Feeding ecology of the crab *Cancer polyodon* in La Herradura Bay, northern Chile. II. Food spectrum and prey consumption

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ABSTRACT: *Cancer polyodon* stomachs were analyzed to determine the dietary breadth and relative importance of prey species of male and female crabs at 2 study sites in La Herradura Bay throughout the year. Of 51 prey items identified, small crustaceans and molluscs of a wide size range predominated at both localities, followed by echinoderms, polychaetes, fish and algae. Cannibalism was high (10 % of total crab production) and showed 2 peaks during winter and summer respectively, indicating recruitment pulses. Significant differences in diet composition were found between sexes, localities, seasons and sizes. Females consumed greater quantities of the deep-burrowing jackknife clam *Tagelus dombei* than males. Most egg-carrying females were found not to feed. In one of the study areas (characterized by a heterogeneous rocky-sandy bottom covered with algae), cirripeds *Austromegabalanus psittacus* and porcellanid crabs *Petrolisthes* spp. were of highest relative importance (6.96 and 6.38 %), while in the other area (a homogeneous sandy bottom without algae) *Tagelus dombei* was by far the most important species (42.2 %) followed by the gastropod *Priene rude* (2.82 %). Small crabs (< 8.0 cm) ingested a higher proportion of molluscs at both study sites, while crustaceans had a higher relative importance in stomachs of large crabs (> 11 cm). Echinoderms and fish were absent in stomachs of small crabs (< 8.0 cm carapace width). Estimates of annual prey consumption/area are given and the crabs' functional role in the shallow water community of La Herradura Bay is discussed.

INTRODUCTION

The food habits of brachyuran crabs attracted attention in the 1960s when it became evident that crab predation could heavily influence the abundance and distribution of their prey species, some of which were of commercial value (Elbing et al. 1964, Muntz et al. 1965, Ropes 1968). Typically, brachyuran crabs are generalists feeding primarily on small molluscs and crustaceans of limited mobility (Williams 1981, 1982, Morales & Antezana 1983, Elner et al. 1985, Haddon & Wear 1987, Rangeley & Thomas 1987, Ryer 1987). Ontogenetical changes in the diet spectrum were attributed to anatomical differentiation of the feeding apparatus ('gastric mill') during growth (Hill 1976, Gotshall 1977, Jewett & Feder 1982, Laughlin 1982, Stevens et al. 1982, Perez & Bellwood 1988). Differences in diet composition were also found between localities and seasons, and were attributed to differing prey availabilities in each environment.

Cancer polyodon (Poeppig, 1836) is the most conspicuous of the 4 species of the genus *Cancer* inhabiting the coastal waters of Chile and Peru (Retamal 1981). Males measure up to almost 20 cm carapace width (CW), while females remain smaller (Garth 1957, Wolff & Soto 1992). It has been fished for decades by divers and captured with traps in the Southeast Pacific (Antezana & Fagetti 1965). Fishing pressure seems to have intensified over the last decade as seen by increased landings (SERNAP 1987, 1988 as cited by Wolff & Soto 1992). In a study area of La Herradura Bay, Wolff & Soto (1992) found average crab densities of 0.15 ind. m^{-2}. The present study is designed to determine the food spectrum and relative importance of prey species of both sexes at 2 distinct localities in La Herradura Bay over 1 yr, and to estimate the prey con-

sumption per area using the results of this and a previous study on feeding periodicity and food consumption (Wolff & Cerda 1992).

MATERIAL AND METHODS

Cancer polyodon were collected by hand in monthly intervals over 1 yr (May 1988 to April 1989) at 2 study sites in La Herradura Bay (Fig. 1). The first site, Marina de Guayacán (MG), is characterized by a rocky sandy bottom covered with red and green algae. The second, Guayacán (G), has a more homogeneous sandy bottom almost without algae. At each sampling, about 15 specimens (total number: 340) were collected from the water at 1.0 to 10.0 m depth between 08:00 and 09:00 h as stomach fullness had been found to be high at this time (Wolff & Cerda 1992). After collection the specimens were killed by an oral injection of formalin (10 %) and transferred to the laboratory to sex the crabs, to measure CW to the nearest 0.1 mm with a calliper and to record fresh weight to the nearest 0.1 g. Subsequently, the carapace was separated from the abdomen and the stomach was extracted and bled on absorbent paper for 5 min to eliminate excessive liquid. Stomach weight was recorded with and without food, and stomach content was emptied into a petri dish for subsequent analysis.

Stomach fullness and stomach content analysis. Relative stomach fullness (RSF) was defined as *in situ* stomach fullness (V_e) divided by the maximum stomach fullness of a crab of the same size (V_m).

$$RSF = V_e/V_m \qquad (1)$$

V_m was obtained by the following method described by Hill (1976): empty stomachs of different-sized crabs were filled with seawater and the displacement volume ($=V_m$) was measured and correlated with CW (Fig. 2). RSF was then obtained using Eq. 1. The stomach content was analyzed by recording the frequency of occurrence of each food item and by using the point assignment method (Hynes 1950). Following this method, a number of points were assigned to a prey item according to a logarithmic scale (base 2: 1, 2, 4, 8, ...) as proposed by Williams (1981) and according to the relative stomach fullness recorded.

After analyzing all samples, total fresh weight of each food item (W_i) was calculated and the following percentages were obtained:

$$\% P_i = (p_i/P) \times 100 \text{ (\% points of prey } i) \qquad (2)$$
$$\% F_i = (f_i/F) \times 100 \text{ (\% of occurrence of prey } i) \qquad (3)$$
$$\% W_i = (w_i/W) \times 100 \text{ (\% of weight of prey } i) \qquad (4)$$

where p_i, f_i and w_i are the point, frequency and weight values for each food item and P, F, W are the point, frequency and weight totals of all food items recorded during the analysis. To overcome the bias of the results from the above methods (as discussed by Hyslop 1980, Williams 1981), the following index of relative importance [Zander 1982 (cited by Tarazona et al. 1988)] was used:

$$MFI = \sqrt{(\%p_i + f_i)/(2 \ w_i)} \qquad (5)$$

where *MFI* is the index of relative importance and % p_i, f_i and w_i as explained above. To see if the diet spectrum varied with season and/or crab size, samples
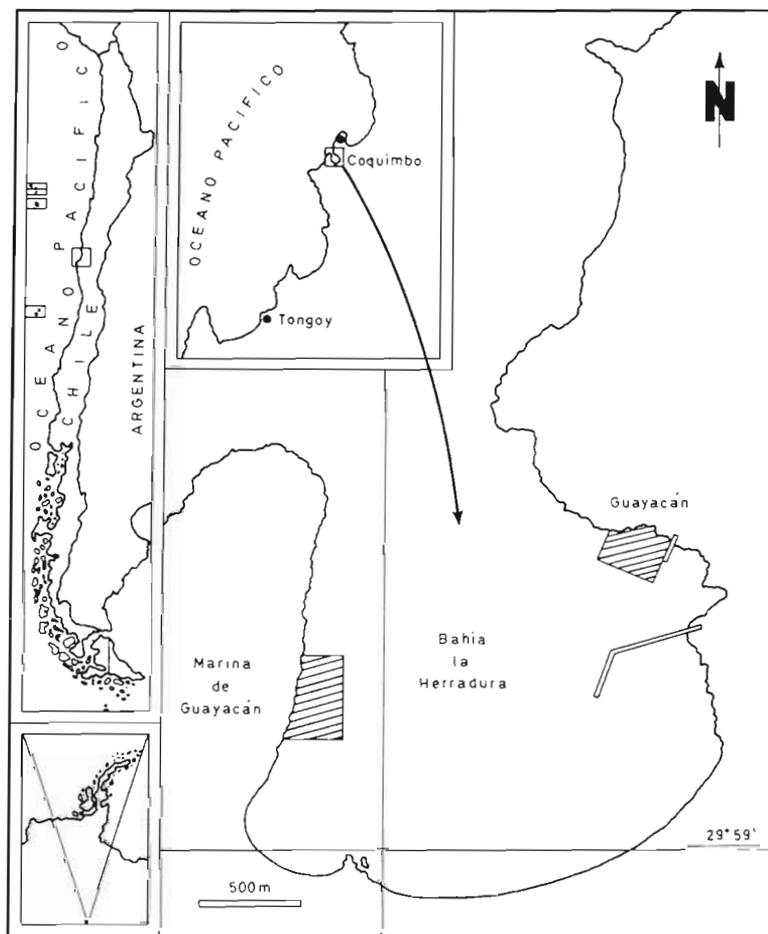

Fig. 1. La Herradura Bay with study sites Marina de Guayacán (MG) and Guayacán (G)
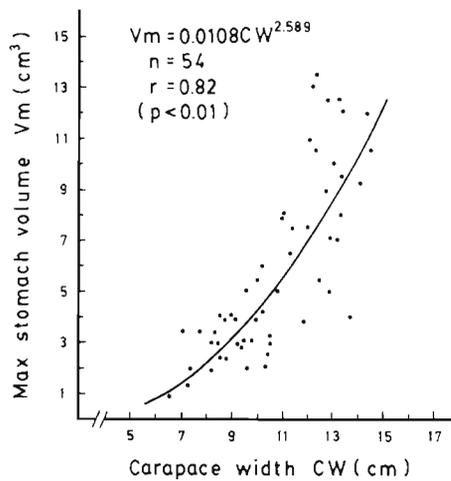
Fig. 2. *Cancer polyodon*. Relationship between maximum stomach volume (V_m) and carapace width (CW)

were grouped for each season as well as into 3 size groups (< 8.0 cm, 8.0 to 11.0 cm and > 11.0 cm CW) for which the *MFI* values for the different prey species were determined.

Prey consumption. Wolff & Cerda (1992) estimated an average food intake of 3.19 % body weight (BW) d^{-1} for crabs of 115 mm CW (size representing the population mode) in the Guayacán area. This average and the percentage of total weight of each prey item recorded were then used to quantify the consumption of each prey item crab^{-1} yr^{-1}. Using the biomass/area estimate of 637 kg 5964 m^{-2} (Wolff & Soto 1992) we estimated prey consumption on an area basis.

RESULTS

A higher percentage (64.8 %) of stomachs analyzed from Site MG (n = 142) contained food compared to those from Site G (58.6 %, n = 203) (X^2 = 1.08; p < 0.025). Average stomach content (%BW) was very similar between study sites (0.49 and 0.48 at Sites MG & G). Crabs were significantly smaller at Site MG (8.3 ± 1.9 cm compared to 10.8 ± 1.7 cm at Site G; t = 12.56, df = 343; p < 0.05) with an almost equal proportion of sexes (1 male : 1.3 females), while at Site G females dominated significantly (1 male : 3.4 females) (X^2 = 5.76; p < 0.05).

Stomach content analysis at both study sites

Of 51 prey items found in the stomachs of *Cancer polyodon*, 28 could be identified to species level (Table 1). Organic material and sand (including unidentifiable parts of shells and carapaces) were defined as additional categories. Crustaceans (including *C.*

Table 1 *Cancer polyodon*. Prey items identified in the stomachs at study sites Marina de Guayacán (MG) and Guayacán (G). *MFI*: index of relative importance; *species of highest importance. The proportions of molluscs and crustaceans were significantly different between Sites G & MG (X^2 = 195.24; df = 7; p < 0.05)

Prey	MFI	
	MG	G
Crustacea		
Crustacea unidentified	1.51	1.42
Isopoda unidentified	0.20	–
Decapoda unidentified	9.46	3.12
Grapsidae unidentified	0.55	–
Leptograpsus variogratus	–	1.13
Paraxanthus barbiger	0.43	–
Cancer polyodon	4.91*	2.47
Corystoides chilensis	0.10	–
Pagurus spp.	0.05	0.67
Pagurus edwardsi	0.50	0.92
Pagurus gaudichaudi	0.56	2.54*
Pagurus perlatus	–	1.51
Petrolisthes sp.	–	0.11
Petrolisthes desmarestii	6.38*	2.53
Rhynochocinetes typus	4.20	0.09
Synalpheus spinifrons	0.83	–
Pilumnoides perlatus	0.12	0.14
Talipus sp.	0.21	–
Eurypanopeus crenatus	0.42	–
Austromegabalanus psittacus	6.46*	0.45
Caprellidae unidentified	0.76	–
Total	**37.86**	**17.81**
Echinodermata		
Tetrapigus niger	0.40	0.27
Loxechinus albus	–	0.09
Total	**0.40**	**0.36**
Polychaeta		
Polychaeta unidentified	0.20	0.09
Phragmatopoma sp.	0.31	–
Total	**0.54**	**0.08**
Total fish	**1.96**	**1.70**
Mollusca		
Mollusca unidentified	0.56	–
Gastropoda unidentified	0.81	2.33
Diloma nigerrima	0.18	0.25
Tegula spp.	2.79	3.93
Turritella cingulatta	0.48	1.85
Prisogaster niger	–	0.30
Nassarius gayi	0.09	–
Priene rude	0.60	2.82*
Polyplacophora unidentified	0.28	0.24
Chiton granosus	2.37	1.77
Bivalvia unident.	4.44	1.44
Ennucula grayi	0.20	0.87
Argopecten purpuratus	1.74	–
Eurhomalea rufa	0.79	0.13
Tagelus dombei	0.07	42.35*
Acmeideae unidentified	1.58	–
Gari solida	–	0.16
Mytilidae unidentified	0.45	0.07
Semimytilus algosus	0.22	–
Brachidontes granulata	1.91	0.07
Total	**20.13**	**59.41**
Algae		
Gracilaria sp.	–	0.09
Polysiphonia sp.	–	0.07
Phaeophyta unidentified	–	0.15
Rhodophyta unidentified	0.84	0.24
Ulva sp.	7.28	–
Total	**8.32**	**0.62**
Organic material	**23.76**	**15.58**
Sand	**7.03**	**4.45**

polyodon) and molluscs constituted over 50 % (*MFI*) of the food at both study sites. At Site MG the cirriped *Austromegabalanus psittacus* and the crab *Petrolisthes desmarestii* were the most important species (*MFI*: 6.46 and 6.38 % respectively), while at Site G the jack-knife clam *Tagelus dombei* was by far the most important food item (*MFI*: 42.35 %) (Table 1). The size spectrum of the prey ranged from < 1 mm (in the case of gastropod *Ennucula grayi*) to several cm (in the case of *T. dombei*). At both study sites, algae represented only a small percentage of the stomach content (8.3 % at Site MG, 0.6 % at Site G). Eighty-seven percent of the algal material at Site MG was represented by the green algae *Ulva* sp. (Table 1), which almost completely filled the stomachs of 2 specimens. At Site MG, crustaceans were consumed in significantly greater quantities than at Site G, and molluscs to a greater extent at Site G (Table 1). Among the crustaceans found in the stomachs, *C. polyodon* constituted the third most important item at Site MG and fifth most important at Site G. Cannibalism peaked between February and April and, more intensively, between August and December (Fig. 3). Out of 113 egg-carrying females analyzed, 102 (90.3 %) had empty stomachs.

Differences in diet composition between sexes were found at Site G (Fig. 4) with females consuming a greater proportion of molluscs than males (x^2 = 40.1; p < 0.01). This difference was very pronounced with regard to consumption of the jackknife clam (*Tagelus dombei*), which constituted 80 % of the molluscs in female stomachs but only 49 % in male stomachs. The proportions of the major taxa in the stomachs collected at different seasons showed significant differences at Sites MG & G (Table 2). At Site MG crustaceans were of greatest importance in summertime, while at Site G the highest amounts of molluscs were consumed during the same period. Small crabs (< 8 cm CW) ingested

a higher proportion of molluscs, while crustaceans had a higher relative importance in stomachs of larger crabs (> 11 cm CW). Echinoderms and fish were absent in stomachs of small crabs (< 8 cm) (Table 2).

Prey consumption at Guayacán (Site G)

Fig. 5 summarizes the consumption of the main prey species by the crab population at Site G together with the population biomass and turnover rate estimated by Wolff & Soto (1992). *Tagelus dombei* was by far the most consumed species (4282.4 kg/637 kg crab biomass yr^{-1} or 718 g m^{-2} yr^{-1}).

DISCUSSION

Our results indicate that *Cancer polyodon* is essentially carnivorous; only a low percentage of algal material was found in the stomachs. Various authors report that brachyuran crabs accidentally ingest algae (Elner 1981, Laughlin 1982, Stevens et al. 1982, Williams 1982, Perez & Bellwood 1988) while Hill (1976) found algae to be part of the diet of juveniles. Jewett & Feder (1982) consider the occurrence of algae in the stomachs as a manifestation of the crabs' opportunistic feeding behaviour. The latter seems to be the case for *C. polyodon*, as the amount of algae found in the stomachs was significantly higher at Site MG (Table 1), where algae are more abundant, than at Site G.

The difference in diet composition between study sites and seasons reflects differences in prey species composition and/or availability. This, and the wide trophic spectrum of 51 food items found, confirms a generalistic and opportunistic feeding behaviour for *Cancer polyodon* which has been reported for other brachyuran crabs (Hill 1976, Laughlin 1982, Ryer 1987, Vannini et al. 1989, Hines et al. 1990). This opportunistic feeding behaviour is exemplified by the high relative importance of the clam *Tagelus dombei* (*MFI*: 42.35 %; see Table 1) in stomachs from Site G, where exploratory diving revealed clam densities of up to 130 ind. m^{-2}. This bivalve was almost absent at Site MG and in the stomachs of specimens caught there. The high consumption of *T. dombei* indicates the enormous excavating ability of *C. polyodon*, as the clam lives buried in the sand at a sediment depth of 15 to 40 cm. According to Auster & Crockett (1984), this is characteristic of carnivorous crabs.

The high relative importance of juvenile *Cancer polyodon* found in the stomachs (*MFI*: 4.91 % at Site MG and 2.47 % at Site G) indicates considerable cannibalistic behaviour. About 10 % of total crab production ends up in the stomachs of the crab population (Fig. 5). As cannibalism peaked during the main spawning pe-
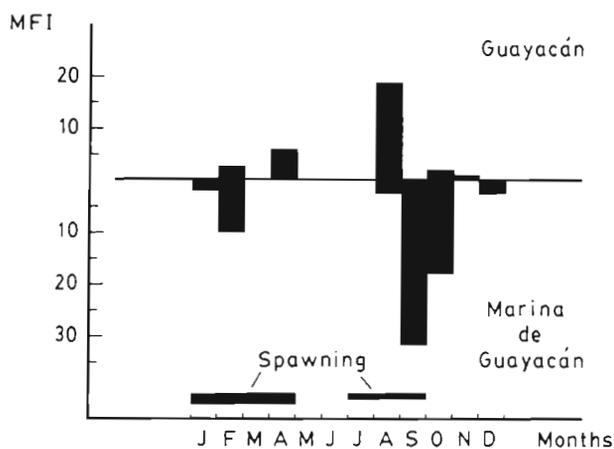

Fig. 3. *Cancer polyodon.* Cannibalism at Sites MG and G as related to spawning pulses
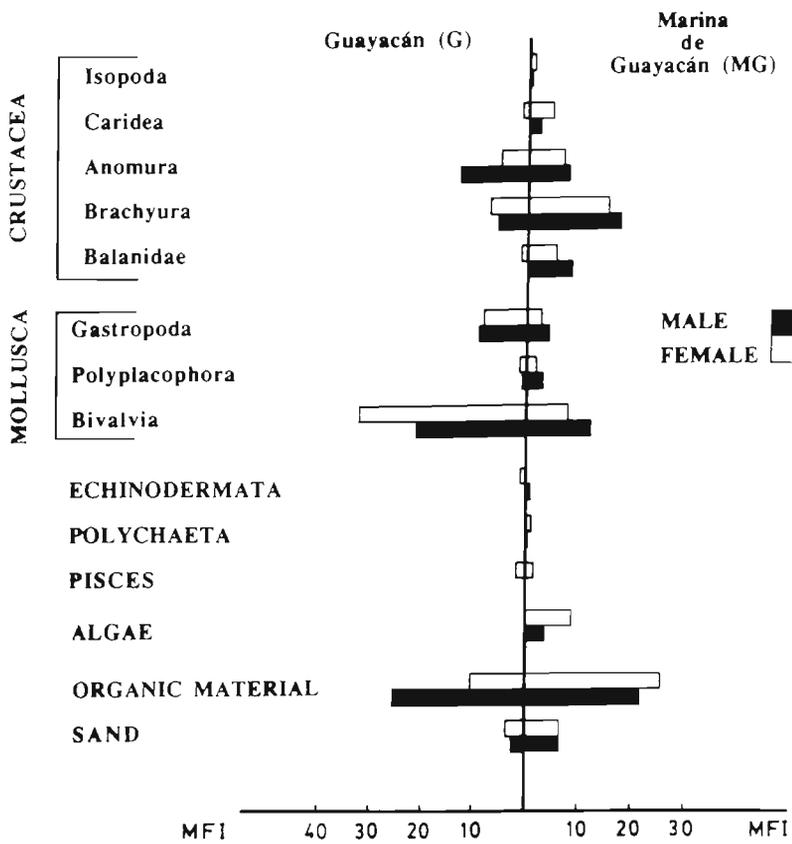
Fig. 4. *Cancer polyodon*. Index of relative importance (MFI) of main food items in male and female stomachs at Sites MG & G, showing females to consume a greater proportion of molluscs than males ($X^2 = 40.1$, df = 3; $p < 0.01$)

riods in summer (January to April) and winter (July to September) (Fig. 3) (Gutierrez & Zuñiga 1976, Wolff & Soto 1992) we assume that most of the juveniles found in the stomachs of the adult population are recruits from the summer and winter spawnings that heavily invade the adult crabs' habitat after ca 6 mo (at 30 to 40 mm CW). The significantly higher proportion of the mollusc *Tagelus dombei* in female stomachs at Site G (80 % compared to 49 % in males), as well as the sex ratio of 1 male to 3–4 females at this site (compared to 1 : 1.3 at Site MG) suggest that male specimens maintain a 'harem' with several females that they defend within their territory, as also proposed by Orensanz & Galucci (1988) and Wolff & Soto (1992). While protecting their harem, males would spend more time at the sediment surface and therefore would more likely prey upon small epibenthic species, like the small crustaceans and molluscs found in their stomachs, rather than on species like *T. dombei* that have to be excavated. The more sedentary females, on the contrary, would be able to excavate prey from the sediment. This hypothesis is substantiated by the fact that at Site
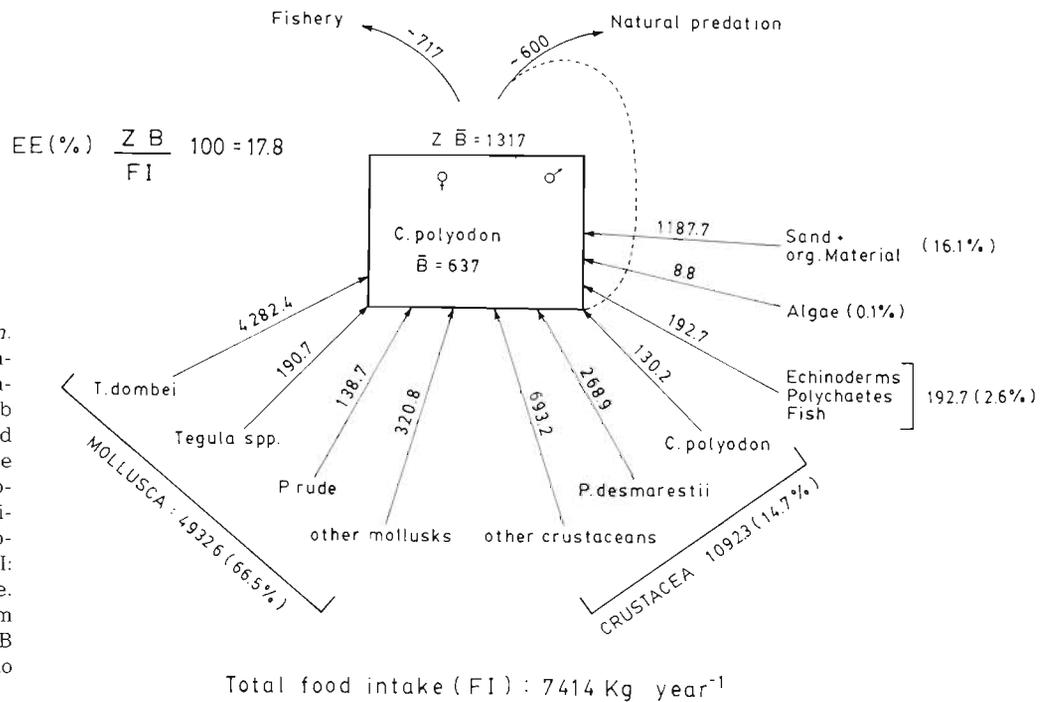

Fig. 5. *Cancer polyodon*. Diagrammatic representation of trophic relationships between the crab population at Site G and its prey. Numbers on the arrows are in kg; EE: population production efficiency; ZB: annual biomass production (kg); FI: total annual food intake. FI and EE values from Wolff & Cerda (1992); ZB values from Wolff & Soto (1992)

Table 2. *Cancer polyodon.* Seasonal values and size group specific values of the index of relative importance (MFI) for the main food categories at 2 study sites, Marina de Guayacán (MG) and Guayacán, (G) with contingency table analysis

Categories	Season							
	Autumn		Winter		Spring		Summer	
	MG	G	MG	G	MG	G	MG	G
Crustacea	32.7	20.2	38.0	16.4	39.1	13.5	48.0	12.0
Mollusca	20.5	45.4	13.3	67.5	25.1	63.3	16.4	73.0
Echinodermata	0.3	1.3	0.7	–	–	–	–	–
Polychaeta	1.1	–	–	–	0.5	–	–	0.2
Pisces	3.3	0.9	0.7	–	4.8	–	–	4.3
Algae	2.0	0.8	14.6	0.6	0.8	–	12.0	–
Organic material	31.8	28.3	27.2	12.6	23.0	18.3	18.0	5.5
Sand	8.2	3.1	5.6	2.8	6.8	5.0	5.6	5.2

Contingency table analysis:		df	χ^2	Cramer's V	p
	MG	21	42.14	0.19	< 0.004 *
	G	21	43.35	0.19	< 0.003 *

Categories	Size groups (cm)					
	Marina de Guayacán (MG)			Guayacán (G)		
	< 8.0	8.0–11	> 11.0	< 8.0	8–11	> 11
Crustacea	32.8	34.1	50.7	13.6	16.9	16.3
Mollusca	21.8	19.8	9.7	68.7	64.0	55.5
Echinodermata	0.0	0.4	2.0	0.0	0.6	0.2
Polychaeta	0.3	0.6	0.0	0.0	0.1	0.0
Pisces	0.0	2.7	13.3	0.0	0.9	1.7
Algae	7.0	9.6	0.0	0.0	0.3	0.2
Organic material	33.8	25.5	22.3	16.4	13.7	20.4
Sand	4.5	7.4	2.0	1.4	3.3	5.7

Contingency table analysis:		df	χ^2	Cramer's V	p
	MG	14	46.8	0.28	< 0.001 *
	G	14	8.7	0.12	< 0.85 ns

* $p < 0.05$; ns: not significant

MG, where most crabs were immature and where the sex ratio of 1:1.3 indicated the non-existence of harems, no significant sex differences in diet composition was found.

Most egg-carrying females seem not to feed (90.3 % had empty stomachs), possibly as an adaptation to avoid predation during egg incubation. The extra weight of their large egg clutches would also make them less mobile and more vulnerable to predation.

Smaller crabs ingest a higher proportion of molluscs, while larger crabs a higher proportion of crustaceans (Fig. 5). This and the fact that fish and echinoderms were absent in stomachs of small crabs suggest size-specific differences in prey accessibility and/or anatomical differences in the feeding apparatus as reported for other crab species (e.g. Hill 1976, Gotshall 1977, Jewett & Feder 1982, Laughlin 1982, Perez & Bellwood 1988).

As shown in Fig. 5, the *Cancer polyodon* population at Site G (average biomass: 637 kg) consumes annually about 12 times its own biomass (7414 kg). The most preyed-upon species is *Tagelus dombei* with 4282.4 kg , followed by the crab *Petrolisthes desmarestii* , the gastropod *Tegula* spp. and several other molluscan species. Through cannibalism about 130 kg of *C. polyodon* are consumed in the total area, which represent tens of thousands of small juveniles (< 5 g) and about 10 % of total production.

The present and the 2 preceding studies show that *Cancer polyodon* can be regarded as an extremely efficient converter of benthic production and as a density regulator for most benthic invertebrates due to its large body size, high abundance and biomass, high daily food intake and population production efficiency and its capacity to detect food patches and to aggregate quickly. Its relative abundance in shallow water areas along the Chilean/Peruvian coast may act as an indicator of benthic productivity in these areas.

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