						0.62
Nitzschia	13	22.8		*	*		*		*						0.5
Melosira	6	10.5		*	*	*	¥	*	*						0.75
Actinoptychus	4	7.01			*	*	*								0.37
Coscinodiscus	4	7.01		*	*					*					0.37
Cocconeis	3	5.2			*			*	*						0.37
Ditilium	2	3.5					*								0.12
Triceratium	1	1.75					*								0.12
Dictiocha	1	1.75		*											0.12
Dinophysis	1	1.75			*										0,12
Plagiogramma	1	1.75			*										0.12

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Fig. 4. Most important diatom genera found during March (A) and September (B) 1990 in benthic red erab stomachs off Baja California. For the complete list of genera see table II.

cells counted. This was the most frequent genus found in 10 of 11 stations (table II). Since some diatom genera were more common (by number of stations) or abundant (number of cells), we derived an importance index for each genus and cruise by multiplying the number of cells from each genus by the number of stations where they appeared. For the March cruise (fig. 4A), only three genera had more than 10 units on the importance index, *Nitzschia* being the most important phytoplankton cell during this period.

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Fig. 5. Number of diatom genera in benthic red crab stomachs according to latitude during March (A) and September (B) 1990 off Baja California.

Another feature of diatom distribution was associated with the number of genera according to latitude. In fig. 5A, the number of genera found in each station indicated that southern stations (between 24° and 25°N) had a higher number of genera than northern stations. Two southern sites provided up to 9 and 10 genera in the langostilla stomachs. The mean value of diatom genera decreased from the south (6.8 \pm 2.3) to north of 25°N (3.5 \pm 2.0).

During the September cruise, only 11 diatom genera were identified, *Cyclotella* being the most abundant cell accounting for 21 out of 57 cells. Four diatom

genera found in this cruise were not recorded in March (*Ditilium, Dictiocha, Dinophysis* and *Plagiogramma*). The mean number of diatom cells per station was notably smaller (7), than in March (73.5) (table II). As a consequence, the importance index was smaller during September, with *Cyclotella* accounting for 22.5 units (fig. 4B). In March, only three genera had more than 10 units on the importance index.

During September, the number of diatom genera diminished in the southern latitudes (24° through 25°N) (fig. 5B) to 3.25 ± 1.9 per station. However, for northern locations, the mean number of genera/station (4 \pm 2.5) was slightly higher to that found in March (3.5).

Zooplankton composition

In March three zooplankton groups were clearly identified in langostilla stomachs: crustaceans, foraminiferans and radiolarians (fig. 6A, B). The relative composition of these groups varied according to depth; the crustaceans were markedly abundant in stations between 100 and 150 m (about 95% and 97%). The next most abundant group was formed by foraminiferans which replaced the crustaceans at depths of 50 and 200 m and represented 84% and 62% of the zooplankton fraction in langostilla stomachs (fig. 6A).

In September the crustaceans were the most important group identified in the stomachs, contributing 87% and 64% of the total zooplankton fraction in the only two strata where langostilla appeared (fig. 6B). The foraminiferans were again the second most important group (13% and 35%) followed by the radiolarians (1%) which were present only at the deeper stations.

DISCUSSION

Changes in the feeding habits of *Pleuroncodes planipes* appear to be associated to the season and depth of collecting. In March, the number of food items was higher at 150 and 200 m compared to September (Rank Sum Test = 38, P > 0.05; Z = 15.8, d.f. 7). Since the benthic langostilla avoids waters above 16°C (Aurioles-Gamboa, 1992), only the deeper strata provided langostilla during September samples. The reduction in stomach contents was probably due to the decreasing availability of organic matter from winter-spring through summer-fall. This trend has at least three probable causes; one is the upwelling which seems to be stronger or have its maximum intensity during the winter and spring (Rodeu, 1972). However, Chelton (1981) suggested that the variability in zooplankton biomass is not the result of upwelling only, but influenced mainly by the California Current. The seasonal variation in the physical characteristics



Fig. 6. Composition of the zooplankton fraction of benthic red crab stomachs during March (A) and September (B) off Baja California.

of the California Current (CC) suggests that its core usually occurs 300-400 km offshore in southern California, but within only 200 km of the Baja California coastline (Lynn & Simpson, 1987). In general, an increase in zooplankton volume is associated with a decrease in water temperature, the two potential sources of cold water being from upwelling and advection (Chelton, 1981). The bottom temperatures registered in the March and September cruises were consistent with this notion. The range of bottom temperatures during September was

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considerably greater. Large-scale advection would play the dominant role in the zooplankton biomass variability of the CC, according to Chelton (1981).

Similar decreasing trend was found for two of the three species that dominate the euphausiid fauna off Baja California (*Nyctiphanes simplex* Hansen, 1911, and *Euphausia eximia* Hansen, 1911) which diminished in abundance from spring through the summer and fall in the same area of the present study (Gómez, 1995). According to that author, the differences in euphausiid yield along the coast is correlated to the upwelling intensity, which has its maximum from March to June and diminishes from July through November.

A third associated factor determining the seasonal reduction of food contents in langostilla stomachs is the red crab density at each station. Due to the retreat of langostilla from the upper 100 m depth during the summer-fall, the crustacean density increases in the areas where the bottom temperature is still below the 16°C (Aurioles-Gamboa, 1992, 1995). The increase in crab density from March to September (4.9-8.1 crabs/m²) may reflect a stronger competition for food during the summer-fall period. Such densities along with the apparent food shortage at that time, would create considerable intraspecific food competition.

The stomach composition revealed that for both cruises, the particulate organic matter (POM) was around 60% of total contents. This suggests that most of the langostilla food is taken as detritus as in many other galatheid species (Nicol, 1932). The POM is considered to be of major importance in the upwelling ecosystem of Baja California (López-Cortes et al., 1990; Lechuga et al., 1993).

The langostilla collected on the continental shelf is a benthic dweller most of the time, performing occasional circadian vertical migrations (Boyd, 1967). In spite of these mass migrations, the crab density on the bottom does not change significantly from day to night (Aurioles-Gamboa, 1992), thus we can assume that most of the detritus is taken directly from the benthos. This is confirmed by the presence of sand and mud grains (inorganic matter) and the abundance of benthic diatoms (*Cocconeis, Melosira, Cyclotella* and some species of the genus *Actinoptychus*) in the stomachs. In the langostilla as in other galatheids, fanning movements of chelipeds generate currents that induce grains of mud or sand to enter the mouth (Nicol, 1932). The grains of sand may serve at least two purposes: as material to grind particles such as crustacean shells or legs, and as nutritional elements since these grains are often covered by organic matter like bacteria or microalgae (Ray & Marshall, 1974; Petchen-Finenko, 1987).

The second most important component in langostilla food was the zooplankton. Crustaceans were relatively more frequent (25-30%) in depths of 150 and 200 m on both cruises (langostilla was only captured at the two deeper strata in September). The crustacean fraction was homogeneous in all strata on both

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cruises, except at the 100 m stations during March, at which phytoplankton cell counts were the highest of all the depths.

The mean number of diatoms per station (73.5 versus 7) and the mean number of genera per station diminished significantly from March to September (Rank Sum Test, Z = 4.25 < 55; P > 0.05). This reduction is probably related to the oceanographic conditions that determine the abundance of phytoplankton. Blackburn (1969) observed that phytoplankton abundance (measured as chlorophyll *a*), was most plentiful in the upwelling season (spring) in areas of cool upwelling areas off Baja California.

In general, the feeding habits of langostilla exhibit evident changes from spring to fall. These major changes are: (1) a reduction in the total number of items counted in the stomachs, and (2) reduction in the number of both phytoplanktonic cells (diatoms) and number of genera. Both parameters seem to reflect a decreasing trend in food availability from winter-spring through summer-fall on the benthos of the continental shelf off Baja California.

Based on the bathymetric strata, the main differences were the dominance of the zooplankton fraction (after POM), composed mainly of crustaceans on the external continental shelf (150-200 m). The grains of sand and mud were also slightly, but consistently, more numerous in the two deeper strata, probably due to the extra sweeping-filtering activity by the langostilla facing a shortage of food and increased density during the fall.

This study confirms the idea that the arrival of langostilla in shallow waters for breeding purposes, coincides with the time when food is plentiful. This not only benefits the breeders but, more importantly, insures the survival of their larvae (Aurioles-Gamboa, 1992).

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