

Population dynamics of *Cancer polyodon* in La Herradura Bay, northern Chile

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ABSTRACT: The objectives of this study were to assess the density and biomass of a local population of *Cancer polyodon* in La Herradura Bay, Chile, and to describe its population dynamics: growth (absolute and relative), mortality (natural and fishing) and spawning. Female crabs grew at a higher von Bertalanffy growth rate ($k = 0.57$) but reached a smaller asymptotic size ($CW_{\infty} = 160.5$ mm) than males ($k = 0.54$, $CW_{\infty} = 198$). A parallel growth study in the laboratory yielded higher k and and lower CW_{∞} values than for wild specimens and lower values for the growth performance index ϕ' . For both sexes, relative growth (post-moult/pre-moult relationship) was better described by a 2-line model instead of a single 'Hiatt-line'. The intersection of the 2 lines is suspected to mark the onset of gonad formation. Age at massive maturity is ca 2 yr in females and males (at 98 and 124 mm CW respectively). Males seem to moult 16 times and females 14 times after the megalopa stage. Spawning occurred over most of the year with pulses in winter and early summer. Average total mortality (Z) was higher in males (2.58) than in females (1.85). A tendency of Z to increase with age indicates that larger specimens are more vulnerable to the traps or have a higher rate of natural mortality (M). M for both sexes was estimated to be between 0.75 and 1.1. Mean annual biomass estimated from Jones' length cohort analysis was 2.4 times and spawning biomass 4 times higher in females than in males. Using the turnover ratio ($Z = P/B$) an average annual production of 221 g m⁻² (fresh weight) was estimated from the density data.

INTRODUCTION

Cancer polyodon Poëppig, 1836 (Brachyura: Cancridae) is distributed in the Pacific from Guayaquil, Ecuador, to the Taitao peninsula, southern Chile (Garth 1959). It is most abundant at 4 to 8 m depth on heterogeneous sand or muddy sand grounds with refuges of rocks, shells and macroalgae but can also be found in deeper waters (to 25 m) and on unstructured sand grounds (Gutierrez & Zuniga 1976, authors' obs.). It is the largest and most common of the crab species inhabiting the coastal waters of Peru and Chile, where it has been fished by divers and captured with traps for decades. Catches in Chile increased from 1124 t in 1980 to 5138 t in 1987 (SERNAP 1980 to 1987). *C. polyodon* preys upon clams and scallops (DiSalvo et al. 1984, Mendo et al. 1987, Augsburg & Vega 1989) and is suspected to be an important regulator for scallop *Argopecten purpuratus* recruitment (Wolff 1987). Some information

exists on its population structure and reproductive cycle in the Bay of Lima, Peru (Talledo & Ishyama 1988), and on its larval development (Quintana 1981). Despite its value as a local food source and its potential as an export product, no resource evaluation has yet been carried out either in Peru or in Chile and very little is known about its functional role in the shallow water community.

The present study is part of a research program aimed to assess the population dynamics of *Cancer polyodon* together with its density and functional role in the shallow water community of La Herradura Bay, northern Chile (Fig. 1). It gives estimates of production and biomass per area, instantaneous rates of growth and mortality, size structure, sex ratio, age at maturity and time of spawning. Most of the data were derived from weekly trap catches, some from hand-collected specimens. Two laboratory growth experiments were conducted to compare growth in the laboratory with growth in the natural habitat.

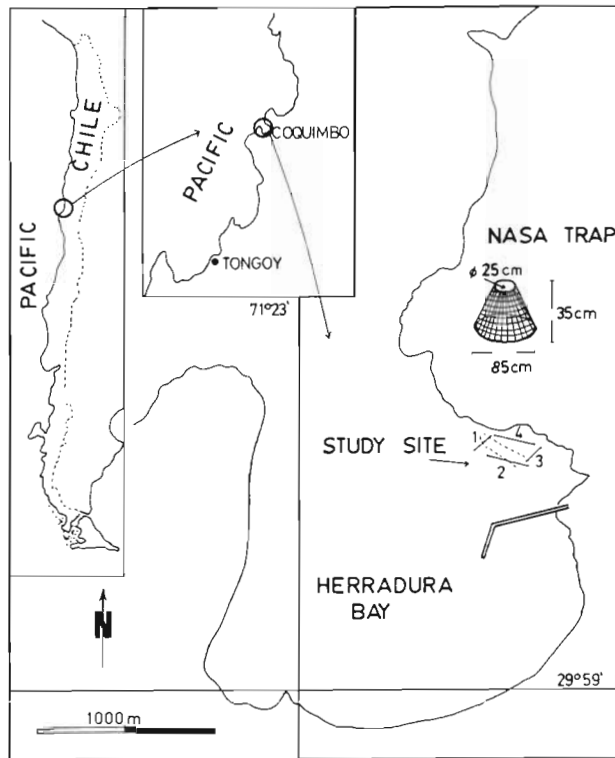


Fig. 1. Study area and trap types used for crab captures. (—) Transects for density estimates; (----) position of traps

MATERIALS AND METHODS

Sampling, measurements and biometric relationships. Weekly crab catches were made in La Herradura Bay from February 1987 to January 1988 using 'Nasa traps' (Fig. 1). Two parallel lines of 10 traps were placed 6 m apart at ca 8 m depth. The traps were baited with sardine or horse mackerel and left for 24 h. Specimens caught were sexed by morphological differences of the abdomen (Gutierrez & Zuniga 1976). The carapace width (CW) and chela width (ChW) were measured to the nearest 0.1 mm using calipers and individual wet weight (W) was registered to the nearest g. Female crabs were inspected for the presence and maturity (colour) of eggs (Gutierrez & Zuniga 1976). Relationships between W and CW and between ChW and CW were described by the allometric equation $Y = aX^b$, which was log-transformed for analysis ($\log Y = \log a + b \log X$); the resulting regression lines of CW versus W of both sexes were compared statistically by covariance analysis. The plot of ChW versus CW in males was inspected for the existence of 2 distinct allometric phases corresponding to premature and mature specimen (see Fig. 2).

Laboratory growth. Experimental design: Two successive growth experiments with sexes separated were

conducted over periods of 7 mo (July 1987 to January 1988 and June 1988 to December 1988). Specimens of 5 to 120 mm CW were collected by hand in La Herradura Bay (Fig. 1) and recently moulted (soft shelled) specimens were transferred to the laboratory and kept under observation for 2 d in 100 l tanks with running sea water. Dead and damaged specimens were discarded. The remaining crabs were placed in six 100 l tanks of running sea water as follows: Eight small specimens (CW: 5 to 30 mm) were put individually into numbered mesh cages of $10 \times 10 \times 15$ cm, which were subsequently installed in Tanks 1 and 2. This experimental design was chosen as preliminary experiments had shown high cannibalism among small individuals when kept in the tank without separation. Eight intermediate-sized specimens (CW: 30 to 50 mm) were individually marked with numbered plastic tags glued onto the carapace and were put into Tanks 3 and 4 in groups of 4 crabs each. Tanks 5 and 6 were supplied with 3 marked specimens (CW: 50 to 120 mm) each. Every second day, each crab was checked and measured if a moult had occurred. The crabs were fed with a surplus of 20 g of fish or mollusc flesh every second day. Remaining food was removed prior to subsequent feeding.

Data analysis: As the number of crabs per experiment (22) was low and both experiments were conducted over almost the same months in consecutive years, the data from both experiments were pooled for analysis.

Absolute growth: The average size at each moult (i.e. instar) and the average intermoult period (d) was calculated for male and female specimens. These data were then used as input for a linear regression model developed by Gulland & Holt (1959) to calculate the von Bertalanffy growth parameters k (instantaneous growth rate) and L_∞ (asymptotic size):

$$(CW_2 - CW_1)/(t_2 - t_1) = a - b[(CW_1 + CW_2)/2], \quad (1)$$

where CW_1 and CW_2 are CW at times t_1 and t_2 ; k is calculated from the slope of the regression ($k = -b$) and the asymptotic size (here CW_∞) from $CW_\infty = a/k$. To obtain an estimate for t_0 , the theoretical age at length zero, an age of 85 d at a size of 3.5 mm was assumed according to Quintana (1981). These values were then inserted into the reordered von Bertalanffy growth equation:

$$t_0 = t + (1/k) \ln(1 - CW_t/CW_\infty) \quad (2)$$

For comparison of the von Bertalanffy growth of *Cancer polyodon* with that of other crab species, the growth performance index ϕ' (Pauly & Munro 1984) was calculated as follows:

$$\phi' = \log k + 2 \log CW_{\infty} \quad (3)$$

Growth per moult: The Hiatt growth diagram (Hiatt 1948) was used to plot the size at instar (CW_n) against the size at the subsequent instar (CW_{n+1}) by a least squares regression line. This line was then tested for an inflection point by a technique described by Somerton (1980). The data were repeatedly divided into 2 groups and regressions were calculated for each group. The residual sum of squares of both lines was then summed and the calculation was repeated with another pair of regression lines until the residual sum of squares approached a minimum. An inflection point exists if the pooled residual sum of squares of a pair of the resulting regression lines is significantly lower than the residual sum of squares of a single line. According to Somerton (1980), the test statistic is:

$$F = \frac{(RSS_1 - RSS_2)/2}{RSS_1/(n - 4)} \quad (4)$$

where RSS_1 and RSS_2 are the residual sums of squares for Models 1 (1 line) and 2 (2 lines) respectively; n is the number of data points; the statistic is distributed as F with 2 and $n - 4$ degrees of freedom.

Field growth. Absolute growth: The CW data of weekly trap catches were pooled into monthly values and subsequently grouped for each sex into size intervals of 12 mm. This relatively wide interval was assumed to be more appropriate because it reduces the possibility of mistaking a moult for an annual mode in the histograms. These data were then analysed using the computer program ELEFAN I (Pauly 1985) that allows for estimation of the von Bertalanffy growth parameters without knowing the age of the individuals. To detect oscillations in the growth rate during the annual cycle, Pauly & Gaschuetz (1979) incorporated the following extended version of the von Bertalanffy growth equation into the program:

$$L_t = L_{\infty}(1 - e^{-k((t-t_0) + (Ck/2\pi) \sin[2\pi(t-t_s)])}) \quad (5)$$

L_t , L_{∞} , and k are parameters as explained above; t_0 is the theoretical age at length zero, C is a constant which represents the amplitude of growth oscillation and t_s is the starting point of the oscillation.

The computation of the growth parameters can be outlined as follows: The length frequency data are first restructured by calculating a running average over 5 length classes and peaks are identified as those parts that are above the corresponding running averages. Von Bertalanffy growth curves are then traced through the length frequency samples for any arbitrary 'seed' input of k and L_{∞} , starting from the basis of each peak and projecting backward and forward in time to meet

all other samples of the sample set or the same sample repeated again and again. The curve that passes through the most peaks and avoids the most troughs yields the best parameter estimates.

Growth per moult: For both sexes, all CW measurements during the study period were pooled, grouped into size class intervals of 1 mm, and histograms drawn. These histograms were analysed for their normally distributed components using the method of Bhattacharya (1967). As distributions proved to be unresolvable, the data were regrouped into size intervals of 2 mm, smoothed using a running average over 3 size intervals and reanalyzed with the Bhattacharya method. The above calculation was done assuming that the size at instar was nearly constant throughout the year and that the normally distributed components would represent CW at instar.

Size at first (massive) maturity (CW_m). Females: In the months of highest incidence of egg-carrying, samples were taken to estimate the size at massive maturity using a method published by Udupa (1986). This method allows the confidence interval for the estimate to be calculated as follows: determination of the proportion of mature females for each size class interval, calculation of the logarithm of the size at first maturity by the formula of Spearman-Kärber (as cited in Udupa 1986) and calculation of the confidence limits based on the standard error of the estimate of mean log size (see Table 2 for the calculation procedure).

Males: A plot of CW versus ChW was drawn using all data over the total size range to look for evidence of an abrupt change in relative growth as indicative for maturity (Somerton 1980). As 2 clearly distinct but overlapping phases were detected, the size at massive maturity was calculated as follows: 2 regression lines were calculated using the log-transformed data for each group of data points excluding the points where both lines overlap; the lines in the middle region were extended and the data points were assigned to the line closest to them, thus classifying them as either juvenile or adult (mature); the so classified data of the overlapping region of the graph were grouped into size intervals of 1 mm, and the size at massive maturity was calculated along with its confidence interval using the method of Udupa (1986) as explained above.

Spawning. Egg colour and percentage of egg-carrying females in the trap catches were determined each month. Females with eggs of dark-reddish to beige colour were classified as fully mature and those with yellow-coloured eggs were classified as immature (Gutierrez & Zuniga 1976).

Total mortality (Z) and natural mortality (M). The same ELEFAN package (Pauly 1985) was used to calculate the instantaneous rate of total mortality via a length-converted catch curve using the same input

data as were used for the growth analysis. The catch curve was established by plotting the logarithm of the number of individuals in a length class divided by the time needed for an average individual to grow through the length class versus their corresponding relative age. Z was computed from the right descending arm of the catch curve. Rough estimates of the instantaneous rate of natural mortality were obtained by 2 empirical formulas. The first (Rikhter & Efanov 1976) relates natural mortality (M ; yr^{-1}) to the age at first (massive) maturity (T_m):

$$M = 1.521/(T_m^{0.72}) - 0.155; \quad (6)$$

the second (Pauly 1980) relates M to the growth parameters k and CW_∞ and the mean annual water temperature (T):

$$\ln M = -0.0152 - 0.27955 \ln L_\infty + 0.6543 \ln k + 0.463 \ln T. \quad (7)$$

Population structure, mean annual biomass and density estimates. Histograms of CW data of specimens caught by the diver and captured with the traps were first drawn separately to assess possible selection effects of the traps. For subsequent population analysis, the CW measurements of all trap and diver catches were pooled into 2 yearly samples of males and females, and divided into size-groups of 6 mm. These data were then used as input for Jones' length-based cohort analysis (Jones 1984) as programmed by Sparre (1987). The program was run with 3 different values of M (around the estimated value) and a terminal exploitation rate ($E = F/Z$) derived from the Z -values of the catch curves and the F -values ($F = Z - M$) estimated. In order to estimate the density of *Cancer polyodon* in the study area, all specimens found on a total area of 600 m^2 were collected. To do so, 2 transects of 100 \times 2 m, and 2 of 50 \times 2 m, were marked with lines on the seafloor (Fig. 1). The collection was done simultaneously by 4 divers on 5 May 1987 during the night hours of highest feeding activity of *C. polyodon* (Wolff & Cerda unpubl.). After sexing and measuring CW , the crabs were returned to the sea.

RESULTS

Biometric relationships

The CW - W relationship was significantly different between sexes ($F = 7.70$, $p < 0.05$):

$$\begin{aligned} \text{Males: } W &= 0.00013 CW^{3.096} \quad (n = 1629) \\ \text{Females: } W &= 0.00050 CW^{2.809} \quad (n = 3079) \end{aligned}$$

The plot of ChW against CW for males showed 2 distinct growth phases for juvenile and mature specimens (Fig. 2).

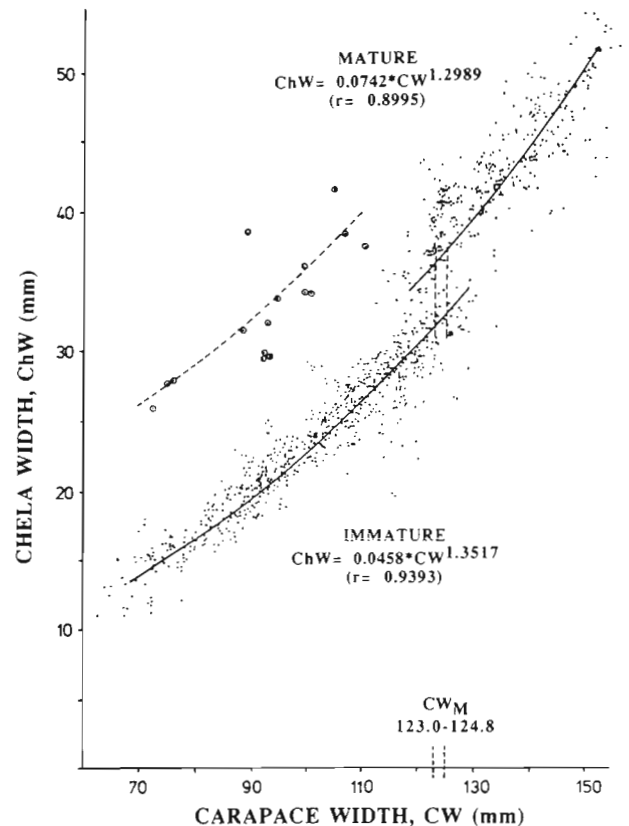


Fig. 2. *Cancer polyodon*. Carapace width (CW) vs chela width (ChW) for males and estimated confidence limits for size at massive maturity (CW_M) (for calculation of CW_M see Table 2); (----) a group of specimens $< CW_M$ with unusually large chelae

Laboratory growth

Absolute growth. Female growth was slower but statistically not significantly different from males for most of the study period (Fig. 3). For both sexes, the growth rate was highest from instars 5+ to 6+; during the subsequent interval (instars 6+ to 7+) the growth rate slowed down by ca 50%. Over the following moulting periods, the growth rate remained nearly constant (Fig. 3). The Gulland & Holt plot indicates wide confidence limits for the parameters CW_∞ and k for both sexes (Fig. 3). The theoretical age at length zero, t_0 , was estimated as 0.25 using the age of 85 d at 3.5 mm CW (Quintana 1981).

Growth per moult. For females and males grown in the laboratory, a 2-line model (see Fig. 4, lines A, B)

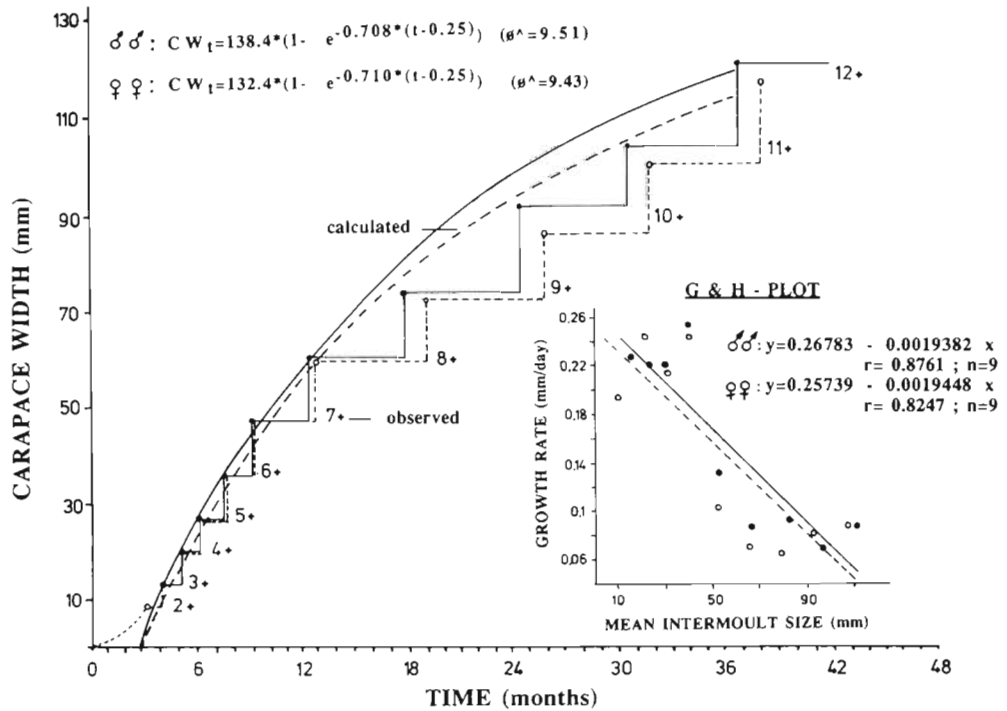


Fig. 3. *Cancer polyodon*. Absolute growth in the laboratory. (---) Females; (—) males

was found to better approximate the post-moult/pre-moult relationship than a single-line model, as the residual sum of squares was significantly lower for the former compared to the latter model (Table 1). The inflection point of both lines lies between instars 7+ and 8+, coinciding with the size where absolute growth dropped markedly (Fig. 3).

Field growth

Absolute growth. The original length frequencies used as input for the ELEFAN I program are seen in Fig. 5, together with the von Bertalanffy growth curves and the corresponding parameter estimates.

Growth per moult. Fig. 6 shows the CW histograms of the pooled data of male and female specimens and the normally distributed components (instars) that were detected using the Bhattacharya method. The instar sizes of both field and laboratory specimens are presented as a 'Hiatt diagram' in Fig. 4.

Size at first maturity (CW_m)

CW_m was found to be in the range 97.1 to 99.1 mm in females and 123.1 to 124.8 mm in males (Table 2, Fig. 2). These sizes correspond to ca 1.9 and 2.1 yr of age respectively. The smallest egg-carrying female found in the study measured only 67 mm CW, indicating that some females might well mature earlier in life. The

same seems to hold true for males as some individuals of sizes below CW_m already exhibit large-sized chelae, characteristic for maturity (Fig. 2, left upper line).

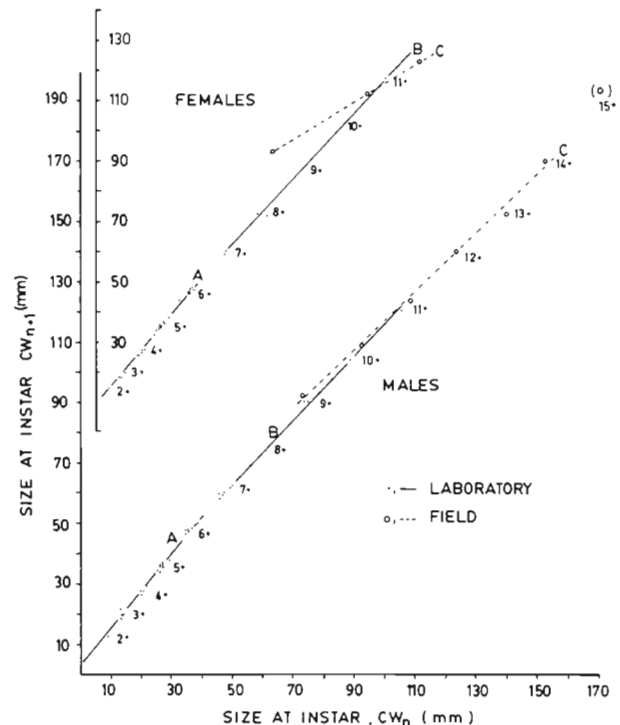


Fig. 4. *Cancer polyodon*. Hiatt diagram for laboratory-held (lines A, B) and field (line C) specimens (sizes correspond to instar numbers to be read from horizontal axis; for regression equations see Table 1)

Table 1. Regression equations for Hiatt diagrams presented in Fig. 4 ($y = CW_{n+1}$, $x = CW_n$)

Line	Equation	r	n	RSS	F
Females					
A	$y = 3.186 + 1.210x$	0.9949	22	11.45	
B	$y = 8.660 + 1.074x$	0.9985	19	24.84	
Sum				36.29	18.61*
A+B	$y = 5.452 + 1.127x$	0.9983	41	71.84	
C	$y = 56.00 + 0.595x$	0.9997	3	-	
Males					
A	$y = 3.364 + 1.212x$	0.9898	23	22.57	
B	$y = 9.859 + 1.063x$	0.9990	18	18.60	
Sum				41.67	24.01*
A+B	$y = 5.990 + 1.120x$	0.9981	41	93.20	
C	$y = 20.92 + 0.957x$	0.9945	6	-	

* 95% level of significance (F-test) for the difference of the residual sum of squares between the 2-line model (RSS A + RSS B) and the 1-line model

Spawning

Spawning probably occurred during the whole year as females with mature eggs were found in all months (Fig. 7). The percentage of females with mature eggs, however, was highest during winter (July and August) and summer (November to Janu-

ary), indicating 2 major spawning pulses during these periods.

Total mortality (Z) and natural mortality (M)

The instantaneous rate of total mortality (Z) as estimated from the catch curve was higher for males than

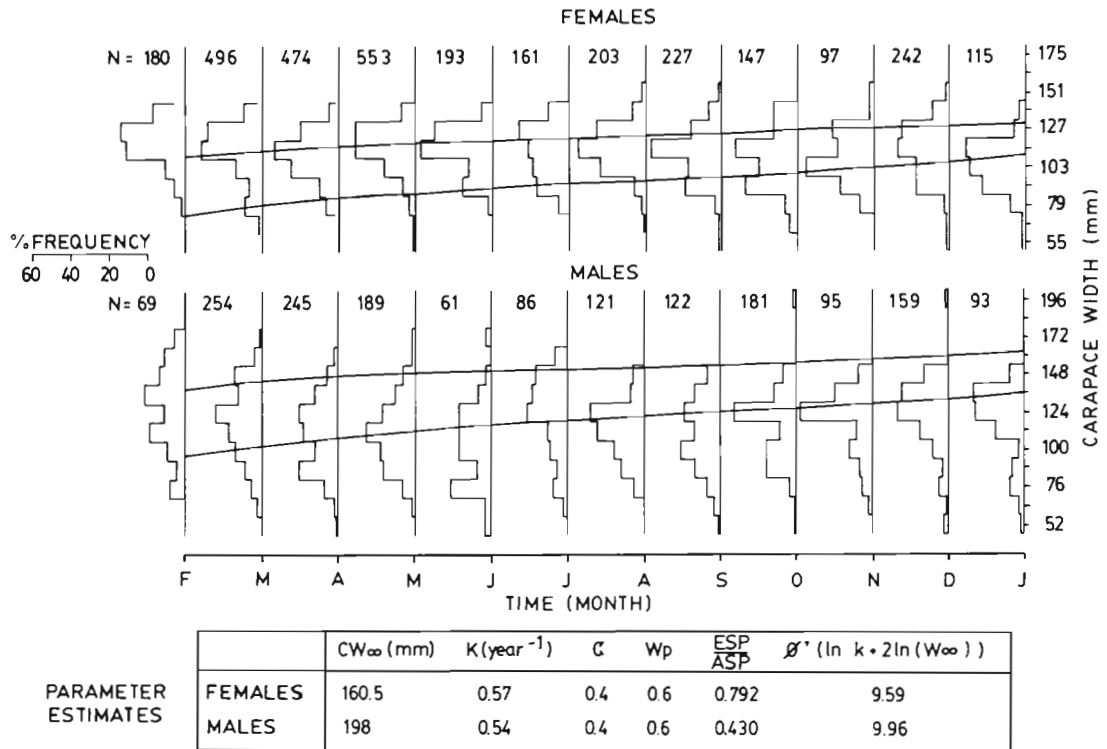


Fig. 5. *Cancer polyodon*. Absolute growth in the natural habitat as derived from ELEFAN analysis. CW_{∞} , k : von Bertalanffy growth parameters; C : constant of growth oscillation; W_p : time of the year when growth is lowest; ESP/ASP : goodness of fit criteria of the ELEFAN program; ϕ' : growth performance index

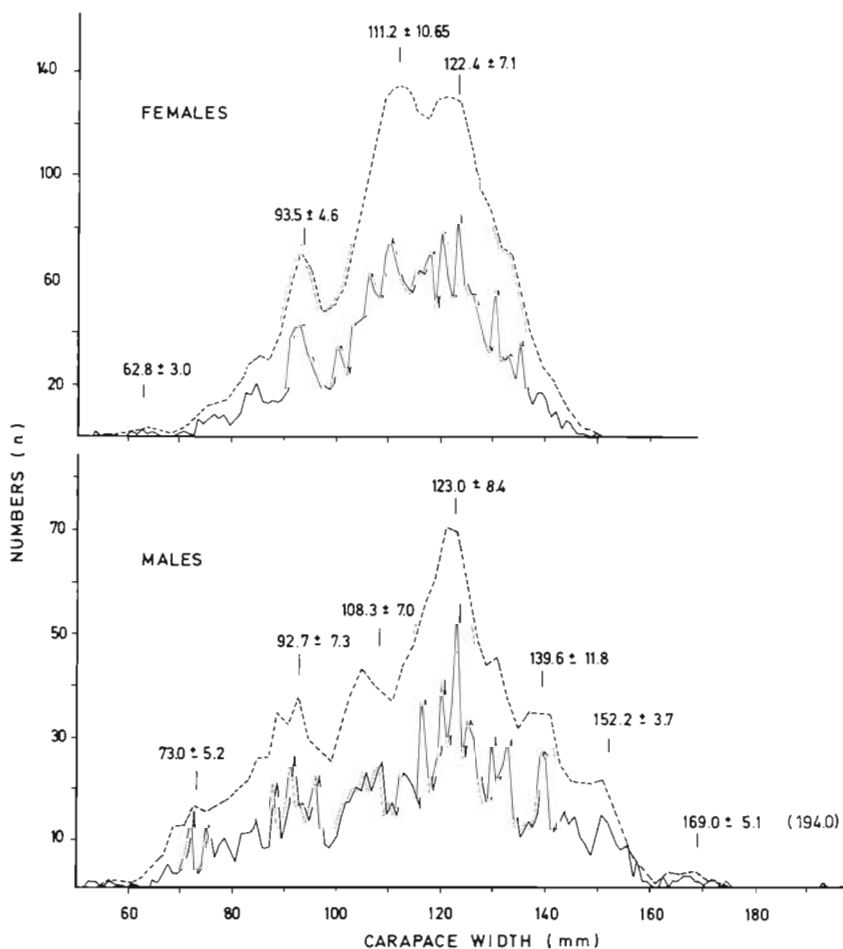


Fig. 6. *Cancer polyodon*. Total catch of females and males. (-----) 2 mm intervals smoothed by a running average over 3 intervals; (—) 1 mm interval; numbers correspond to size of instars

for females (2.56 compared to 1.85) (Fig. 8). The cohort analysis (Table 3) as well as the good fit of the quadratic regression to the catch curve data (Fig. 8)

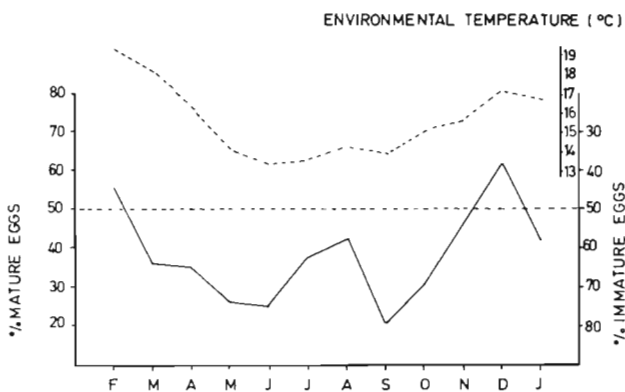


Fig. 7. *Cancer polyodon*. Proportion of mature and immature eggs of females and environmental temperature during the study period

indicate a general increase of *Z* with size for both sexes. Exploitation was heavy above 110 mm CW. Based on the age of first massive maturity, natural mortality was estimated as 0.80 and 0.74 for females and males respectively. Inserting the growth parameters calculated in this study and the mean annual water temperature of ca 14.5 °C into Pauly's formula resulted in *M*-values of 1.00 for females and 0.99 for males.

Population structure, mean annual biomass and density estimates

The mean annual biomass of females was 2.4 times greater than that of males (378 to 525 kg compared to 166 to 204 kg for the range of *M*-values used; Table 3). The size range of the captured specimens was different for both sexes. Females were caught from sizes of 55 mm CW onwards, while the smallest male measured 76 mm CW; the last length group that contributed a significant number of male specimens was 166 to 172 mm compared with 139 to 145 mm in females. Exploitation was more intense for

males than females over all intervals. Despite the large difference in total and spawning biomass between sexes, the yield of females was only 36 % higher than that of males, mainly due to higher average sizes and weights of males. The comparison of the pooled trap catches with the pooled diver catches did not show any significant differences (Fig. 9), indicating that the trap catches can be considered representative for the population structure in the study area. The monthly catches varied during the year in a similar way for females and males, being highest during the mid to late summer months (February to April) (Fig. 10). Thereafter they dropped markedly in May and increased slightly until August (females) and September (males) before reaching a second minimum in October.

The average density in the 4 transects of a total area of 600 m² was 0.15 ind. m⁻² (53.4 g fresh weight m⁻²). Average sex ratio (female:males) over the 4 transects was 2.3:1 (range from 1.5:1 to 3.0:1).

Table 2. *Cancer polyodon*. Size at massive maturity (CW_m) for males and females and its calculation by the method of Udupa (1986). ML_i = midlength of size-group i ; N_i = total no. in size-group i ; M_i = no. of mature specimens in size-group i ; $P_i = M_i/N_i$

ML_i	$\ln ML_i$	N_i	M_i	P_i	$\ln ML_{i+1} - \ln M_i$	$1 - P_i$	$P_i \frac{1 - P_i}{N_i - 1}$
Females							
83.5	4.4248	6	1	0.17	0.0353	0.83	0.0282
86.5	4.4601	6	1	0.17	0.0341	0.83	0.0282
89.5	4.4942	5	1	0.21	0.0330	0.80	0.0400
92.5	4.5272	13	4	0.31	0.0319	0.69	0.0178
95.5	4.5591	7	3	0.43	0.0310	0.57	0.0409
98.5	4.5901	6	3	0.50	0.0300	0.50	0.0500
101.5	4.6201	11	7	0.64	0.0291	0.36	0.0230
104.5	4.6492	10	7	0.70	0.0283	0.30	0.0233
107.5	4.6775	19	16	0.84	0.0275	0.16	0.0075
110.5	4.7050	7	6	0.85	0.0268	0.15	0.0213
113.5	4.7318	9	8	0.89	0.0261	0.11	0.0122
116.5	4.7579	8	7	0.88	0.0254	0.12	0.0151
119.5	4.7833	11	10	0.91	0.0248	0.09	0.0082
122.5	4.8081	12	11	0.92	0.0242	0.08	0.0067
125.5	4.8323	2	1	0.50	0.0236	0.50	0.2500
128.5	4.8559 ^a	2	2	1.00	–	0.00	–
Sum		134	88	9.91	0.0287 ^b	6.09	0.5724
Males							
116.5	4.7579	29	1	0.03	0.0085	0.97	0.0010
117.5	4.7664	25	8	0.32	0.0085	0.68	0.0091
118.5	4.7749	12	4	0.33	0.0084	0.67	0.0201
119.5	4.7833	21	1	0.05	0.0083	0.95	0.0024
120.5	4.7916	24	4	0.17	0.0083	0.83	0.0061
121.5	4.7999	21	10	0.48	0.0082	0.52	0.0124
122.5	4.8081	26	14	0.54	0.0081	0.46	0.0099
123.5	4.8162	42	30	0.71	0.0081	0.29	0.0050
124.5	4.8243	17	12	0.71	0.0080	0.29	0.0129
125.5	4.8323	21	8	0.38	0.0079	0.62	0.0118
126.5	4.8402	17	12	0.71	0.0079	0.29	0.0129
127.5	4.8481	10	6	0.61	0.0078	0.40	0.0267
128.5	4.8559	9	4	0.48	0.0078	0.52	0.0312
129.5	4.8637	10	5	0.50	0.0077	0.50	0.0278
130.5	4.8714	16	15	0.94	0.0076	0.06	0.0038
131.5	4.8790	9	8	0.89	0.0076	0.11	0.0122
132.5	4.8866 ^a	13	13	1.00	–	0.00	–
Sum		322	155	8.84	0.0080 ^b	8.16	0.2054
<i>Calculation procedure:</i> $\ln CW_m = X_k + X/2 - \sum P_i$ where $X_k = \ln$ size at which 100% of specimens are mature (^a); $X =$ average \ln size increment (^b). 95% confidence intervals (CI) = $\text{antilog} \left[\ln CW_m \pm 1.96 \sqrt{X^2 \sum P_i (1-P_i) / (N_i - 1)} \right]$							
<i>Results:</i> Females: $CW_m = 98.09$ (CI: 97.05 to 99.13) Males: $CW_m = 123.95$ (CI: 123.09 to 124.81)							

DISCUSSION

Growth, biometric relationships and size at massive maturity

The difference found in weight and asymptotic size for females and males of *Cancer polyodon* is a commonly reported feature of brachyuran crabs [Krouse (1972, 1976) for *Cancer irrotatus*; Donaldson et al.

(1981) for *Chionoecetes bairdi*; Gonzalez Gurriaran (1985) for *Macropipus puber*; Orensanz & Galucci (1988) for *Cancer magister*, *Cancer gracilis* and *Cancer productus*; Wenner & Stokes (1984) for *Menippe mercenaria*]. The similar growth found for immature specimens of both sexes in the laboratory (Fig. 3) has also been described for the brachyuran crabs in the above-cited reports. According to the von Bertalanffy growth curves calculated for laboratory-reared and wild spec-

imens, the former grew with a higher instantaneous growth rate (higher k -value) but approached a smaller asymptotic size (CW_{∞}) compared to the latter (Figs. 3 & 5). The higher growth rate could be attributed to more favourable food conditions in the laboratory (higher amounts and digestability of food, as only shell-free meat was supplied) and to the avoidance of energy expenditure for territorial behaviour and cannibalism. The smaller asymptotic size could indicate that space was growth limiting for larger specimens. We think that the simple and most widely used von Bertalanffy model reasonably describes the growth of *C. polyodon* (at least for the later juvenile and adult phases) because of the following: (1) visual inspection of the growth curves passing through the frequency histograms showed a reasonable fit (Fig. 5); (2) the ELE-FAN analysis yielded CW_{∞} -values for males and females of 198.0 mm and 160.5 mm respectively, near to the maximum sizes found in this study of 194.5 mm for males and 151 mm for females; (3) the growth oscillation found ($C = 0.4$) was consistent with the relationship with annual temperature found by Pauly (1984) for shrimps and fish and findings for other invertebrates of the same latitude, such as the scallop *Argopecten purpuratus* (Etchepare et al. 1989) and the sea urchin *Tetrapygus niger* (Stotz pers. comm.).

Male and female *Cancer polyodon* moult on an average 7 times during the first year, 3 during the second and 2 during the third year of life (Figs. 4, 5 & 6). The terminal moult seems to be 16+ in males and 14+ in

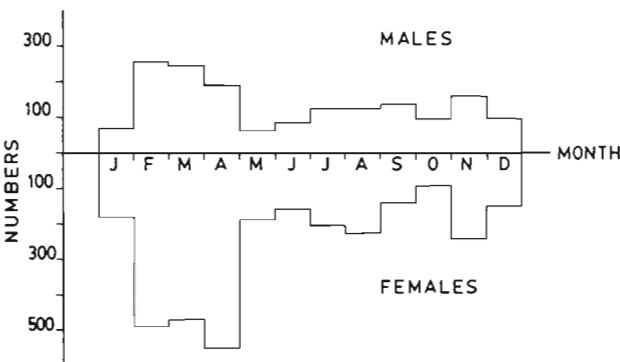


Fig. 9. *Cancer polyodon*. Size frequency of trap and diver catches

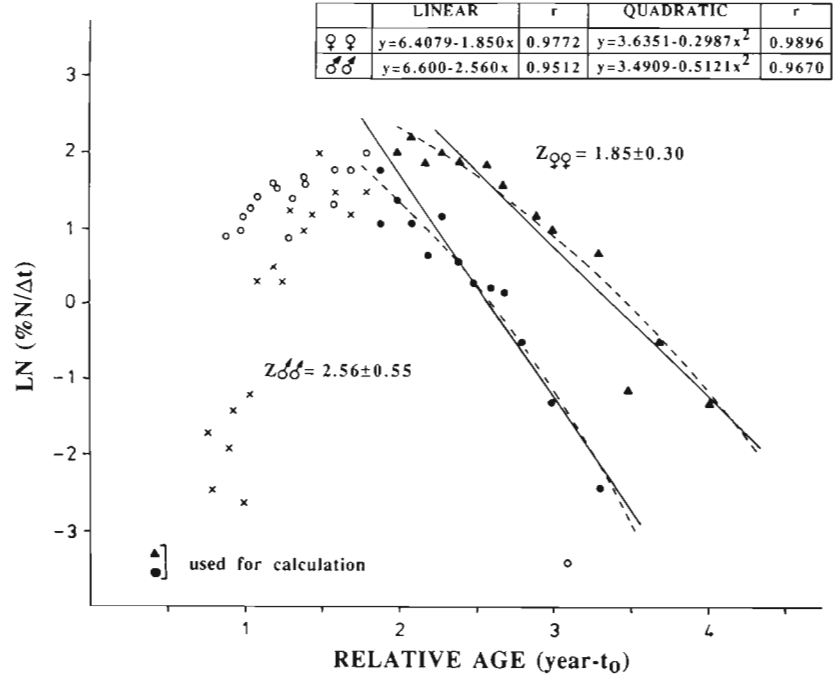


Fig. 8. *Cancer polyodon*. Catch curves for females and males with estimates of instantaneous rates of total mortality (Z). (—) Linear regression; (---) quadratic regression

females. Gutierrez & Zuniga (1976) reported only 15 instars for males of the same species. As the percentage of specimens of instar 16+ was very low in the present study (2 out of 1633), it is probable that the above authors did not find such large specimens during their study. Orensanz & Galucci (1988) found lower instar numbers for *C. magister* (13), *C. oregonensis* (11), *C. productus* (13) and *C. gracilis* (12) but cited reports of 16 instars for *C. magister* (Poole 1967, Collier 1983). Gonzales Gurriaran (1985) and Melville-Smith (1989) reported instar numbers of 17 for *Macropipus puber* and 16 for *Geryon maritae*. This indicates that instar

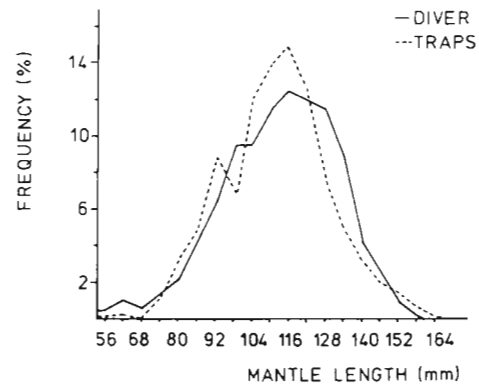


Fig. 10. *Cancer polyodon*. Monthly catches of females and males

Table 3. *Cancer polyodon*. Cohort analysis for females and males. *i*: size group. *ML_i*: midlength (cm); *W_i*: mean individual wet weight; *t_i*: time needed for an average individual to grow through size group; *C_i*: numbers caught; *N_i*: numbers reaching lower limit of size interval; *F_i*, *Z_i*, *M_i*: instantaneous rates of fishing, total and natural mortality; *E_i*: exploitation rate; *N_i*: average number in size group

<i>i</i>	<i>ML_i</i>	<i>W_i</i>	<i>t_i</i>	<i>C_i</i>	<i>N_i</i>			<i>F_i</i>			<i>Z_i</i>			<i>E_i</i>			<i>N_i</i>				
					<i>M=0.75</i>	<i>M=0.90</i>	<i>M=1.05</i>	<i>M=0.75</i>	<i>M=0.90</i>	<i>M=1.05</i>	<i>M=0.75</i>	<i>M=0.90</i>	<i>M=1.05</i>	<i>M=0.75</i>	<i>M=0.90</i>	<i>M=1.05</i>	<i>M=0.75</i>	<i>M=0.90</i>	<i>M=1.05</i>	<i>M=0.75</i>	<i>M=0.90</i>
Females																					
1	58	44.9	0.105	6	10725	14233	19135	0.01	0.00	0.00	0.76	0.91	1.06	0.01	0.00	0.00	10312	13580	18117		
2	64	59.2	0.111	10	9910	12947	17135	0.01	0.01	0.01	0.76	0.91	1.06	0.01	0.01	0.01	9504	12315	16166		
3	70	76.2	0.118	12	9108	11704	15235	0.01	0.01	0.01	0.76	0.91	1.06	0.01	0.01	0.01	8709	11095	14317		
4	76	96.0	0.127	50	8322	10507	13437	0.05	0.04	0.03	0.80	0.94	1.08	0.06	0.04	0.03	7914	9904	12554		
5	82	118.8	0.137	87	7519	9324	11711	0.09	0.07	0.06	0.84	0.97	1.11	0.11	0.07	0.05	7104	8731	10865		
6	88	144.9	0.148	132	6704	8162	10062	0.14	0.12	0.10	0.89	1.02	1.15	0.16	0.12	0.08	6280	7577	9253		
7	94	174.4	0.161	267	5875	7020	8489	0.31	0.26	0.22	1.06	1.16	1.27	0.29	0.22	0.17	5402	6403	7677		
8	100	207.5	0.177	221	4954	5822	6918	0.28	0.24	0.20	1.03	1.14	1.25	0.27	0.21	0.16	4530	5273	6204		
9	106	244.4	0.197	374	4130	4758	5539	0.52	0.45	0.39	1.27	1.36	1.45	0.41	0.34	0.27	3655	4176	4821		
10	112	285.2	0.221	464	3216	3642	4166	0.77	0.68	0.60	1.52	1.58	1.65	0.50	0.43	0.36	2732	3073	3489		
11	118	330.3	0.253	470	2297	2564	2887	1.00	0.90	0.80	1.75	1.80	1.86	0.57	0.50	0.43	1857	2060	2305		
12	124	379.7	0.294	446	1473	1622	1802	1.36	1.25	1.13	2.12	2.15	2.18	0.65	0.58	0.52	1097	1203	1330		
13	130	433.6	0.352	301	782	854	940	1.56	1.44	1.32	2.31	2.34	2.37	0.68	0.62	0.56	535	581	637		
14	136	492.1	0.440	168	336	365	398	1.83	1.70	1.57	2.58	2.60	2.62	0.71	0.65	0.60	201	217	237		
15	142	555.6	0.584	67	99	108	118	2.27	2.12	1.94	3.02	3.02	3.00	0.75	0.70	0.65	47	50	55		
16	148	624.1	0.874	6	10	12	14	1.04	0.90	0.76	1.79	1.80	1.82	0.58	0.50	0.42	5	6	7		
17	154	697.8	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Sum																					
Yield = 932 kg																					
Males																					
1	79	97.5	0.093	61	3301	3886	4585	0.21	0.18	0.15	0.95	1.08	1.19	0.21	0.16	0.15	3157	3697	4338		
2	85	122.3	0.098	83	3018	3514	4100	0.29	0.25	0.22	1.04	1.16	1.27	0.28	0.22	0.22	2868	3321	3855		
3	91	151.1	0.104	113	2724	3136	3620	0.42	0.37	0.32	1.17	1.27	1.37	0.36	0.29	0.29	2564	2938	3374		
4	97	184.1	0.110	90	2411	2748	3139	0.36	0.32	0.28	1.11	1.22	1.33	0.32	0.26	0.26	2269	2571	2921		
5	103	221.7	0.117	130	2133	2402	2713	0.52	0.50	0.45	1.31	1.40	1.49	0.43	0.36	0.36	1977	2216	2489		
6	109	264.1	0.125	127	1829	2039	2277	0.60	0.54	0.49	1.35	1.45	1.54	0.45	0.38	0.38	1683	1865	2072		
7	115	311.8	0.134	176	1545	1701	1879	0.95	0.87	0.79	1.70	1.77	1.84	0.56	0.49	0.49	1381	1515	1666		
8	121	365.0	0.14	231	1229	1342	1469	1.52	1.40	1.28	2.27	2.30	2.33	0.67	0.61	0.61	1048	1142	1248		
9	127	424.0	0.157	164	884	962	1049	1.39	1.28	1.18	2.14	2.18	2.23	0.65	0.59	0.59	752	815	885		
10	133	489.1	0.171	147	632	682	739	1.65	1.53	1.42	2.40	2.43	2.47	0.69	0.63	0.63	518	558	603		
11	139	560.7	0.188	120	418	449	483	1.92	1.79	1.67	2.67	2.69	2.72	0.72	0.67	0.67	328	352	378		
12	145	639.1	0.210	81	251	268	288	2.00	1.87	1.75	2.75	2.78	2.80	0.73	0.68	0.68	191	203	218		
13	151	724.5	0.237	69	139	148	159	3.08	2.89	2.70	3.83	3.79	3.75	0.80	0.70	0.76	92	98	105		
14	157	817.4	0.271	25	54	58	63	2.52	2.33	2.14	3.27	3.23	3.19	0.77	0.72	0.72	35	39	42		
15	163	918.1	0.318	4	21	23	26	0.75	0.69	0.63	1.50	1.59	1.68	0.50	0.43	0.43	17	18	20		
16	169	1026.8	0.385	8	13	14	15	1.75	1.57	1.40	3.48	3.47	3.45	0.78	0.74	0.74	7	8	8		
17	175	1143.9	0.486	2	3	3	3	1.75	1.60	1.45	2.50	2.51	2.49	0.70	0.64	0.64	2	2	2		
18	181	1269.7	0.661	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
19	187	1404.6	1.036	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
20	193	1548.9	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Sum																					
Yield = 599 kg																					
Mean annual biomass (kg)																					
Spawning biomass (kg)																					
					<i>M=0.75</i>					<i>M=0.90</i>					<i>M=1.05</i>						
					166	183	204	204	166	183	204	166	183	204	166	183	204	166	183	204	204
					55	60	64	64	55	60	64	55	60	64	55	60	64	55	60	64	

number may vary between species of brachyuran crabs.

The reduction of the absolute growth rate by about 50 % in both sexes of *Cancer polyodon* from instar 7+ to 8+ (Fig. 3) coincides with the intersection of the 2 fitted lines describing the premoult-postmoult relationship (Fig. 4). Donaldson et al. (1981) found a similar inflection point in the Hiatt diagram for *C. bairdi* within the same size range and attributed it to a change in lifestyle, i.e. migration to deeper waters. Perhaps the abrupt change in absolute growth in *C. polyodon* and the 'change in lifestyle' of *C. bairdi* are associated with a metabolic (hormonal) change marking the onset of gonad formation. The above-mentioned authors substantiate this, as they report a long time span (ca 2 yr) between ovary formation and appearance of orange ova in *C. bairdi*. While most female specimens of *C. polyodon* mature at instar 11+ (or 10+) and most males at instar 12+, some individuals seem to mature earlier. The smallest egg-carrying female measured only 67 mm and some males of little more than 70 mm CW had very big chelae, indicating maturity (Fig. 2).

Larger size at maturity, greater robustness, bigger chelae and larger size of males, as well as the predominance of females over most of the study period (Fig. 10) suggest a polygynous mating system in which one male might occupy and defend a group of females. This has been reported for species of *Cancer* by Cleaver (1949), Butler (1960), Snow & Neilson (1966) and Orensanz & Galucci (1988).

Spawning

Spawning peaked during July/August and November/December (Fig. 7) which coincides well with the observations of Gutierrez & Zuniga (1976) for the same species at Mejillones, about 800 km to the north of La Herradura Bay. They also found less intense spawning in winter (July to September) and a more intense spawning during the summer (January to April).

Mortality

Total mortality of both sexes ($Z = 2.6$ and 1.85 for males and females respectively) was low when compared with the calculated Z -value (9.2) for the heavily exploited Dungeness crab *Cancer magister* in British Columbia, Canada (Smith & Jamieson 1989). Gonzalez Gurriaran (1985) estimated Z -values of 1.53 for males and 1.79 for females for the commercially exploited crab *Macropipus puber* in Galicia, Spain, which are

close to our values. As seen from the cohort analysis (Table 3), and from Fig. 8, the Z -values tend to increase with size in both sexes. This could be due to either increasing fishing and/or higher natural mortality with age. Orensanz & Galluci (1988) found dead and moribund *C. productus*, *C. gracilis* and *C. magister* in the field and think that senescence might be the most important source of adult mortality in these species. Hankin et al. (1985) also observed increased mortality with age in female *C. magister* and attributed this partly to senescence with concomitant shell deterioration. Hill (1975) reported an increase in mortality from the second to third year of the portunid crab *Scylla serrata*. Our diving observations did not give evidence, however, that senescence is an important source for natural mortality in *C. polyodon* as moribund individuals of older ages were not found. Smith & Jamieson (1989) suggest that natural mortality might increase in *C. magister* as intermoult period increases. They demonstrated that a quadratic regression fitted the data of the catch curve slightly better than a linear regression coinciding with our results (Fig. 8). Fishing mortality could also have increased with size of *C. polyodon*, if the catchability of larger crabs is higher. Larger crabs can presumably walk faster and travel longer distances and therefore might have competitive advantages over smaller crabs when entering the trap. Diving observations suggest that larger crabs are better retained in traps because of their size and inferior swimming capacity. Our estimates for the instantaneous rates of natural mortality (M) were similar for both sexes but differed according to the method employed. Rikhter & Evanov's formula yielded lower M -values (by 20 to 25 %) than Pauly's formula. As both formulas employed were considered to yield only rough estimates for M , it seemed advisable to use an envelope of M -values for the cohort analysis (Table 3).

Population structure, mean annual biomass and density

The maximum biomass of males is near the size at massive maturity and displaced to the right of the size at massive maturity in females (Fig. 6). This suggests that natural selection favours offspring production over biomass maximization in females and coincides with the fact that females in general are smaller and less robust than males. The wide confidence intervals for the size-at-instar, as obtained from the Bhattacharya analysis (Fig. 6), indicate individual variability probably due to environmental heterogeneity or genetic variation.

During September and October, the catch was lowest (Fig. 10), possibly due to migration of females (and

males?) or burying into the sand after moulting. In these months the sex ratio approached 1:1, whereas it was 2 to 3 females per male during the rest of the year. Crabs < 55 mm CW were not caught in the study area (depth range ca 4 to 10 m), either by the traps or by the diver (Fig. 9). The smaller specimens used for the laboratory experiments (Fig. 3) had to be collected between rocks in the intertidal area. It thus appears that the megalopa larvae settle in this area and do not successfully invade the deeper sandy bottom area until they reach at least 55 mm CW. A very high proportion of small crabs in the stomachs of older individuals (Cerdeira & Wolff unpubl.) indicates strong cannibalism of smaller by larger crabs. The average crab density and biomass of 0.15 individuals or 53.4 g m⁻² on a total area of 600 m² found in May can be considered as a low limit estimate as May was a month of low captures (Fig. 10). Assuming proportionality to catches, density should have ranged between 0.15 and 0.5 crabs m⁻². As mean biomass for both sexes in the area effectively fished by the traps was estimated as 544 to 729 kg (Table 3), the extent of this area can roughly be estimated as 5964 m² (taking 0.3 crabs m⁻² and 637 kg as average density and biomass values).

Based on the Z-values estimated in this study, annual biomass production was thus about 1317 kg/5964 m² or 221 g crab biomass m⁻². Our density estimates are higher than those reported by Orensanz & Galucci (1988) for *C. gracilis* (0.026 to 0.096 as an average and 0.4 crabs m⁻² in exceptionally dense aggregates) and Gonzalez Gurriaran (1985) for *Macropipus puber* (0.0008 to 0.08 crabs m⁻² corresponding to 0.02 to 2.02 g fresh weight m⁻²).

The high biomass, density and production of *Cancer polyodon* in the study area suggest favourable food conditions (high densities and productivities of prey species).

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