

Feeding ecology of the crab *Cancer polyodon* in La Herradura Bay, northern Chile. I. Feeding chronology, food intake, and gross growth and ecological efficiency

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ABSTRACT: Feeding activity pattern and food intake of the crab *Cancer polyodon* were determined from crab stomach samples taken at 3 to 4 h intervals on 2 days per season in 1988 and 1989. The gross growth efficiency (K_1) and the ecological (= population production) efficiency (EE) were calculated in conjunction with growth and production data from a previous study. *C. polyodon* feeds at night and to a lesser extent during the day. Feeding chronology differed markedly among seasons: in winter, night feeding lasted about twice as long (13 to 15 h) as in spring, but maximum stomach fullness reached only 0.35 % BW (body weight) compared to 0.62 % BW in spring. Summer feeding resembled the spring pattern and autumn feeding the winter pattern. Daily food intake was estimated from the stomach content data and a laboratory-derived evacuation rate using the Elliott & Persson model. Daily rations increased from 2.8 (\pm 0.71) % BW in winter to 4.4 (\pm 0.64) % BW in summer and decreased to 2.7 (\pm 0.37) % BW in autumn (annual average: 3.19 % BW). K_1 (weight gain as % of total food ingested) was lower for females (5.3) than for males (10.3), as females convert a high fraction of ingested food into egg production instead of growth. EE [(population biomass production)/(food ingested)] was estimated at 17.8 %.

INTRODUCTION

Cancer polyodon is a shallow-water brachyuran crab distributed from Ecuador to southern Chile. It is the largest and most common of a variety of crab species inhabiting the coastal waters of Peru and Chile, where it has been fished by divers and captured with traps for many decades. It is known as a predator of clams and scallops (DiSalvo et al. 1984, Augsburger & Vega 1989) and is suspected to be an important regulator of scallop *Argopecten purpuratus* recruitment (Wolff 1987). Most published reports on natural feeding of brachyuran crabs have focussed on the dietary range and shown cangrid crabs to be food generalists, preying upon small molluscs and crustaceans of limited mobility (Elner 1981, Williams 1981, 1982, Morales & Antezana 1983, Elner et al. 1985, Haddon & Wear 1987, Rangeley & Thomas 1987,

among others). Ontogenetical, geographical, seasonal and sex differences in the dietary range have also been reported (Hill 1976, Gotshall 1977, Jewett & Feder 1982, Laughlin 1982, Stevens et al. 1982, Perez & Bellwood 1988). Some authors have described the feeding technique of the crabs (Elbing et al. 1964, Elner 1978, Zipser & Vermeij 1978, Asson-Batres 1986, Davidson 1986); others have analysed crab feeding in the light of optimal foraging theory (Elner & Hughes 1978, Morales & Antezana 1983, Chilton & Bull 1986, Rangeley & Thomas 1987).

The focus of the investigation presented here was the determination of feeding chronology, daily food intake, gross growth efficiency and ecological efficiency of *Cancer polyodon*. The study was part of a research program aimed at assessing the functional role of *C. polyodon* in the shallow-water community of La Herradura Bay, Chile. The population dynamics of

this species have been characterized by Wolff & Soto (1992). An analysis of the food spectrum will be presented later.

Previous diving observations by us have shown that *Cancer polyodon* forage during the night, while they seem to rest during daylight hours, buried in the sand. Based on this observation we addressed the following questions: Are the crabs exclusively night feeders? Is the feeding behaviour reflected in the stomach content over the course of a day? How do seasonal changes in water temperature and night length affect their feeding behaviour and daily rations? We conducted a laboratory study on gastric evacuation and calculated the daily rations based on this rate and on the stomach content data of the field-collected specimens, using the model of Elliott & Persson (1978).

MATERIAL AND METHODS

Sampling and sample treatment. On 2 days per season in 1988–89, 7 samples of 15 crabs each were hand-collected by a diver within the study area (Fig. 1) at 3 to 4 h intervals, at a water depth of 5 to 8 m. Immediately after collection, moulting and egg-carrying specimens were sorted out and returned to the water; the remaining specimens were killed by oral

injection of formalin (10 %), stored in plastic bags and transferred to the laboratory for analysis. The crabs were sexed, the carapace width (CW) was measured to the nearest 0.1 mm with a calliper and the fresh weight was registered to the nearest 0.1 g. Subsequently the carapace was separated from the abdomen and the stomach was extracted and bled on absorbing paper for several minutes to eliminate excess liquid. The stomach was then emptied and the content weighed to the nearest 0.1 g.

Determination of gastric evacuation rate. Six similar-sized crabs (average CW = 115 mm) were kept individually in 30 l tanks of seawater ($14.5 \pm 0.5^\circ\text{C}$, 35 ‰ S) and fed with clam meat [1.5 % of body weight (BW)]. Only those crabs that had eaten all the food offered within 15 min were subsequently used for the experiment. After intervals of 1.5, 3, 4.5 and 6 h, 1 crab was sacrificed to determine the stomach content. This experiment was repeated 10 times and the stomach contents after each interval were averaged. These averages were used to calculate the gastric evacuation rate (for each interval) from the following equation:

$$S_t = S_0 e^{-Rt} \quad (1)$$

where S_t and S_0 are the stomach contents at time t after food ingestion and at the start of evacuation, and R is the gastric evacuation rate (h^{-1}). The R values of each time interval were averaged and a confidence interval calculated.

In addition, we calculated R values from the steepest parts of the descending portion of the feeding curves (R = underlined numbers in Fig. 2) assuming that within these intervals only evacuation had occurred, and compared these values with the laboratory-derived rate.

Daily rations (r_d) were calculated from the laboratory-derived evacuation rate and the Elliott & Persson (1978) model:

$$r_d = \sum_1^n C_{\Delta t} \quad (2)$$

where $C_{\Delta t}$ = quantity of food consumed during an interval Δt between 2 successive sampling times t and $t + 1$, and n = number of intervals per day. In our study there were always 7 such intervals. $C_{\Delta t}$ is defined as:

$$C_{\Delta t} = RT(S_{t+1} - S_t e^{-RT}) / (1 - e^{-RT}) \quad (3)$$

where S_{t+1} and S_t = mean stomach contents at 2 successive sampling times; R = evacuation rate; and T = interval length in hours.

Computation of standard deviation for daily ration estimates. The errors around the daily ration estimates from the Elliott & Persson model were computed using a method known as 'bootstrap' (Efron 1981). This non-

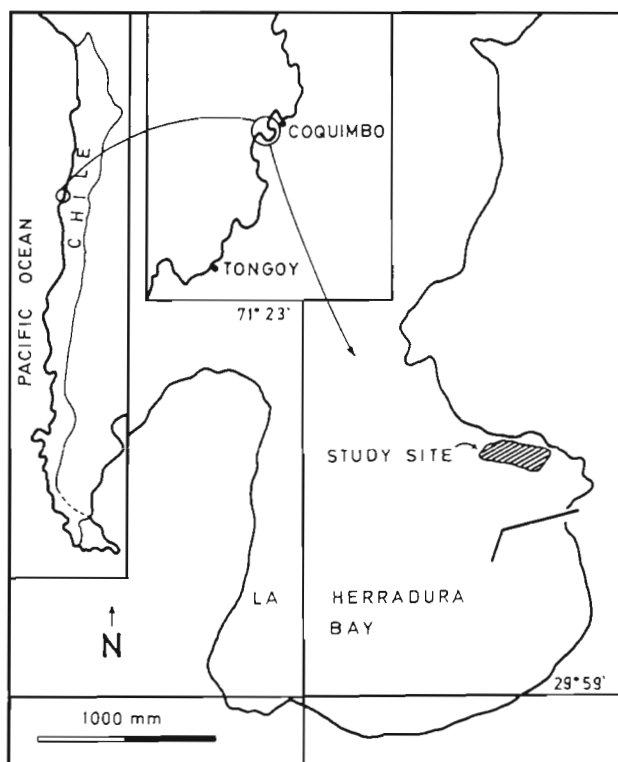


Fig. 1. La Herradura Bay, Chile, with study site

parametric method can be applied when the data are not normally distributed (such as the stomach contents in the present case) and even when the underlying distribution of the parameter is unknown. A necessary assumption of this method is that the original sample is representative for the population from which it is drawn. Following this method random subsamples (of the original sample size) were repeatedly taken from each sample (obtaining each time similar but not identical averages for stomach content at a sampling time), and Eq. 3 was calculated. This procedure was repeated 1000 times, producing a frequency distribution of daily rations from which the average values and standard deviations were computed.

Gross growth efficiency (K_1) and ecological efficiency (EE). Daily weight increments of female and male *Cancer polyodon* were calculated from the following equations (Wolff & Soto 1992):

$$\begin{aligned} \text{Males: } CW_t &= 198(1 - e^{-0.54(t-0.25)}); \\ W_t &= 0.00013 CW_t^{3.096}; \\ \text{Females: } CW_t &= 160.5(1 - e^{-0.57(t-0.25)}); \\ W_t &= 0.00050 CW_t^{2.809} \end{aligned}$$

where CW_t and W_t = carapace width (m) and wet weight (g) respectively at age t (yr).

For the calculation the weight of an average crab of 115 mm CW (Wolff & Soto 1992) was determined, its size increment d^{-1} was calculated and this size was then re-transformed into weight. K_1 was then estimated as follows:

$$K_1 = \frac{(\text{daily weight increment, g wet wt})}{(\text{daily ration, g wet wt})} \quad (4)$$

EE was calculated as:

$$EE = ZBr_a \quad (5)$$

where Z and B = average instantaneous mortality rate (yr^{-1}) of the population and the average annual biomass, estimated as 2.07 and 637 kg respectively (Wolff & Soto op. cit.); and r_a = annual amount of food ingested, which is given by $B \times (\text{daily food consumption in \% BW}) \times 365$.

RESULTS

Feeding pattern

The average stomach fullness of specimens collected showed a cyclic pattern for all days sampled (Fig. 2). The general pattern was similar for the 2 days per season but differed markedly among seasons. Maximum stomach content occurred earlier at night and was higher in spring and summer (0.6 to 0.7 % BW) than in winter and autumn (0.4 to 0.5 % BW). The

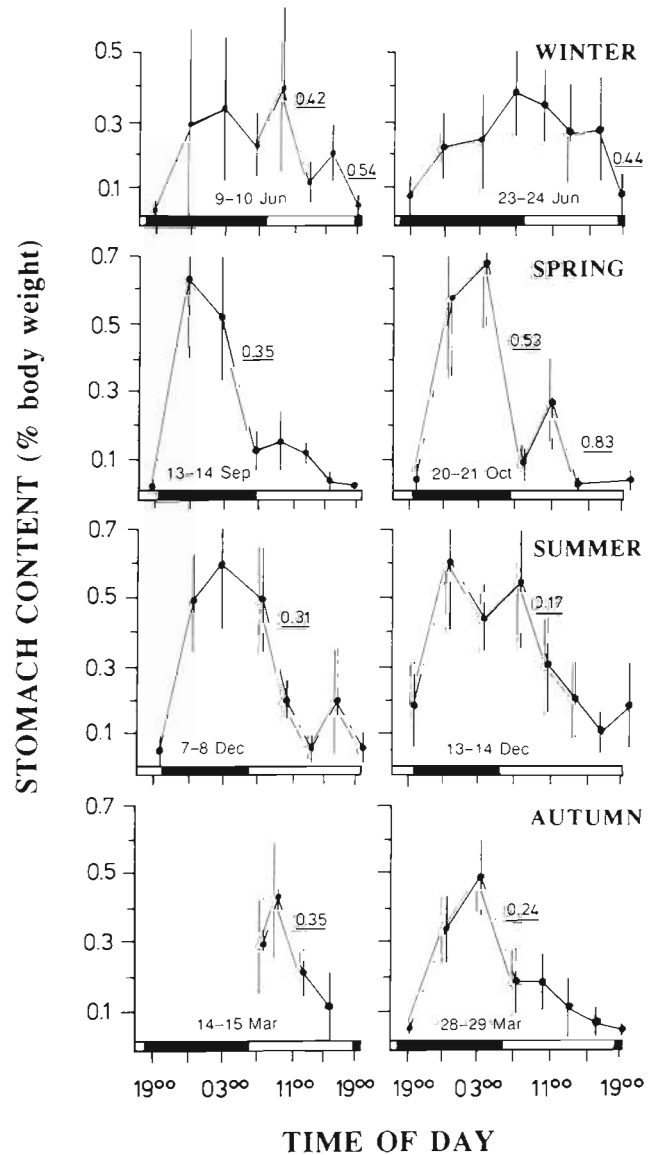


Fig. 2. *Cancer polyodon*. Average stomach content (± 1 SE) at different times on 2 days per season (austral winter, spring and summer 1988, and autumn 1989). Underlined numbers are calculated evacuation rates, R , between 2 sampling times assuming no food intake; black and white bars on horizontal axes show length of night and day

highest feeding activity occurred during the night hours but daytime feeding also occurred. Lowest stomach contents were generally found just before sunset.

Daily ration estimates

Fig. 3 shows the gastric evacuation curve and the evacuation rate ($R = 0.506$) obtained for the laboratory-fed specimens. Daily rations increased from winter

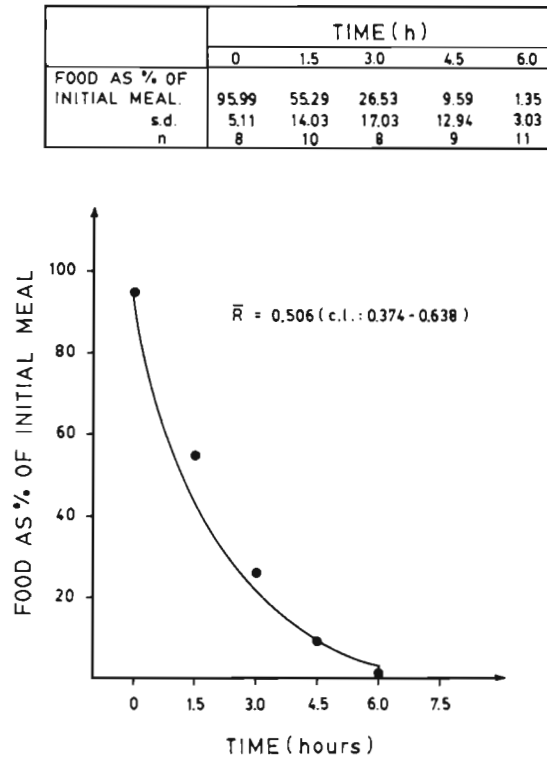


Fig. 3. *Cancer polyodon*. Gastric evacuation curve calculated from laboratory-fed specimens at $14 \pm 0.5^\circ\text{C}$

through spring and summer, and decreased thereafter (Fig. 4). They were significantly different (t -test, $p < 0.05$) between all seasons and days, except for the last winter and first spring day ($t = 1.2$; $df = 999$, $p < 0.05$). The annual average was 3.19 % BW (Fig. 4).

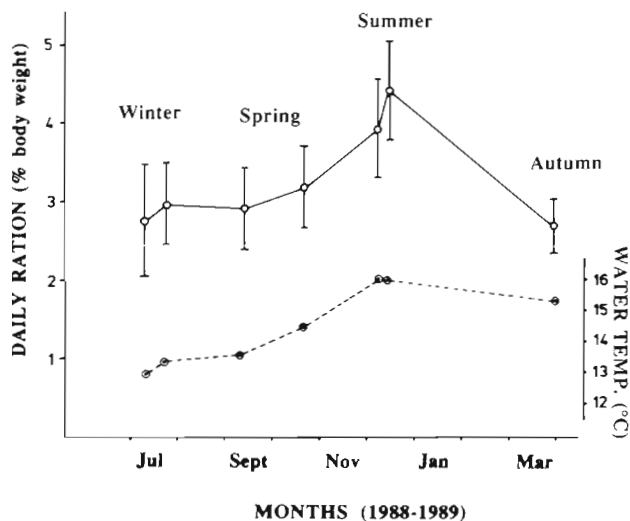


Fig. 4. *Cancer polyodon*. Seasonal changes in daily ration (± 1 SD), calculated for each sampling day (upper curve) in relation to *in situ* temperature (lower curve)

Gross growth and ecological efficiency

According to the growth curves and size-weight relationships for both sexes (see above) a female of 115 mm CW increases its body weight by about 0.52 g d^{-1} at a body weight of 307 g. Using our average ration estimate of 3.19 % BW, K_1 can be calculated as follows:

$$K_1 (\text{females}) = 100 [0.52 \text{ g} / (307 \times 0.0319)] = 5.3 \%$$

$$K_1 (\text{males}) = 100 [1.03 \text{ g} / (312 \times 0.0319)] = 10.3 \%$$

Using Eq. 5 we obtain:

$$EE = 100 (2.07 \times 637) / (637 \times 0.0319 \times 365) = 17.8 \%$$

DISCUSSION

Feeding pattern and food intake estimates

Our initial assumption that *Cancer polyodon* feeds only at night and rests during the daytime was shown to be erroneous, as minor feeding was also found during the day (Fig. 2). The highest feeding activity occurs over the night hours, however, and most crabs appear to cease feeding at sunrise or shortly beforehand, then start again when the food is evacuated, which takes about 6 h (Fig. 3). Crabs that cease feeding at sunrise may thus start feeding again in the early afternoon hours. This is partly confirmed by our results (Fig. 2).

The seasonal variation in duration and intensity of night-time feeding followed the changes in water temperature and night length over the year (Fig. 4). It seems that at increasing temperatures in spring (and possibly also due to the shortening of the night) crabs feed more actively during the initial night hours, resulting in faster food saturation and a shortened night feeding period. A similar feeding pattern prevails in summer, when temperatures are highest (Fig. 4). The total daily food intake (Fig. 4) also showed a clear relation with the water temperature, except for the autumn estimate, which was lower than the 2 winter estimates even though temperature in autumn was higher than in spring.

This could be explained by a depletion of the crabs' food source during late summer and autumn, when crab densities are highest (Wolff & Soto 1992). The abrupt decrease in density by about 60 % at the end of autumn is also indicative of this. Virnstein (1977) reported lowest faunal densities of shallow-water subtidal communities in Chesapeake Bay, USA, in late summer and fall, after crabs and fish had been feeding on the infauna, and highest densities in winter and spring when these predators were absent or less

active. Dare & Edwards (1976) and DiSalvo et al. (1984) reported on the capacity of cangrid crabs (*Carcinus maenas* and *Cancer polyodon* respectively) to detect dense patches of prey and to aggregate quickly. This capacity and the high daily rations suggest that *C. polyodon* and probably cangrid crabs in general are extremely efficient regulators of their benthic prey's abundances.

Stomach fullness was highly variable among individuals (see SE bars in Fig. 2) and cannot be treated like a normally distributed data set. Individual success in finding and ingesting food is not only a function of the crabs' activity but also of competition among crabs, which increases with crab density. During night diving it was observed that specimens holding a prey item were attacked by other crabs trying to take the prey away; other specimens aggressively lifted their chela against one another. This agrees with observations of Scheibling (1984) on *Cancer irroratus* from Nova Scotia, who found that crabs fought for possession of prey and that, out of 8 crabs attracted to a piece of bait, only 1 fed at a time. His observations were also made at the end of summer, the time of highest crab densities. Such resulting high variability in the stomach contents among individual specimens can be adequately handled with the bootstrap method, as this study shows. By the use of the random resampling procedure, the variability of the original individual stomach contents in a sample is taken into account and is reflected in the variability of the resulting mean values which are used for the daily ration estimates and the corresponding error estimates.

Our estimates of daily food intake were obtained using a constant, laboratory-derived evacuation rate at a water temperature of 14 ± 0.5 °C. As evacuation (and feeding) is temperature-dependent, R will vary among the seasons with *in situ* temperature. However, this variation was probably small, as the temperature range among the sampling days was narrow (13.0 to 16.0 °C). Fig. 2 gives some indication that our laboratory-derived R value (0.506) is a reasonable estimate for the *in situ* rate, as the R values obtained from the steepest parts of the descending portion of the feeding curves (Fig. 2) ranged from 0.17 to 0.86 with an average around 0.40. Two values (0.54, 0.53) were near the laboratory-derived rate.

This study is the first to estimate daily rations of adult cangrid crabs in the field, and consequently references for direct comparisons of daily food uptake are lacking. Some authors, however, have reported on the predation potential of cangrid crabs. Lake et al. (1987) found that *Cancer pagurus* (10.5 cm CW) consumes 25 to 31 *Pecten maximus* of 5 cm shell height and 71 to 85 *P. maximus* of 4 cm shell height within 5 d. Scheibling (op. cit.) reported predation rates of 1 sea urchin

crab⁻¹ d⁻¹ and 3.2 mussels (3 to 4 cm shell length) crab⁻¹ d⁻¹ for *Cancer irroratus* (60 to 100 mm CW) in the laboratory. The latter amounts to ca 5.3 % BW assuming 150 g BW for a crab of 80 mm CW (after Krouse 1972) and 2.5 g as the weight of the mussels. This rough estimate is similar to our daily ration estimates for the summer period.

Daily rations of cangrid crabs cannot be generalized to other crustaceans. For adult lobsters *Homarus americanus*, Jahnig (1973) reported daily rations <1 % BW to maintain their slow growth. Branford (1979) obtained values in the 0.5 to 1.5 % range. These reports and our results suggest substantial differences in daily rations between crabs and lobsters and they should not be grouped into quantitative ecosystem box models, as has been done before (Polovina 1984).

Gross growth efficiency and ecological efficiency

The K_1 values of our study (5.3 and 10.3 % for females and males respectively) are low compared to the 20 to 30 % value reported by Barnes & Mann (1980) for macroinvertebrates of temperate waters. They are also lower than those for most fish, which usually range from 15 to 30 % (Bardach et al. 1972, Caddy & Sharp 1986). Lane et al. (1979), however, calculated lower K_1 values of 12 % for the benthic-feeding diamond turbot *Hypsopsetta guttulata* (>25 g), assuming 80 % digestion of ingested food. In *Cancer polyodon*, a significant proportion of the stomach content is made up of undigestible hard parts and sand (we estimate this to be about 40 %), so that only a part of the ingested food can be digested. However, K_1 values are intended to express weight gain as % of total food ingested, without differentiating digestible and non-digestible components.

The difference in the K_1 values between sexes is explained by the fact that females convert a significant fraction of ingested food into egg production instead of somatic growth. Paul & Fuji (1989), for example, found that female *Chionoecetes bairdi* allocated over 20 % of their energy to their egg clutches.

According to our findings, about 18 % of the food ingested by the crab population was converted into population biomass. Based on the population biomass-per-area estimate of 637 kg per 5964 m² (Wolff & Soto 1992), the crabs should have removed about 1.25 kg of their prey m⁻² yr⁻¹. Our EE estimate is near the 20 % value for overall efficiency for most marine benthic invertebrates (10 to 30 %) (Mann 1982).

The results of the present study indicate that the food ingested by *Cancer polyodon* is more efficiently converted into population biomass than individual bio-

mass due to the high population turnover ($Z = 2.07$) compared to temperate invertebrates of similar sizes (Mann 1982). This might be explained by the almost constant recruitment of juveniles to the adult population (Wolff & Soto op. cit.) and the compensatory 'thinning out' through cannibalism. This strategy not only keeps the turnover high, but also compensates for occasional food shortages or excessive densities of crabs. The next report will concentrate on the food spectrum of *Cancer polyodon* and the relative consumption of the different prey species.

Acknowledgements. This research was financially supported by project D.G.I. Universidad Catolica del Norte # 68.71. Our sincere thanks go to M.Sc. Rachel Wolff and Dr Sabine Dittmann for their constructive suggestions, to Dr Thomas Brey for writing the bootstrap program and to 3 unknown referees, whose critical reading helped to improve the manuscript.

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This article was presented by J. E. Winter, Valdivia, Chile

Manuscript first received: February 15, 1992

Revised version accepted: October 13, 1992