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TITLE XII

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WORKING PAPER SERIES

Working Paper No. 47

"Comparative Study of Postlarval Life-History
Schedules in Four Sympatric Species of Cancer
(Decapoda: Brachyura: Cancridae)"

by

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PREFACE

The Bay of Nicoya is located on the Pacific coast of Costa Rica. It is the location of a cooperative research project on the stock assessment and the management of the artisanal fisheries in the bay. These fisheries are primarily on four species of the group known as corvinas. There is a commercial, quite industrialized fishery on shrimp in the mouth of the Bay and in the Pacific Ocean and a relatively small number of shrimp are also caught in the gillnets set for corvina. There are, in addition, other fisheries on molluscs and on crustacea in the Bay that are carried out entirely artisanally. These fisheries are soon to enter into the research sphere of the research project.

The methods and ideas presented in this working paper are derived primarily from Garrison Bay which is a north temperate homologue to the Bay of Nicoya. Both bays are shallow, subjected to seasonal input of fresh water and extremely muddy. Whereas many of the shallow parts of the Bay of Nicoya are bordered by mangrove or mangal, large parts of Garrison Bay's more shallow areas are covered by eel grass. Since it is well-known that many of the energy flow pathways in tropical and temperate water estuaries are highly dependent upon the structure and function of mangals and eel grass environments, respectively, we are able to take advantage of the Garrison Bay homologue.

Principle elements in the energetic pathways in both environments are macroinvertebrates such as the crustaceans (crabs) described herein. The methods presented in this report are not at all specific to the genus Cancer but are widely applicable to molting invertebrates, in general. For example, species in the genus Cancer to which we have applied the methods include individuals where maximum carapace size is 20 mm to another species whose maximum is an order of magnitude greater. Such methodology will be a valuable guide for data collection and analysis as our research project begins to include investigations of how the benthos contributes both in the energy pathways and in the artisanal fisheries.

COMPARATIVE STUDY OF POSTLARVAL LIFE-HISTORY SCHEDULES IN FOUR SYMPATRIC SPECIES OF *CANCER* (DECAPODA: BRACHYURA: CANCRIDAE)

José M. Orensanz and Vincent F. Gallucci

ABSTRACT

Size-at-instar, growth-per-molt, reproductive schedules, and morphometric allometries were investigated in four sympatric species of *Cancer* (*magister*, the Dungeness crab, *gracilis*, *productus*, and *oregonensis*) in Garrison Bay, North Puget Sound. Complementary observations were made on mating systems, mortality, habitat utilization patterns, and feeding. Numerical methods were successfully employed to discriminate instars in size-frequency distributions. Growth pattern, contrary to our expectation, was determinate in the four species. Geographic variation in prereproductive growth rate of *C. magister* is attributed to environmental factors. It is suggested that an independent stock may inhabit the Strait of Georgia-North Puget Sound area.

Observations on mating behavior suggest that these polygynic species have different types of mating systems, leaning towards resource defense in *C. oregonensis*, female defense in *C. gracilis* (and perhaps also in *C. productus*), and explosive breeding assemblages in *C. magister*. Degree of sexual dimorphism is consistent with this hypothesis. Adult males of *C. gracilis*, *C. productus*, and *C. oregonensis* have proportionally larger chelae than females; no significant dimorphism was detected in *C. magister*. Male *C. gracilis* and *C. productus* show two clear allometric phases in the chela-carapace size relation.

Contemporary studies of diversity within decapod guilds have frequently been done with food-resource partitioning as an explicit or implicit hypothesis. In contrast, we stress the importance of habitat, mating systems, and sexual selection as primary mechanisms underlying the diversification of this genus.

The paleontological record indicates that the genus *Cancer* originated during the Eocene, presumably in the Northeast Pacific, and was well diversified in the Miocene (about 15 million years ago) (Nations, 1975). Nations (1975, 1979) postulated a radiation from this area (center of origin) into the Northwest Pacific, the North Atlantic, the Southeast Pacific, and then to New Zealand. The genus is at present restricted to cold temperate waters, and is maximally diversified in the Northeast Pacific, where we conducted our studies.

Four species coexist in Garrison Bay (the study area), a small, shallow embayment in North Puget Sound. There are many publications dealing with one of them, *Cancer magister* (the Dungeness crab), but little is known about the other three (*C. productus*, *C. gracilis*, and *C. oregonensis*). Nevertheless, even for *C. magister* there are unexplained discrepancies between the life-history schedules reported for different geographic areas. One goal of the present study was to assemble and compare (within and between species) such schedules for the four species. Whenever possible we tried to

extend the discussion to other species in the genus, and to summarize alternative hypotheses that might explain regularities or unexpected discrepancies.

A second objective was to use the comparative approach to look at the processes underlying the diversification of the genus in the past, and the coexistence of congeners in extant guilds. Many contemporary studies of diversity within decapod guilds have been done with food-resource partitioning as an explicit or implicit hypothesis (see Lawton and Elnor, 1985, for *Cancer*). In contrast, we stress the importance of habitat, the structure of mating systems, and sexual selection as primary mechanisms underlying the diversification of this genus.

The Study Area

Garrison Bay (Fig. 1) is a small (2×1 km) and shallow (4 m maximum depth at MLW) bay on the northwest coast of San Juan Island, North Puget Sound. Our study was conducted on the east coast, in the English Camp National Historical Park. Large red algae (*Gigartina*) define the physiognomy of the central (deepest) part. The shal-

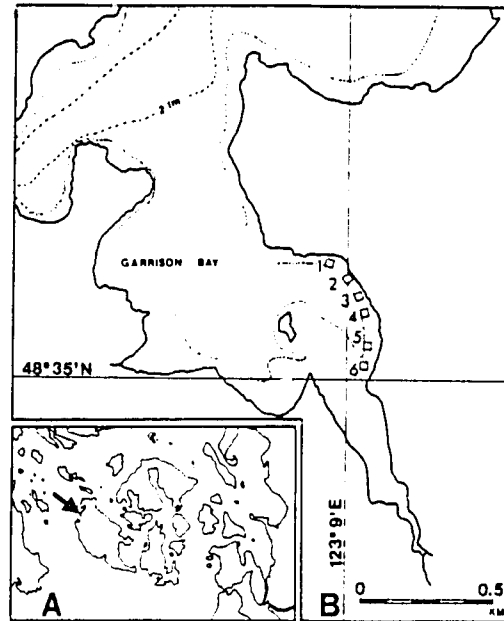


Fig. 1. The study area of four sympatric species of *Cancer*. A. San Juan Archipelago, North Puget Sound. B. Garrison Bay. Squares correspond to the large quadrats.

low subtidal belt is covered by eelgrass (*Zostera*) beds. Soft bottoms, ranging from sandy in the north to muddy in the south, predominate in intertidal and shallow subtidal zones. The flats are interrupted by occasional small rocky outcrops. Water temperature in the shallow subtidal zone ranges from 4°C in winter to 19°C in summer. Water overlying intertidal flats reaches freezing point during cold, nocturnal winter low tides. Salinity ranges from 26–28‰ (winter minimum) to around 30‰ (late summer), and can be lower in localized areas of fresh-water runoff.

The Species Guild

The four species of *Cancer* coexisting in the bay have a fossil record in the Northeast Pacific back to the Pliocene, and closely related counterparts occur in the Miocene of the same area (Nations, 1975, 1979). All of them range from California to Alaska, being distributed over the Oregonian and Aleutian biogeographic provinces (Table 1). Systematics, distribution, and natural history have been sketched by Holmes (1900), Way (1917), Weymouth (1910), Schmitt (1921),

Rathbun (1930), Knudsen (1964), Ricketts and Calvin (1968), Garth and Abbott (1980), and Hart (1982).

Patterns of microhabitat use observed by us in Garrison Bay are similar to those reported by Knudsen (1964) and Way (1917) in Puget Sound and by other authors (Cleaver, 1949; Hart, 1982; Schmitt, 1921) elsewhere; *C. magister* is always found in sand or muddy sand grounds, inshore and offshore; *C. gracilis* in eelgrass beds and in muddy bottoms of sheltered environments; *C. productus* in protected rocky outcrops and in areas of bays and estuaries where the bottom is composed of gravel, rocks, shells, or hard-packed sand; *C. oregonensis* in structurally complex substrates, like protected rocky areas, mussel and barnacle beds, and algal holdfasts.

Garrison Bay functions as a "nursery area" for *C. magister*. Megalopae settle in sandy areas in the north. Early benthic instars are restricted to intertidal and shallow subtidal areas. During daytime and low tides they seek refuge under objects lying on the beach, mostly stranded algae (a similar use of refugia was reported by Armstrong and Gunderson, 1985, for Grays Harbor). As the crabs grow, their range gradually expands to the subtidal and onto muddy areas to the south, where they overlap with *C. gracilis*. The latter was always observed in shallow subtidal muddy areas bordering the eelgrass belt. *Cancer productus* and *C. oregonensis* settle on spatially complex substrates (rocky outcrops, mussel and barnacle patches, etc.). *Cancer oregonensis* is restricted to these refuge-rich habitats for its entire life. *Cancer productus*, instead, leaves them as it grows, shifting to open grounds or to larger hiding places. Foraging areas of *C. magister*, *C. gracilis*, and *C. productus* overlap. Adults move into the intertidal zone during nocturnal high tides, feeding mostly upon polychaetes and bivalves. Interspecific aggressive encounters were never observed in the field. *Cancer oregonensis* and juvenile *C. productus* have similar habitat requirements. Structured substrates are in limited supply in the bay; their artificial expansion results in increased settlement of both species. Interference competition for refuge space, although not documented, is likely to occur.

MATERIAL AND METHODS

Measurements, Terms, and Abbreviations

Abbreviations are as follows: ChH, Chela Height (maximum height of the propodus, as in Nations, 1975, fig. 2, A); CL, Carapace Length (megalopae only, from tip to tip of the rostral and dorsal spines); CW, Carapace Width (tenth anterolateral spines always included); MCS, Minimum Copulating Size; MOS, Minimum Ovigerous Size (females only); MPS, Minimum Precopulatory Embrace Size (females only); OSR, Operative Sex Ratio; PW, maximum Pleon (abdomen) Width (measured only in females); SFD, Size-Frequency Distribution; and W, total Weight (measured only in live specimens with no missing or regenerating appendages).

The word "instar" always refers to crab instars, which are numbered starting from crab instar 1. Crab instars of *C. magister* are partitioned in 2 sets to facilitate comparison with other studies. Instars below and above an average carapace width of 100 mm are labeled, respectively, as "J" (for juvenile) and "A" (for adult), and denoted as "instar J number" or "instar A number." The last "J" instar (irrespective of its number) is denoted as "instar J-." We were not able to find the earliest crab instars of *C. gracilis*. Their numbering, in consequence, involves back-calculating average size-at-instar to a hypothetical crab instar 1. To denote this conditional identification, such instar numbers are followed by a character (for example: "instar 9").

When analysis of the relative growth of two structures reveals a change in the value of the allometric coefficients at some size, the two resulting patterns, groups are labeled (following adherence to the "size-equilibrium hypothesis" of Hartnoll, 1978b) "Phase 1" and "Phase 2" (or, equivalently, juvenile and adult phases).

Plots of postmolt versus premolt sizes are called "Hiatt Diagrams" (Hiatt, 1948; Somerton, 1980a) or "Gray-Newcombe Diagrams" (Botsford, 1985). If the parameters of a model fitted to a Hiatt diagram and the size of one instar ("anchor") are specified, the sizes of the other instars can be estimated. This extrapolation procedure is called "Hiatt-projection." When a breakpoint in the Hiatt diagram is identified (Material and Methods, *Growth Increments*), the corresponding premolt size is abbreviated "CW*."

When the life history of a year class is discussed, "Year 1" refers to the *calendar* year during which the megalopae settled to the bottom. Other "Years" are numbered subsequently. "Cohort" and "year class" are not used interchangeably, since some year classes are composed of more than one cohort.

Field Collections

Qualitative Collections.—Specimens were collected in the intertidal and upper subtidal zones, along the east coast of Garrison Bay, between 1981 and 1985. These included live and dead individuals, as well as molt casts. Deeper areas of the bay were trawled on 14 July 1984 and 9 September 1985.

Additional collections came from other localities around San Juan Island: Eagle Cove and False Bay (juvenile *Cancer magister*), the beach of the Friday Harbor Laboratories (*C. productus*), trawling by re-

Table 1. General information on the four species of *Cancer*, and their closest Miocene counterparts.

Subgenus	Species	Stratigraphic range	Present geographic range	Bathymetric range	Closest/oldest relative	Stratigraphic range	Geographic location of findings
<i>Cancer sensu stricto</i>	<i>productus</i> Randall, 1839	Middle Pliocene to Recent	Kodiak, Alaska, to Laguna Beach, California	0–80 m	<i>chaneyi</i> Nations, 1975	Middle Miocene to Upper Pliocene	San Joaquin Basin to Los Angeles
<i>Glochocarcinus</i> Nations, 1975	<i>oregonensis</i> (Dana, 1852)	Middle Pliocene to Recent	Pribilof Island, Alaska, to Santa Barbara, California	0–136 m	<i>affinis</i> Nations, 1975	Middle Miocene to Upper Pliocene	Coos Bay, Oregon, to San Diego
<i>Metacarcinus</i> Milne Edwards, 1862	<i>magister</i> Dana, 1852	Lower Pliocene to Recent	Unalaska, Alaska, to Monterey Bay, California (*)	0–180 m	<i>coosensis</i> Nations, 1975	Middle Miocene to Lower Pliocene	Coos Bay, Oregon, to Central California
<i>Metacarcinus</i> Milne Edwards, 1862	<i>gracilis</i> Dana, 1852	Upper Pliocene to Recent	Prince William Sound, Alaska, to Gulf of Viscaño, Baja California	0–143 m	<i>dauidi</i> Nations, 1968	Middle Miocene to Middle Pliocene	San Joaquin Basin, California

(*) An old record from Magdalena Bay, Baja California, remains unconfirmed. There is a recent record of a single specimen from Japan.

Table 2. Dimensions of the large plots in Garrison Bay, San Juan Archipelago, North Puget Sound (locations shown in Fig. 1).

Plot	Area (m ²)	
	Upper half (midintertidal)	Lower half (low intertidal)
1	253	253
2	197	219
3	191	356
4	190	190
5	140	140
6	180	180

search boats (adult *C. oregonensis* and *C. gracilis*), and the water supply system of the laboratory (megalopae and juveniles of *C. oregonensis* and *C. productus*).

Measurements taken from each specimen included CW (always recorded), ChH, PW, and W. The latter three were sometimes omitted due to time or logistic limitations. Also recorded were sex, missing or regenerated appendages, general condition of the shell, and (for females) presence/absence and condition (color, degree of extrusion and hatching) of the egg mass. Special attention was paid in the field to the observation of mating activity. Pairs found in precopulatory embraces were taken to the laboratory, and kept until the female molted and hardened. Partners recoupled soon after being placed in tanks with running sea water.

Quantitative Samples.—Large plots were marked in the middle and low intertidal (Fig. 1, Table 2). Each plot was partitioned into upper and lower halves. Plots were scanned in low-mid tide on 15 occasions between February 1983 and June 1984. Crabs sampled within each plot were taken to the laboratory, measured, and released in their areas of origin. One or two pereopodal dactyls of the individuals returned to the field were clipped following a coded pattern. The clip removed half of the dactyl, and was recognizable after at least one molt.

A different quantitative sampling routine was conducted in the north sector during 1984, its purpose being to investigate the pattern of recruitment of *C. magister*. Only the SFDs were utilized in this study.

Laboratory Observations

Megalopae of *C. productus* and *C. oregonensis* were obtained from the water system of the Friday Harbor Laboratories during the summers of 1982 and 1983. Part of the megalopae were preserved, and part were individually raised in small screen containers with running sea water. When hardened, some crabs in each instar (as well as molt casts) were stored in 70% ethanol. Carapace outlines of megalopae and crab instars 1–4 were drawn with a camera lucida attached to a stereoscopic microscope, and measured.

Growth of juvenile *C. magister* was closely monitored from late spring to early fall of 1982, and instar-specific information was obtained from several samples brought alive from the field and kept under laboratory conditions for variable periods of time. Pre- and postmolt size and sex were recorded for each molting episode. A detailed log of molting dates was kept

for 2 subsamples: (a) 19 instar J1 specimens brought from Eagle Cove in May 1982, for which growth was followed through instar J3, and (b) 76 instar J4 crabs brought from Garrison Bay on 18 June 1982, among which 20 reached instar J9. Both batches corresponded to a single cohort of the 1982 year class; no significant difference in size of instar J3 was found between subsamples from the two sites.

Crabs of the 4 species were brought from the field and kept in tanks with running sea water (fed with clam meat) for variable periods of time, usually until they molted. Precopulatory embracement and female molting were frequently observed for all the species. Pre- and postmolt sizes, information on mating partners, and general ancillary information were routinely recorded. In total, 443 molting events were fully documented.

Data Analyses

Growth Increments.—Allocation of increment observations is summarized in Table 3. Straight lines were fitted to Hiatt diagrams according to the following three models (Somerton, 1980a):

$$Y_i = A + BX_i + \epsilon_i \quad (1)$$

$$Y_i = A - BX_i + \epsilon_i \quad \text{for } X_i < X^* \quad (2)$$

$$Y_i = C + DX_i + \epsilon_i \quad \text{for } X_i > X^* \quad (3)$$

$$Y_i = A - BX_i + \epsilon_i \quad \text{for } X_i < X^* \quad (3)$$

$$Y_i = Y^* + D(X_i - X^*) + \epsilon_i \quad \text{for } X_i > X^*$$

$$Y^* = A - BX^*$$

where X_i and Y_i are the i -th pair of pre- and postmolt size observations; ϵ_i is an error term assumed to be distributed as $N(0, \sigma^2)$; and A , B , C , D , and X^* are free parameters. Program HIATT (Somerton, 1978) was used to estimate the parameters in models (1) and (3). A statistical test was used to determine whether model (3) fitted the data better than model (1). The test statistic (Draper and Smith, 1966; Somerton, 1978) is:

$$F = \frac{(RSS1 - RSS3)/2}{RSS3/(N-3)} \quad (4)$$

where $RSS1$ and $RSS3$ are the residual sum of squares (RSS) for, respectively, models (1) and (3), and N is the number of data points. This statistic is distributed as F with 2 and $N-3$ degrees of freedom. Model (2) was fitted to assist in comparisons with earlier studies.

Somerton (1980a) compared model (3) with model (2) and with a hyperbolic model proposed by Mauchline (1976) and concluded that model (3) is superior to both. Botsford (1985) noted that the difference in the quality of the fittings is so small that it is largely irrelevant. We made use of model (3), when appropriate, for two reasons: it yields information on size at sexual maturity in females, and is easily combined with polymodal SFD dissection methods (Material and Methods, *Size-Frequency Distributions*).

Changes in Relative Growth.—Growth of ChH (in both sexes) and PW (in females only) relative to CW was described by the allometric equation [$Y = aX^b$]. All the analyses were done with log-transformed measurements [$\log(Y) = \log(b) + a \cdot \log(X)$]. The analyses were done in two steps: (a) to determine whether there is

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significant size-dependent change in the value of the allometric coefficients (Hartnoll, 1978b), and (b) to discriminate the phases and estimate the value of the allometric coefficients in each phase (Hartnoll, 1978b; Somerton, 1980b).

There is no recipe for the first step. The size range over which both allometric phases overlap is estimated in different ways depending on the type of information available (Hartnoll, 1978b). We took two approaches:

(a) An algorithm similar to program HIATT (Material and Methods, *Growth Increments*) was used to partition the data pairs into two groups, and to determine whether two lines (one for each partition) fit the data significantly better than a single line. If they do, this is a good indication of the existence of two allometric phases. The opposite is not true: if two lines were not to fit the data significantly better than one (for any partition), it would not unequivocally establish the presence of only one allometric phase, due to the usually high size overlap between phases. This approach was suggested to us by Dr. D. Somerton (personal communication).

(b) A second approach was used only for the [ChH: CW] relationship. We found no evidence of multiple allometric phases for the chelae of the females. Therefore, an assessment can be done by inspecting plots of observed male ChH residuals versus CW, using the line fitted to female data (Results, *Males: Carapace-Chela Allometry*). This graphical method was previously used by Weymouth and Mackay (1936, fig. 3).

When the existence of two allometric phases was detected and a size range of overlap could be assessed, we used program MATURE (Somerton, 1979, 1980b) to fit the allometric model to the two groups and to classify the points within the overlap zone. The program assigns crabs to either of the two phases using nonhierarchical cluster analysis.

Size-Frequency Distributions (SFD).—Computer programs structured along the lines suggested by Macdonald and Pitcher (1979) and Schnute and Fournier (1980) were adapted or written to analyze SFDs (see these publications for a detailed presentation of the general approach). Listings of FORTRAN subroutines and a worked example are available from the authors upon request.

It is assumed that the observed SFD is a mixture of K normal distributions, one for each of K instars in our particular case. The mean, variance, and relative abundance of each component distribution in the mixture are then estimated. Data from a sample were grouped over M size intervals (not necessarily equal). The theoretical distribution was fitted by finding parameter values that minimize the discrepancy between the theoretical distribution and the observed histogram. Discrepancy was measured by

$$-2n \sum_{j=1}^M \hat{p}_j \log(\hat{p}_j / \bar{p}_j) \quad (5)$$

where \hat{p}_j denotes the theoretical probability that an individual belongs to the j th size interval, n is the total number of individuals in the sample, n_j is the number that fall into the j th size interval, $[\hat{p}_j = n_j/n]$ is the observed relative frequency of the j th size interval, and ϕ is a $R \times 1$ array of parameters. Minimization of (5)

Table 3. Allocation by species and sexes of growth increment observations in *Cancer*. Range of premolt size (CW) between parentheses.

Species	Males	Females	Unsexed juveniles
<i>C. magister</i>	77 (7, 80)	67 (21, 110)	67 (6, 50)
<i>C. gracilis</i>	31 (12, 80)	63 (26, 86)	—
<i>C. productus</i>	30 (7, 85)	39 (16, 84)	—
<i>C. oregonensis</i>	24 (8, 32)	45 (10, 40)	—

or a chi-square criterion leads to approximately the same estimates with the same asymptotic statistical properties. The minimized value of either criterion can be used to test the goodness-of-fit of the model. The null distribution is asymptotically chi-squared with $M - R - 1$ d.f.

All our programs alternate between iterative calculations and constrained direct-search optimization, for which the Nelder-Mead (SIMPLEX) algorithm was used. Three basic procedures were tried, in which the following parameters were estimated by the direct-search method:

(a) The means and standard deviations (Macdonald-Pitcher's method).

(b) The two parameters of a Hiatt line, one mean, the two parameters of a linear relationship between means and standard deviations, and $K - 1$ proportions. This parallels the Schnute-Fournier approach, with the difference that growth structure is introduced by means of the Hiatt line instead of the von Bertalanffy growth model.

(c) The means, and the two parameters of a linear relationship between means and standard deviations. A hybrid of the preceding two yielded the best results: rapid convergence to meaningful parameter combinations, with relative economy of degrees of freedom. (In (a) and (c) the direct search alternated with iterative calculations for the estimation of the proportions.)

Assumptions of normal SFD for individual instars, and of a linear relationship between means and standard deviations ($\sigma = a + b\mu$), were empirically supported by data from laboratory reared cohorts. Hiatt diagrams provided ancillary information to evaluate K (the number of instars in the mixture), and to project means and variances (Nicholson, 1979).

Data from Other Published Studies.—CL of megalopae were extracted from illustrations in publications dealing with larval development, using the graphic scales provided by the authors.

CW data from authors who excluded the tenth anterolateral spines in measurements of *C. magister* were converted with the relationship:

$$Y = -0.029 + 1.0715X \text{ (Butler, 1961),}$$

where X and Y are the respective widths excluding and including the spines.

The growth scheme for Dungeness crab in Grays Harbor (Discussion, Intraspecific Variation in *Cancer magister*) was assembled using size-at-instar figures and illustrations given by Cleaver (1949). Part of the data in his fig. 4 were digitized.

Table 4. Coefficients of linear models fitted to Hiatt diagrams, and statistical comparisons.

A. Coefficients estimated by fitting one line (model 1) and two lines (model 3) to female Hiatt diagrams.									
Species of Cancer	CW*	One line fitted (model 1)			Two lines fitted (model 3)				
		N	Slope	Intercept	Lower line			Upper line	
					N	Slope	Intercept	N	Slope
<i>magister</i>	92	67	1.21	3.39	63	1.27	0.95	4	0.61
<i>gracilis</i>	46	64	1.04	11.16	15	1.38	-2.97	49	0.93
<i>productus</i>	40	39	1.27	1.77	18	1.38	-1.43	21	1.23
<i>oregonensis</i>	45	23	1.08	3.11	27	1.19	1.25	18	0.97

B. Tests of whether two straight lines (model 3) fit female Hiatt diagrams significantly better than a single straight line (model 1); RSS1 and RSS3: residual sums of squares of, respectively, models 1 and 3.						
Species of Cancer	N	RSS1	RSS3	F	d.f.	Significance
<i>magister</i>	67	741.5	537.5	12.15	2,64	**
<i>gracilis</i>	64	239.9	114.6	33.36	2,61	**
<i>productus</i>	39	190.0	178.5	1.16	2,36	NS
<i>oregonensis</i>	45	68.8	60.1	3.02	2,42	NS

C. Comparison of straight lines fitted to male and prepuberty female Hiatt diagrams (covariance analyses).						
Species of Cancer	Groups compared	Interactions		Factors		d.f.
		F	Significance	F	Significance	
<i>magister</i>	females < 93 and males	3.77	*	—	—	1,136
<i>gracilis</i>	females < 46 and males	1.24	NS	1.35	NS	1,43
<i>productus</i>	females and males	1.03	NS	1.50	NS	1,65
<i>oregonensis</i>	females and males	7.27	**	—	—	1,65

D. Coefficients estimated for straight lines fitted to Hiatt diagrams, models (1) and (2).				
Species of Cancer	Group	N	Intercept (SE)	Slope (SE)
<i>magister</i>	males	77	1.044 (0.510)	1.273 (0.013)
<i>magister</i>	females < 93	64	1.074 (0.889)	1.270 (0.019)
<i>gracilis</i>	males and females < 49	47	1.866 (0.949)	1.239 (0.023)
<i>gracilis</i>	females > 49	43	17.264 (1.339)	0.940 (0.022)
<i>productus</i>	males and females	69	1.088 (0.851)	1.293 (0.017)
<i>oregonensis</i>	males	24	0.772 (0.629)	1.195 (0.035)
<i>oregonensis</i>	females > 10	45	3.105 (0.574)	1.076 (0.025)

RESULTS

Growth Increments

No evidence was found for a change in male growth-increment patterns within the size ranges explored. Models (2) and (3) (two lines) did not fit the data better than a single straight line. For *C. magister* the data did not extend to the sizes where a change might be expected, and this is probably the case also for *C. productus*.

Model (3) (two lines) fitted the data significantly better than model (1) (a single line) for the females of *C. magister* and *C. gracilis* (Table 4A, B). The premolt carapace width corresponding to the intersection point of the two lines (CW*) was 92 mm for *C. magister* and 46 mm for *C. gracilis*. The number of observations for *C. magister* larger

than 93 mm (premolt size) was insufficient to estimate reliably the parameters of a linear model for the postpuberty females.

Model (3) (two lines) did not significantly improve the fit of the data for the females of *C. oregonensis* and *C. productus* (Table 4A) when compared with model (1) (one line). In *C. productus* the lack of a break-point cannot be explained solely by the size range explored. In *C. oregonensis* the size range (10–40 mm) may be above the break-point, as suggested by the high value of the intercept in model (1) (Table 4D) and by the fact that MOS = 10 mm (Results, *Observed MOS and MCS, and Consistency with Morphometric Results*).

Covariance analysis was used to compare the lines fitted to males and prepuberty fe-

Table 5. Morphometric allometries. CW': carapace width at which the partition into two groups yields the lowest SS.

A. Male chelae: exploration of allometric phases with Somerton's method.										
Species of <i>Cancer</i>	Size range	CW'	Lower line			Upper line		F	d.f.	Signifi- cance
			Intercept	Slope	d.f.	Slope	d.f.			
<i>magister</i>	8-187	—	(no significance minimum found for the total SS, $N = 302$)							
<i>gracilis</i>	11-114	61	-1.80	1.08	137	1.21	186	16.48	2,323	**
<i>productus</i>	7-160	76	-1.92	1.10	57	1.26	43	10.32	2,100	**
<i>oregonensis</i>	8-42	22	-1.57	1.16	52	1.32	56	0.97	2,108	NS

B. Male chelae: results of fitting two lines (one to each allometric phase) with program MATURE.										
Species of <i>Cancer</i>	Boundaries (CW, in mm)	Lower line			Upper line			F	d.f.	Signifi- cance
		Intercept	Slope	N	Intercept	Slope	N			
<i>gracilis</i>	70, 85	-1.92	1.11	240	-1.67	1.07	198	41.174	2,434	**
<i>productus</i>	70, 87	-1.87	1.08	64	-2.00	1.13	39	18.688	2,99	**

C. Female pleon: exploration of allometric phases with Somerton's method.										
Species of <i>Cancer</i>	Size range	CW'	Lower line			Upper line		F	d.f.	Signifi- cance
			Intercept	Slope	d.f.	Slope	d.f.			
<i>magister</i>	15-181	93	-2.83	1.28	56	1.52	52	30.48	2,108	**
<i>gracilis</i>	26-106	44	-3.64	1.62	7	1.34	428	12.82	2,435	**
<i>productus</i>	16-128	43	-2.88	1.33	41	1.44	59	3.57	2,100	*
<i>oregonensis</i>	9-45	18	-1.73	1.07	42	1.19	81	0.51	2,123	NS

males of *C. magister* and *C. gracilis*, and to males and females (all sizes) of *C. productus* and *C. oregonensis* (Table 4C). The slopes were significantly different between males and prepuberty females of *C. magister*, and between males and females of *C. oregonensis*. No significant difference was found between males and prepuberty females of *C. gracilis*, or between males and females of *C. productus*. Consequently, data for males and prepuberty females of *C. gracilis*, and of male and female *C. productus*, were respectively pooled. The statistically significant difference between young male and female *C. magister* appears to be of little biological relevance for our study.

Table 4D contains the parameters estimated for models (1) and (2). Although model (3) is formally more appropriate than model (2), we include parameters estimated for the latter because it was previously used for species of *Cancer*.

Size of Sexual Maturity

Males: Carapace-Chela Allometry.—No indication of sexual dimorphism or allometric phases was found in *C. magister* (Fig. 2, Table 5A) within the size range studied, which extends generously below and above

the size of sexual maturity inferred from reproductive behavior.

In *C. gracilis* and *C. productus* there is good evidence of the existence of two distinct phases (Fig. 2, Table 5A, B). These overlap over the size range (70–85 mm) for *C. gracilis* and (70–87 mm) for *C. productus*. Table 5B contains the coefficients of the allometric equation estimated for each of the phases, for the two species, using program MATURE.

In *C. oregonensis* the graphical method (Fig. 2) showed clear sexual dimorphism expressed earlier than in the other species. Neither the graphical method (Fig. 2) nor Somerton's method (Table 5A) revealed clear allometric phases.

Females: Carapace-Abdomen Allometry.—The analyses showed evidence of two phases in *C. magister*, *C. gracilis*, and *C. productus* (Table 5C). No such evidence was found for *C. oregonensis*, but for this species the size range of the females measured (9–45 mm) is probably above the puberty molt (MOS = 10 mm).

Observed MOS and MCS, and Consistency with Morphometric Results.—Measured size ranges of crabs involved in reproductive activities are summarized in Table 6.

Table 6. Measured size ranges of crabs involved in reproductive activities (sample sizes between parentheses).

Species of <i>Cancer</i>	Mating males	Females in precopula	Ovigerous females
<i>magister</i>	135 (2)	107–109 (2)	151–172 (3)
<i>gracilis</i>	71–111 (58)	39–85 (61)*	54–100 (242)
<i>productus</i>	64–147 (11)	49–114 (9)	70–129 (7)
<i>oregonensis</i>	25–41 (15)	17–35 (19)	10–43 (37)

* Excluding a single, outlying (CW = 39 mm) precopulating female *C. gracilis*, the remaining 60 females were larger (CW > 47 mm).

No morphological correlate of the size at sexual maturity was found in the males of *C. magister*. For *C. productus* and *C. oregonensis* MCS was close to or slightly below the lowest boundary of the range of overlap between the two allometric phases, indicating that change in relative chela height is related to sexual maturity.

Females of *C. magister* show a significant change in both relative growth-per-molt and abdominal width at (CW* = 93 mm). This is the average size of instar J+ (Results, Size-at-Instar Schedules). Observed MPS corresponds to the next instar (A1). This suggests that at least some females mate one instar late with respect to the expression of size-dependent morphological changes usually associated with the onset of sexual maturity.

In females of *C. gracilis* MPS (47 mm), CW* (46 mm), and the average size at which there is an increase in relative abdominal width (44 mm) are all very close to each other, suggesting that these morphological changes are effectively associated with puberty. MPS and average size of abdominal enlargement were, respectively, 49 and 43 mm in the females of *C. productus*, showing a pattern similar to that of *C. gracilis*. The difference between abdominal allometric phases, however, was less defined.

Size-at-Instar Schedules

Megalopae of *C. productus* and *C. oregonensis* were similar in size (CL ~ 4.2–4.3 mm). Megalopae of *C. magister* were much larger, up to (CL = 9.3 mm). We were unable to obtain megalopae of *C. gracilis*.

The first column of Tables 7 and 8 summarizes the size-at-instar data for laboratory-reared instars 1–4 of *C. productus* and *C. oregonensis* raised from megalopae obtained from the laboratory water system.

Tables 7–10 present the size-at-instar schedules resulting from the dissection of

polymodal frequency distribution of individuals of the four species collected in Garrison Bay. Goodness of fit tests led in all cases to rejection of the hypothesis that the differences between the observed and estimated SFDs were statistically significant ($P < 0.05$). For each size-at-instar vector we also present the corresponding Hiatt-projected size-at-instars (Tables 7–10). Back-calculated (extrapolated) average size-at-instar starting from field averages match closely the size-at-instar from the laboratory reared animals, making it possible to number the instars discriminated in the field SFDs. Table 11 contains coefficients for straight lines fitted to the (CW:W) relationship using log-transformed values. These can be used to convert size-at-instar schedules into weight figures.

The first field of Table 9 contains size-at-instar corresponding to laboratory-reared *C. magister* of the 1982 year class (cohort A: Results, *Cancer magister*), instars J2–J6. They closely match the schedule of the laboratory-reared group (instars J1–J9) and the Hiatt-projection (Table 9). This particular cohort went through 9 J-instars. The initial size of the 1984 year class (cohort A) was smaller than that of its 1982 homologue (which also settled earlier). Size-at-instar were consequently lower, suggesting the possibility of some interannual variability in the number of J-instars (9 or 10). This also points to the risk of pooling animals of different cohorts in SFD analyses: the mixture can lead to an overestimation of the number of instars. No difference was found between males and females of the J-instars. Size-at-instar for A-instars are summarized in Table 12.

No specimens of the earliest instars of *C. gracilis* were available for this study. The size at instar 1 can to some extent be guessed from the literature. Table 13 summarizes sizes of the megalopae of several species.

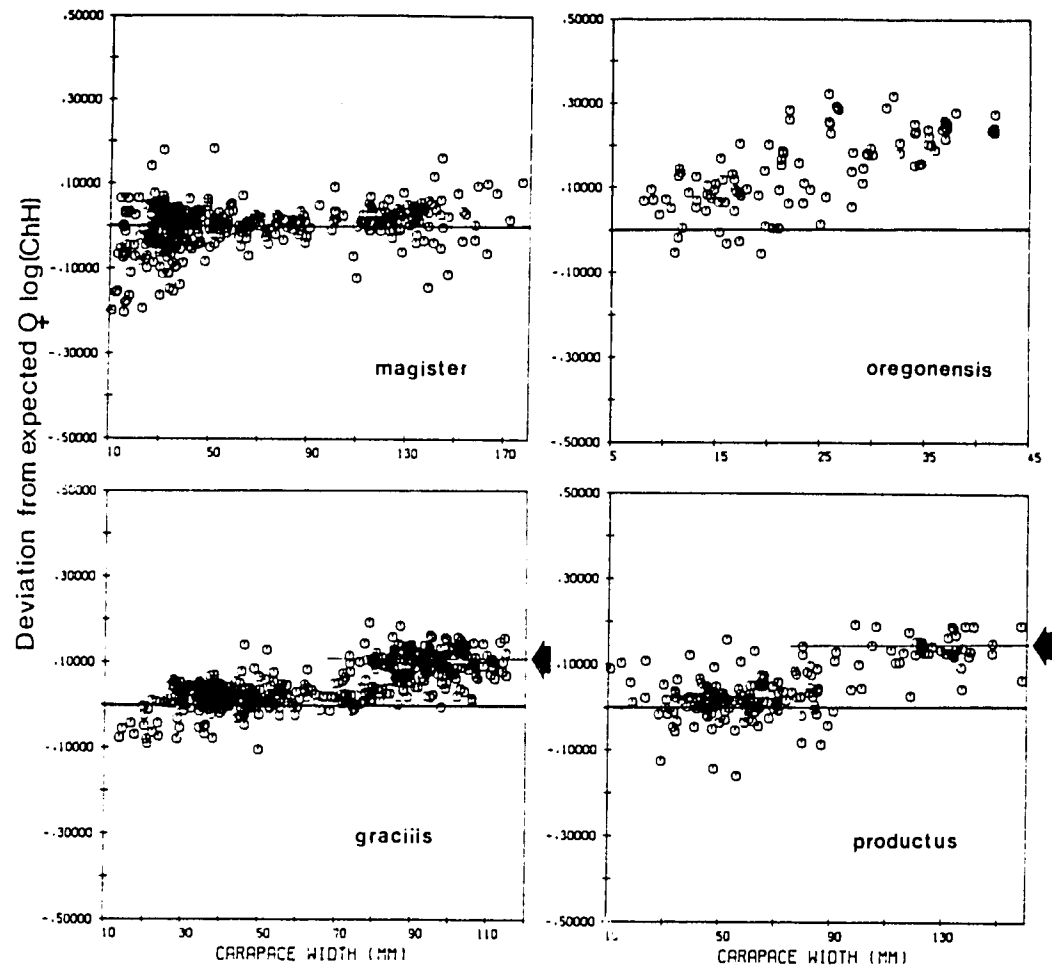


Fig. 2. Size-dependent deviations of male $\log(\text{ChH})$ from expected female $\log(\text{ChH})$, showing male allometric phases and sexual dimorphism in the size of the chelae. Arrows indicate phase 2 (adult) in *Cancer gracilis* and *C. productus*.

Instar 1 can be expected to fall in the interval ($2 \text{ mm} < \text{CW} < 3 \text{ mm}$). Average size of the first modal group of the 1982 cohort that could be discriminated in the SFD was ($\text{CW} \sim 30 \text{ mm}$). Smaller specimens were available, but not in numbers large enough to estimate average instar sizes. Back-calculating the size-at-instar schedule from the Hiatt diagram, the smallest group discriminated in the SFD was assumed to be instar 7' (Table 10). If our guess for instar 1 is correct, the 1982 cohort went through 12 instars. The size estimated for male instar 11' is an underestimate. This group was poorly represented in our samples, due to the fact that the 1981 year class (to which most of our data correspond) went through instar 11 during the fall of 1982, a period

for which we have very few observations. The specimens measured were obtained during late summer, were the first to enter the instar, and for that reason were the smallest within it. Instar 11' aside, males and females started to diverge in average size by instar 9', which corresponds to the onset of female sexual maturity (Results, *Observed MOS and MCS, and Consistency with Morphometric Results*).

Different pieces of information allowed the assembly of complete schedules for *C. productus* and *C. oregonensis* (Tables 7, 8). Male *C. productus* in instars 9–12 were $\sim 4 \text{ mm}$ larger than their female counterparts. The average size at instar 13 could not be adequately assessed due to the scarcity of large specimens in the main study area. No

Table 7. Average size-at-instar: *Cancer productus*. \bar{x} and Hiatt-projections correspond to CW. Anchor for the Hiatt-projections underlined. a and b: coefficients of linear relationship between means and standard deviations of the component distributions in the mixture. Projection of male size-at-instar done with straight line fitted to male data alone. $Y_i = 0.651 + 1.307X_i$.

Instar	Juveniles (laboratory-reared)			Males			Females	
	\bar{x}	SD	N	Field (SFD)		Hiatt-projection	Field (SFD)	
				\bar{x}	P		\bar{x}	P
1	3.74	0.20	98	—	—	(3.7)	—	—
2	5.73	0.34	30	—	—	(5.5)	—	—
3	8.01	0.75	15	—	—	7.9	—	—
4	11.62	1.04	5	—	—	10.9	—	—
5	—	—	—	—	—	15.0	—	—
6	—	—	—	—	—	20.2	—	—
7	—	—	—	—	—	27.1	—	—
8	—	—	—	—	—	36.1	—	—
9	—	—	—	46.0	0.24	47.7	42.0	0.39
10	—	—	—	63.0	0.30	<u>63.1</u>	58.7	0.28
11	—	—	—	82.0	0.17	83.1	78.1	0.13
12	—	—	—	109.9	0.03	109.3	107.3	0.07
13	—	—	—	128.8	0.26	143.5	117.8	0.13
a	—	—	—	-0.821	—	—	-0.711	—
b	—	—	—	0.108	—	—	0.104	—
χ^2	—	—	—	15.3	—	—	23.9	—
d.f.	—	—	—	16	—	—	18	—
N	—	—	—	201	—	—	199	—

significant difference was found between average size-at-instar of male and female *C. oregonensis* of instars 5–10 (Table 8); the result of pooling sexes is shown in the last column of Table 8.

Maximum known sizes for the four species are summarized in Table 14. We report

maximum size records for female *C. magister*, *C. gracilis*, and *C. productus*.

Mortality

Little information was obtained in the field on sources of mortality for juvenile crabs. Cannibalism occurs among young-of-

Table 8. Average size-at-instar: *Cancer oregonensis*. Conventions as in Table 7. Hiatt-projection of males utilized parameters shown in Table 4D.

Instar	Juveniles (laboratory-reared)			Males			Females		Pooled sexes	
	\bar{x}	SD	N	Field (SFD)		Hiatt-projection	Field (SFD)		Field (SFD)	
				\bar{x}	P		\bar{x}	P	\bar{x}	P
1	3.41	0.18	81	—	—	(3.9)	—	—	—	—
2	5.00	0.49	27	—	—	(5.5)	—	—	—	—
3	7.20	0.53	16	—	—	7.3	—	—	—	—
4	9.75	0.56	4	—	—	9.5	—	—	—	—
5	—	—	—	11.6	0.11	12.2	12.0	0.11	11.9	0.11
6	—	—	—	15.3	0.24	<u>15.3</u>	16.2	0.25	15.8	0.24
7	—	—	—	19.9	0.11	19.1	20.8	0.20	20.7	0.17
8	—	—	—	24.5	0.18	23.6	26.6	0.10	25.7	0.15
9	—	—	—	30.9	0.07	28.9	30.7	0.16	33.1	0.24
10	—	—	—	35.9	0.29	35.4	35.4	0.18	37.5	0.09
a	—	—	—	-0.646	—	—	-0.335	—	-0.340	—
b	—	—	—	0.122	—	—	0.125	—	0.119	—
χ^2	—	—	—	15.8	—	—	14.0	—	9.9	—
d.f.	—	—	—	6	—	—	7	—	7	—
N	—	—	—	187	—	—	206	—	393	—

Table 9. Average size-at-instar: *Cancer magister*. Conventions as in Table 7. Hiatt-projections were done with straight lines fitted to pooled (males, females, and unsexed juveniles) data. The regression equation is $Y_i = 2.51 + 1.235X_i$.

Instar	1982 Year-class						1984 Year-class		
	Laboratory reared			Hiatt-projection	Field (SFD)		Hiatt-projection	Field (SFD)	
	\bar{x}	SD	N		\bar{x}	P		\bar{x}	P
1	7.9	0.50	19	7.9	—	—	7.1	7.1	0.31
2	12.5	0.86	39	12.3	12.6	0.03	11.3	10.5	0.15
3	17.8	1.56	22	17.7	17.6	0.26	16.4	15.2	0.21
4	26.1	1.59	62	24.3	25.8	0.52	22.8	20.8	0.13
5	33.9	2.20	103	32.7	34.8	0.10	30.7	28.8	0.13
6	45.1	3.57	52	42.9	43.8	0.09	40.4	42.7	0.07
7	57.6	4.90	52	55.5	—	—	—	—	—
8	72.0	5.35	43	71.0	—	—	—	—	—
9	90.6	6.14	5	90.2	—	—	—	—	—
a					-0.58			-0.29	
b					0.09			0.10	
χ^2					28.17			15.14	
d.f.					20			19	
N					501			597	

the-year *C. magister*, but its importance was not assessed. Bird predation is restricted to intertidal juveniles, and to large crabs in poor health condition. Mass mortality of adult *C. gracilis* was observed in January 1984, as a result of the combination of very low tides and freezing temperatures.

The most important apparent source of mortality of adult *C. productus* and *C. gracilis* was senescence. Data on crabs found dead or moribund in the field, and whose

condition is attributable to senescence or disease, are summarized in Table 15.

Crabs of all species are frequently found wounded or lacking appendages, as has been documented also by other authors (Durkin *et al.*, 1984). At least part of these injuries are attributable to partial predation by fishes, reported here for the first time. In the fall of 1985 we found many legs of adult *C. gracilis* and of large juveniles of *C. magister* in the stomach contents of staghorn scul-

Table 10. Average size-at-instar: *Cancer gracilis*. Conventions as in Table 7. See Table 4 for parameters utilized in Hiatt-projection.

Instar	Males			females		
	Field (SFD)		Hiatt-projection	Field (SFD)		Hiatt-projection
	\bar{x}	P		\bar{x}	P	
1	—	—	(2.4)	—	—	(2.3)
2	—	—	(4.9)	—	—	(4.7)
3	—	—	(7.9)	—	—	(7.7)
4	—	—	11.7	—	—	(11.4)
5	—	—	16.3	—	—	(16.1)
6	—	—	22.1	—	—	(21.8)
7	29.7	0.06	29.2	31.4	0.05	28.8
8	38.1	0.12	38.1	37.6	0.09	37.6
9	49.3	0.17	49.1	47.3	0.12	48.4
10	62.4	0.04	62.7	61.7	0.09	61.8
11	73.1	0.09	79.5	76.6	0.42	75.4
12	95.6	0.52	100.4	86.2	0.23	88.1
a	-0.72			-0.65		
b	0.104			0.100		
χ^2	24.5			40.0		
d.f.	32			27		
N	436			824		

Table 11. Parameters of straight lines fitted to the log-transformed carapace width versus total fresh-weight relationship.

Species of Cancer	Sex	Intercept (SE)	Slope (SE)	N	Size range (CW, in mm)
<i>magister</i>	male	-8.41 (0.068)	2.89 (0.016)	158	13, 186
<i>magister</i>	nonovigerous female	-8.31 (0.060)	2.86 (0.014)	137	21, 182
<i>gracilis</i>	male	-9.38 (0.084)	3.19 (0.019)	213	19, 115
<i>gracilis</i>	nonovigerous female	-8.94 (0.095)	3.06 (0.022)	274	30, 105
<i>gracilis</i>	ovigerous female	-8.04 (0.295)	2.90 (0.068)	150	54, 94
<i>productus</i>	male	-8.25 (0.129)	2.84 (0.030)	105	8, 161
<i>productus</i>	nonovigerous female	-8.61 (0.114)	2.91 (0.029)	108	15, 130
<i>oregonensis</i>	male	-7.28 (0.215)	2.79 (0.065)	65	10, 42
<i>oregonensis</i>	nonovigerous female	-7.45 (0.235)	2.82 (0.072)	81	11, 45
<i>oregonensis</i>	ovigerous female	-8.22 (0.316)	3.12 (0.101)	31	10, 43

pins, *Leptocottus armatus*. At least in some cases these appendages belonged to recently molted crabs.

Postlarval Life-History Schedules

Cancer magister.—Megalopae start to appear in the bay in May, and can be found in the area as late as August. Molting into crab instar J1 peaks in late May or early June. Settlement over the study period followed a pattern of alternating strong and weak years, high in 1982 and 1984, low in 1983 and 1985.

The growth of crabs settled during late spring in 1982 was followed in the field and in laboratory-reared animals. The growth schedule of the laboratory stock closely matched that observed in the field, both in size-at-instar and timing (Results, Size-at-Instar Schedules: Tables 9 and 16; Fig. 3). The cohort, on the average, reached instar J8 by November of Year 1, and instar J9 by February of Year 2 (1983).

While most Year 2 crabs belong in instar J9 at the onset of the spring, we have recurrently observed a second group, less abundant and smaller in size (Fig. 4). These range between 20 and 40 mm in CW by late April or early May. We refer to that pattern as "bimodal recruitment," and designate the two groups as cohorts A (large) and B (small).

Cohort B megalopae settle in late summer (August). We have not followed the growth of cohort B as closely as we did with cohort A, but the growth of late summer settlers was documented by Mackay and Weymouth (1935) for Boundary Bay (southern Strait of Georgia), 20 miles (32.2 km) from our study site. The growth curve implicit in

their data (Fig. 3) correctly predicts the size of cohort B at the onset of the spring of Year 2. Assuming that Mackay and Weymouths' size-at-instar schedule applies to Garrison Bay cohort B crabs, these reach instars J7 or J8 by the spring of Year 2. The size of instar J1 documented by Mackay and Weymouth (cohort B, \bar{x} = 5.2 mm) is smaller than what we observed for cohort A (\bar{x} = 7.1–7.9 mm). Coincidentally, Dungeness crab megalopae observed in the Friday Harbor area in late summer are smaller than those of the late-spring batch, but compatible with sizes reported by Mackay and Weymouth.

Past the spring of Year 2 we can account only for members of cohort A. Only field data are available beyond this point. Molt from instar J9 to A1 took place in early-midspring; this is the least documented step in our data base. In this molting episode the crabs crossed the 100-mm CW boundary, frequently associated with the onset of sexual maturity.

Molting from instar A1 to A2 extended over the late spring and summer of Year 2. On the average, females molted before males (molting peak in June versus July).

Males started molting to instar A3 in Au-

Table 12. *Cancer magister*. Estimated size-at-instar of A-instars.

Instar	Males		Females	
	\bar{x}	SD	\bar{x}	SD
A1	109.3	8.57	107.5	8.51
A2	131.2	10.39	131.4	10.53
A3	165.5	13.26	160.5	13.00
N	161		72	

12

Table 13. Size of the megalopae of various species of *Cancer*. T°C: temperature at which larvae were reared, in °C.

Species	CL	Source	Author
<i>amphioetus</i>	2.3	Laboratory-reared, 15°C	Iwata and Konishi, 1981
<i>antennarius</i>	2.7	Laboratory-reared, 13.8°C	Roesijadi, 1976
<i>anthonyi</i>	2.2	Laboratory-reared, 17.5°C	Trask, 1974
<i>anthonyi</i>	1.8	Laboratory-reared, 18–22°C	Anderson, 1978
<i>borealis</i>	2.1	Laboratory-reared, 20°C	Sastry, 1977b
<i>edwardsi</i>	4.3	Chile, 13.5–14.6°C	Quintana, 1983
<i>gracilis</i>	2.8	Laboratory-reared, 17°C	Ally, 1975
<i>irroratus</i>	2.5	Laboratory-reared, 15°C	Sastry, 1977a
<i>magister</i>	10.2	Laboratory-reared, 51°F	Poole, 1966
<i>magister</i>	8.7	Oregon	Waldron, 1958
<i>magister</i>	9.3	Northern Puget Sound	This study
<i>oregonensis</i>	4.2	Northern Puget Sound	This study
<i>pagurus</i>	3.3	Laboratory-reared	Ingle, 1981
<i>productus</i>	4.0	Laboratory-reared, 11°C	Trask, 1970
<i>productus</i>	4.3	Northern Puget Sound	This study

gust of Year 3. Molting continued during September, and presumably during October. Thus, molting from instar A1 to A2 of Year 2 males preceded (on the average) molting from instar A2 to A3 of Year 3 crabs. It is uncertain at which instar males start leaving the bay, but no healthy individuals were found beyond instar A3 or Year 3.

Most females entered instar A2 in May and June of Year 2, and all those observed were embraced by larger males. Complete observations were made on two couples captured in mid-June 1983. The Year 2 females molted from instar A1 (CW = 107.6 and 109.2 mm) to instar A2 (CW = 126.0 and 134.2 mm), while embraced by Year 3, instar A2 males (CW = 135 mm). The females were sacrificed in September for ob-

servation of the gonads: both had ripe orange ovaries. Most females seem to leave the bay after mating (i.e., while in instar A2). However, fresh casts indicated that at least a few females molted into instar A3 in the bay. No ovigerous females were observed over the study period. Instar A3 females in poor health or recently dead (not because of predation) were found in small numbers year-round.

Thus, while most females leave the bay after mating, following puberty molt (spring of Year 2), at least a considerable number of males stay in the bay for more than one year, until mating (instar A2) and subsequently molting into instar A3 during the late summer and early fall of Year 3. This results in a strongly biased sex ratio of samples of adults (instar A1 and larger) obtained in the bay, especially in late summer and fall.

Cancer gracilis.—Virtually all the results

Table 14. Maximum known sizes (CW, in mm), by species and sex. Data are from Butler (1961), Cleaver (1949), Garth and Abbott (1980), Hankin *et al.* (1985), Hart (1982), Rathbun (1930), and this study. Underlined figures are maximum records reported here.

Species of <i>Cancer</i>	Male	Female	Estimated mean maximum number of instars
<i>magister</i>	254 ¹	<u>182</u>	13 ²
<i>gracilis</i>	115	<u>106</u>	12
<i>productus</i>	180	<u>167</u>	13
<i>oregonensis</i>	49.5	47	11

¹ Males larger than 210 mm are rarely found. This maximum size record corresponds to an exceptional specimen reported by Cleaver.

² Garrison Bay (see Discussion, Intraspecific Variation in *Cancer magister*, and Table 22).

Table 15. Size of crabs found dead or moribund in the field. Only crabs whose condition was attributable to senescence or disease are included.

Group	N	Size range	Approximate instars
<i>Cancer magister</i> , males	10	127–186	A2–A3
<i>Cancer magister</i> , females	5	144–170	A3
<i>Cancer gracilis</i> , males	15	80–114	11'–12'
<i>Cancer gracilis</i> , females	23	63–106	11'–12'
<i>Cancer productus</i> , males	24	91–159	12–13
<i>Cancer productus</i> , females	27	102–167	12–13

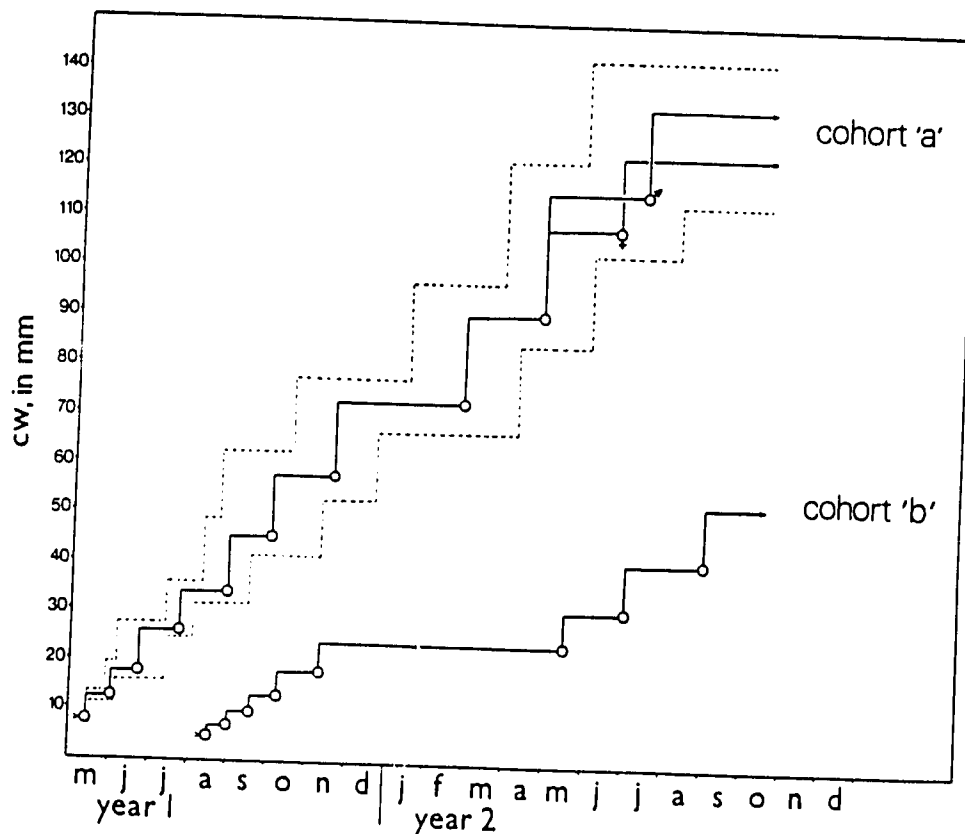


Fig. 3. *Cancer magister*. Schematic representation of growth in North Puget Sound. Cohort a (late spring settlers), data for the 1982 year-class; the envelope corresponds to one SD above and below average size-at-instar, and before and after average molting date. Cohort b (late summer settlers), extracted from Mackay (1935) data (Boundary Bay). Circles indicate average or approximate occurrence of molting.

correspond to a single cohort that presumably settled into the bay during the late summer or early fall of 1981, and was followed from the early winter of 1982 (instar 7' 8') until it vanished during the winter of 1984. Figure 5 is a schematic representation of the

postlarval life history of that particular cohort.

Molting into instar 9' peaked by late March, and into instar 10' by late May. The first mating season took place over the summer of Year 2. Some females mated with

Table 16. Growth schedule for laboratory-reared *Cancer magister*, 1982 year-class (cohort A, subsamples for which a detailed log of molting dates was kept). See Table 9 for complete information on size-at-instar schedule from the sample.

Instar	Average size (mm)	Average date at which molted into next instar (*)	SD	N	Average time spent in instar (days)
1	7.96	0.37 (13 May)	0.00	19	—
2	12.47	0.42 (11 June)	0.01	22	18.2
3	17.80	—	—	—	—
4	26.09	0.56 (22 July)	0.03	62	—
5	33.95	0.66 (28 August)	0.05	27	36.5
6	45.07	0.75 (30 September)	0.11	25	32.8
7	57.61	0.88 (17 November)	0.09	26	47.5
8	72.04	1.15 (24 February)	0.12	20	98.5
9	90.56	—	—	—	—

(*) In years, counted starting 1 January 1982 (corresponding date between parentheses).

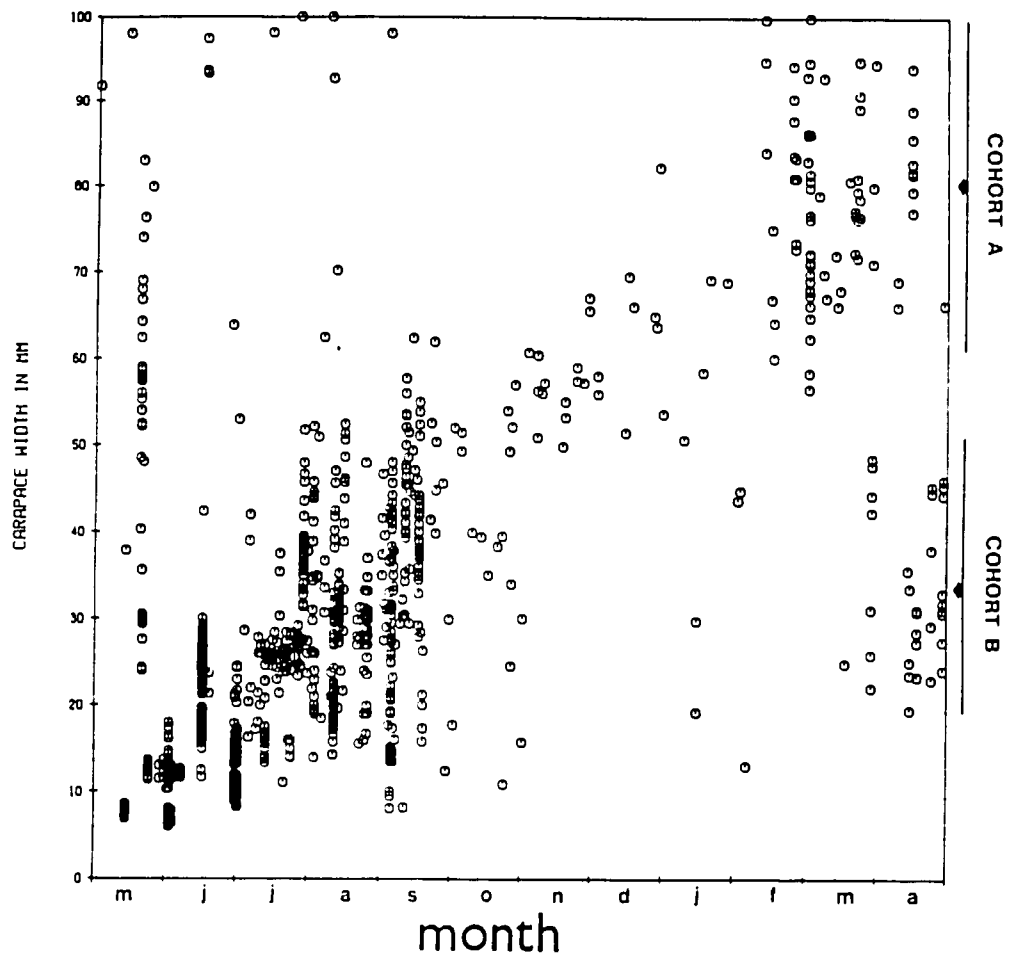


Fig. 4. *Cancer magister*, specimens smaller than CW = 100 mm obtained from the field. Years and sexes pooled.

older males while molting from instar 9' to 10', but most mated for the first time while passing from instar 10' to 11'. A few females mated early in the season and spawned in early summer; eggs were being carried as early as June, and hatched between July and September.

During Year 3 spawning started in early winter. The percentage of ovigerous females peaked in March and then declined over the year (Table 17). Females carrying eggs during the winter of Year 3 were mostly instar 11', but a few were instar 10' or 12' (the last most likely survivors of an older cohort). Molting (mostly from instar 11' to 12') and mating was most intense over the summer (June to August); smaller females tended to molt earlier in the season. The few females carrying eggs by late summer (August/September)

were on average larger than those carrying eggs in the preceding winter (Fig. 6), and were mostly in instar 12'. Some females might well have had two spawnings over Year 3 (winter and summer). This could be achieved in two ways: (a) one spawning before and another after mating over the late spring or early summer, or (b) two spawnings with sperm produced by a single copulation in Year 2. The distribution of ovigerous females per instar indicates that (a) was more likely to occur.

Male molting from instar 11' to 12' apparently peaked during the fall of Year 2 or the early winter of Year 3. So, by the next peak of mating activity, during the summer of Year 3, most males were one instar ahead (12' versus 11') of females of the same cohort. Unlike what happened during the first

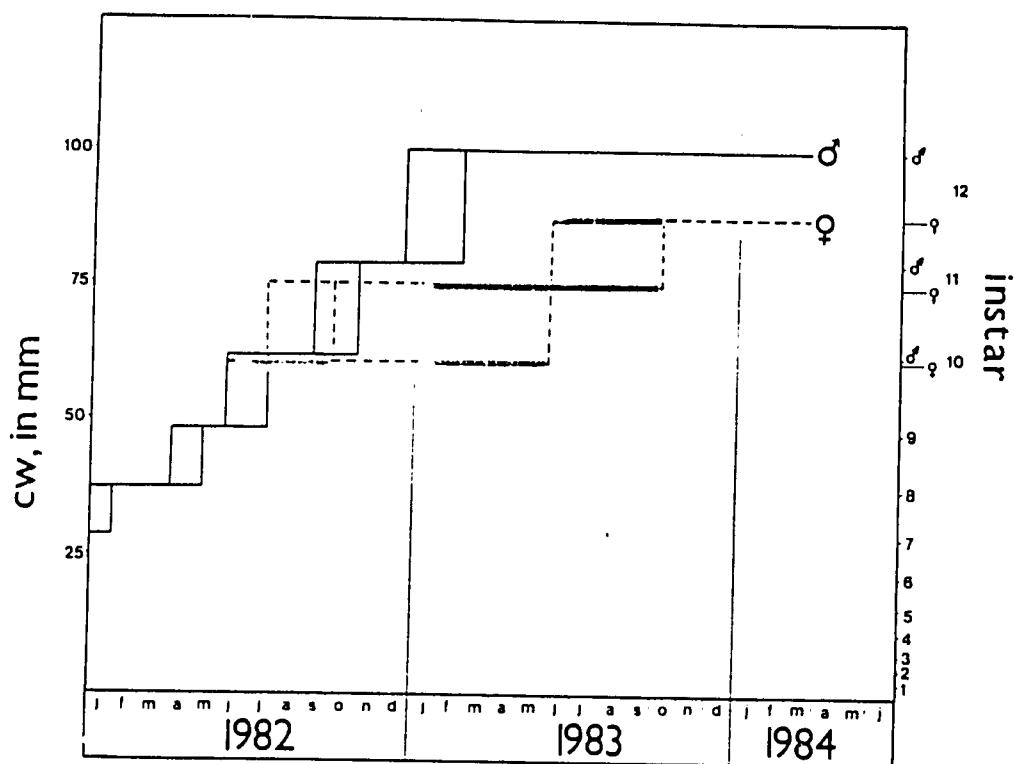


Fig. 5. *Cancer gracilis*, schematic representation of growth of the 1981 year-class during 1982-1984. Solid lines = juveniles and males; dashed lines = females; hatched lines = periods over which females were carrying eggs.

mating season (summer of Year 2), when males were monopolized by older males, females mated with males of their same cohort during the second mating season (summer of Year 3).

Density dropped in the study area over 1983. Figures obtained from the large plots (Material and Methods, *Quantitative Samples*), giving a preliminary indication of survival, are summarized in Table 18. Instar 12' is the terminal one for most *C. gracilis*,

if not for all (Results, Size-at-Instar Schedules). Senescent instar 12' females were found dead or moribund starting in the summer of Year 3. During the early winter of Year 4, a combination of very low tides and extremely cold nights resulted in mass mortality. Few were observed afterwards.

Had the cohort survived, most females might have had their second and last spawning season over Year 4, while in instar 12', and males might have had a chance to mate with females from younger cohorts. Thus, the maximum number of spawning seasons for a female may potentially be 3 (instars

Table 17. *Cancer gracilis*. Percentage of ovigerous females by month, 1983.

Month	N	Ovigerous (%)	Hatching or recently hatched (%)	Clean pleopods (%)
February	91	54.9	4.4	40.7
March	73	65.8	15.1	19.2
April	29	37.9	12.5	34.5
June	7	42.9	4.7	14.3
July	86	23.3	20.9	55.8
August	104	7.7	12.5	79.8
September	40	7.5	17.5	75.0

Table 18. *Cancer gracilis*. Density estimates from large plots, by season, 1983-1984.

Season	Number of crabs counted	Number of m ² scanned	Mean density (crabs/m ²)	Per. range
Winter, 1983	104	1,078	0.0965	1-11
Spring, 1983	124	3,190	0.0389	2-6
Summer, 1983	199	5,356	0.0371	2-7
Fall, 1983			—	—
Winter, 1984	22	831	0.0265	1-18

16'

Table 19. Sex ratios for the four species (all non sex-selective samples pooled).

Species of <i>Cancer</i>	N (males)	N (females)	N (males)/ N (females)
<i>magister</i> , CW < 110	143	145	0.98
<i>magister</i> , CW > 110	119	46	2.59
<i>gracilis</i> , CW < 30	19	19	1.00
<i>gracilis</i> , CW > 30	257	590	0.43
<i>productus</i> , CW > 40	62	65	0.95
<i>oregonensis</i> , CW > 10	29	62	0.47

10', 11', 12') but may be more often 2 (instars 11' and 12'), and was truncated to 1 (11') for most females of the 1981 year class.

Cancer productus.—Settlement of megalopae in the Friday Harbor area peaked between early July and early August in 1982 and 1983. The 1981 year class was the best represented in Garrison Bay during the study period. Molting from instar 9 to instar 10 was well documented in May 1982 (Year 2). This was shown to be the puberty molt for both sexes. Instar 10 males are already able to mate (laboratory observations). Females mate for the first time while molting from instar 9 to 10. Thus, sexual maturity is reached before one year after settlement. Most crabs were in instars 12 and 13 during the summer of Year 3 (1983). Many of them were moribund or dying from senescence or disease.

Mating was observed in the Friday Harbor area from May to September, matching the period reported by Knudsen (1964: June to September). No ovigerous females were observed in Garrison Bay; most of the crabs found in winter were adult males. Mature females presumably emigrate to deeper areas before hatching; this is also suggested by observations made by Knudsen (1964) in South Puget Sound. Females seem to emigrate in November–December, and return to the shallows in May–June.

Cancer oregonensis.—Settlement peaks in summer, coincidently with *C. productus*. Mating was observed from April to September. Ovigerous females were found from early November to April/May. The size of the smallest berried females indicates that puberty is reached in the molt from instar 4 to 5. Thus, at least some females may mate for the first time during the fall of Year 1, a few months after settlement.

Table 20. *Cancer gracilis*. Composition by sexes of samples from aggregates and background areas.

	Ovigerous Males	Ovigerous females	Non-ovigerous females	Females per male
Aggregates				
24 June 1982	16	12	27	2.4
15 September 1982	6	0	13	2.2
8–9 July 1983	50	20	64	1.7
9 August 1983	7	7	61	9.7
Totals	79	39	165	2.4
Background				
June–September 1982	9	7	2	1.0
June–July 1983	17	7	5	0.7
August–September 1983	51	5	48	1.0
Totals	77	19	55	0.96

Mating and Sex Ratio

Mating was observed in all four species. In all of them there is a precopula (usually lasting a few days). The copula takes place while the female is soft, and a short postcopulatory embrace follows. Males can presumably detect when a mature female is approaching molting.

Sex ratio patterns resulting from pooling all individuals sampled, in ways unlikely to be sex-selective, are summarized in Table 19.

Field observation of *C. gracilis* over the 1982 and 1983 summers revealed that crabs form very dense aggregates at some times and locations. Detailed measurements and observations were done on aggregates found on 24 June and 15 September 1982, and 8–9 July and 9 August 1983. The density in the last (which coincided with one of the large quadrats) was estimated at 0.4 crabs m² (probably an underestimate). This corresponds to ~2.5 m² per crab, and is about 10 times the average density observed over the summer (Results, Postlarval Life-History Schedules). The density at the core of the aggregates (observations made in 1982 and in July 1983) was of the order of one crab per square meter or even higher. Sex ratios from aggregates and background areas are summarized in Table 20. The samples consistently show a disproportionate abundance of females within the aggregates, even when we were likely to have biased the samples in favor of males. Most females, particularly ovigerous ones, were buried in the

mud, and for that reason were more difficult to locate. Ovigerous females buried in a similar way have been reported for *C. magister* (Diamond and Hankin, 1985) and *C. pagurus* (Howard, 1982). Most males were active, wandering above the sediment; on a few occasions males engaged in agonistic contests. Some males and females were in precopulatory embraces on all occasions. Samples taken over background areas (low density) over the same summers (the 1983 counts are from the sampling plots) show a very different picture, with sexes equally represented, or sex ratio slightly biased in favor of males (Table 20).

No such aggregates were observed in the other species. On several occasions, during the summer, adults of *C. productus* were found in heterosexual monogamous pairs. This pattern is reflected in the overall observed sex ratio, which does not depart significantly from unity. Garrison Bay may be a marginal environment for *C. productus*, and the pattern observed may be atypical for the species.

Specimens of *C. oregonensis* were never observed far from their refuges. Specimens occupying crevices or spaces under stones in the field seem to be distributed in small "harems," composed of a large male and a few smaller females. The overall observed sex ratio (~2 females per male on the average) reflects this pattern.

DISCUSSION

The Bonus of Discrete Growth

The lack of growth marks on exoskeletons has hindered studies on crustacean natural history. The discreteness of growth-by-molts, however, offers an edge that has not been fully exploited. Size increment-per-molt data come in two formats: Hiatt diagrams and their relatives, and size-at-instar schedules which can be derived, among other types of data, from SFDs (Hartnoll, 1982).

The usefulness of representations of expected growth increment per molt given premolt size has been widely acknowledged, and different models have been proposed (Botsford, 1985). The analysis of SFDs (their natural complement) has received, by contrast, little attention. It is thus paradoxical that the first analytical dissection of a polymodal frequency distribution (Pearson,

1894) was exemplified with a crab SFD! Hartnoll (1978a, 1982, 1983) has discussed the value of SFDs, and the circumstances that might render them useless. We have found only a short mention (Warner, 1985) of the use of numerical methods in the dissection of crab SFDs; most studies have relied on graphical techniques or ocular inspection. Ours is (as far as we know) the first study to make extensive use of numerical methods for polymodal SFD analysis in a crustacean, and to incorporate growth structure into it. Caution, however, is advised in the use of these techniques. Their usefulness is maximal when the data come (as in our case) from a single cohort whose members grew under similar conditions. Potential problems are of two types:

- (a) Mixtures of cohorts can produce multimodality for each instar, masking any pattern or leading to erroneous interpretations.
- (b) If increments-per-molt are small and/or standard deviations are large, modes can be rendered indistinguishable. Environmental heterogeneity or protracted settlement can increase variance of size-at-instar even within a single cohort, and erase all useful information (Hartnoll, 1978a, 1982, 1983).

When these difficulties can be overcome, the analysis of discrete growth facilitates some insights. The apparent contrast in the number of juvenile instars between estuarine and marine populations of Dungeness crab (Discussion, Intraspecific Variation in *Cancer magister*) constitutes an example. This case also illustrates the use that can be made of the decomposition of the growth process in size increments per molt and frequency of molting, since each of these two components can be specifically affected by different environmental factors.

Interspecific Comparisons

Early Life History.—Data on larval development is now available for a number of species (Table 13). There is wide interspecific variation in the size of the megalopae, as well as some intraspecific variation (Discussion, Intraspecific Variation in *Cancer magister*). Megalopae of *Cancer* can be broadly grouped into small (CL ~ 2–3 mm: *amphioetus*, *antennarius*, *anthonyi*, *borealis*, *gracilis*, *irroratus*), medium (CL ~ 4 mm:

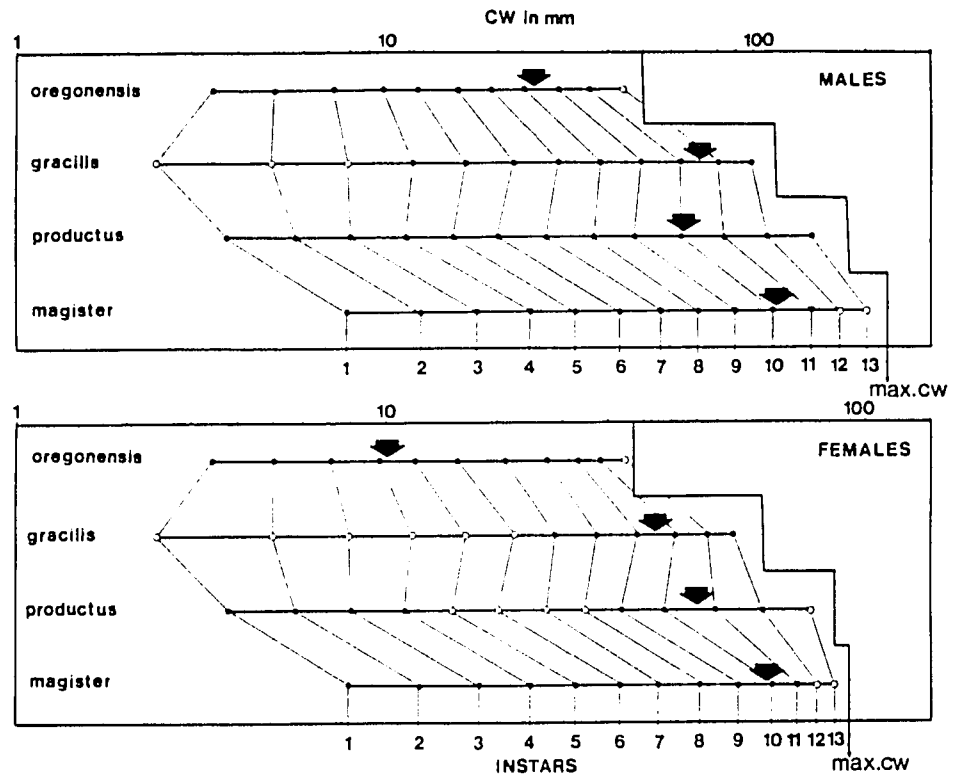


Fig. 6. Schematic representation of postlarval life-history schedules in the four species of *Cancer* studied (males and females). Size is in log scale. Arrows indicate MCS for males, and MOS for females. Open circles indicate that values were interpolated or extrapolated.

productus, *edwardsi*, *oregonensis*, *pagurus*), and large CL ~ 8–10 mm: *magister*). The pattern is not related to biogeographic or phylogenetic affiliation, but may have ecological correlates.

Megalopae of *C. magister* are the largest in the genus. They settle onto relatively open sandy areas, where they are exposed to fish predation. Large initial size may reduce the length of the period during which these megalopae are exposed to predation by the small fishes that are abundant in Dungeness crab nursery grounds.

We were unsuccessful in finding the earliest crab instars of *C. gracilis* in our benthic surveys. Weymouth (1910) and Garth and Abbott (1980) reported the association of these with pelagic medusae off California. This might be also the case in North Puget Sound; our three smallest specimens were obtained on the north part of the Bay on 5 September 1982, coincidentally with a large stranding of jellyfishes.

Growth and Sexual Maturity.—The average maximum number of crab instars varied from 11 in *C. oregonensis* to 13 in *C. magister* and *C. productus* (Fig. 6). The number of instars within a species varies because of environmental influences on growth rate and size-at-settlement (Discussion, Intraspecific Variation in *Cancer magister*), but the number of potentially reproductive male instars is three in most cases. The effective number can be contingently lower, due to mortality from causes other than senescence. Results for the females are also comparable, with one notable exception: judging from MOS, 8 out of 11 instars of *C. oregonensis* are potentially reproductive. Females of all species studied have the potential to spawn more than once while in each postpuberty instar (Knudsen, 1964; Ebert *et al.*, 1983).

“Stretching” of the life-history schedule (Fig. 6) involves settlement size, size-specific growth-per-molt increments, and number of instars. This last component was

Table 21. Lines fitted to Hiatt diagrams, extracted from the literature.

Species of <i>Cancer</i>	Group	Area	Intercept	Slope	Author
<i>magister</i>	adult males	southeast Alaska	36.6	0.953	7
<i>magister</i>	adult females	southeast Alaska	27.8	0.924	7
<i>magister</i>	pooled sexes, < 29	British Columbia	1.620	1.220	2
<i>magister</i>	males > 83	British Columbia	19.0	1.070	2
<i>magister</i>	females > 88	British Columbia	31.6	0.892	2
<i>magister</i>	males < 100	central California	1.053	1.223	4
<i>magister</i>	males > 100	central California	19.5	1.051	4
<i>irroratus</i>	pooled sexes	Maine	0.566	1.274	8
<i>irroratus</i>	males	Chesapeake Bay	3.925	1.161	5
<i>irroratus</i>	pooled sexes, < 35	Rhode Island	-1.265	1.371	9
<i>irroratus</i>	females > 35	Rhode Island	12.95	0.948	9
<i>irroratus</i>	laboratory males > 35	Rhode Island	-1.604	1.332	9
<i>irroratus</i>	field males > 35	Rhode Island	11.45	1.033	9
<i>pagurus</i>	male > 90	eastern England	8.99	1.269	6
<i>pagurus</i>	females > 90	eastern England	19.68	1.096	6
<i>pagurus</i>	males > 90	southwest England	9.45	1.180	1
<i>pagurus</i>	females > 90	southwest England	24.67	1.030	1
<i>antennarius</i>	females > 64	central California	16.02	1.001	3

(1) Bennett (1974), (2) Butler (1961), (3) Carroll (1982), (4) Collier (1983), (5) Haefer *et al.* (1975), (6) Hancock and Edwards (1967), (7) Koeneman (1985), (8) Krouse (1976), (9) Reilly and Saila (1978).

surprisingly conservative; although *C. oregonensis* and *C. magister* have dramatically different sizes (reported maximum males sizes are, respectively, 50 and 254 mm), the maximum average number of instars is, respectively, 11 and 13 in the sympatric populations studied by us.

Hartnoll (1985) classified crustacean patterns of growth and reproduction according to whether growth is indeterminate or determinate, to the number of postpuberty instars, and to the distribution of egg-laying among instars. He considered a single species of *Cancer*, *C. pagurus*, which is said to have indeterminate growth, and sometimes more than one egg-laying per postpuberty instar (Pearson, 1908; Hartnoll, 1985, table 1, fig. 3). In the case of indeterminate growth molting continues indefinitely after puberty until death, with no clear terminal anecdydysis. The life-history schedules of the species studied by us seem to be more determinate, closer to the patterns reported for *Portunus sanguinolentus* or *Carcinus maenas* (Hartnoll, 1985).

Our study shows that in *C. gracilis*, *C. productus*, and *C. oregonensis* there is a certain average size, associated with an average terminal instar, at which crabs die of physiological senescence following their last reproductive season. This was best documented for *C. gracilis* and *C. productus*. Hankin *et al.* (1985) found evidence of physiological senescence in large females of

C. magister. The size and/or instar at which senescence occurs seems to be part of the life-history program of each species. There are no obvious mechanical or environmentally related constraints that might hamper growth to a larger size in *C. gracilis*, considering that *C. magister*, sympatric and morphologically very similar, grows to a much larger size.

Data on life-history schedules have been published for some other species of *Cancer*. Coefficients of regressions fitted to Hiatt diagrams in previous studies are summarized in Table 21. Size-at-instar schedules have been published for the following four species: (1) *C. magister*: Butler, 1961; Cleaver, 1949; Collier, 1983; Mackay and Weymouth, 1935; Poole, 1967. (2) *C. irroratus*: Reilly and Saila, 1978; Krouse, 1976. These two studies are inconsistent with each other (Bigford, 1979): Reilly and Saila's instar 1 seems to correspond to Krouse's 3 or 4. Krouse's data for early crab instars seem the most complete; also, his instar 1 is consistent with the size of the megalopa published by Sastry (1977a, table 13) and with size-at-instar of laboratory-reared crabs (Bigford, 1979). (3) *C. anthonyi*: Anderson and Ford, 1976. This study dealt exclusively with laboratory-reared crabs. (4) *C. antennarius*: Carroll, 1982. Carroll's schedule was not actually observed, but guessed from comparison with Butler's (1961) data on *C. magister*.

Comparisons are difficult due to the heterogeneity of approaches followed in different studies. However, rough calculations utilizing Hiatt diagram regression coefficients (Table 21), size-at-settlement (Table 13), and known maximum sizes, suggest that postlarval life-history schedules of several other species are very similar to those reported here. This might be so even for *C. pagurus*: given maximum known size (about 280 mm for males), size at sexual maturity (MOS = 115 mm, male maturity ~ 110 mm; Edwards, 1979), and data on size increments per molt (Table 21; Bennett, 1974; Hancock and Edwards, 1967), the average maximum number of postpuberty instars may be 3, as is apparently the case for most other species.

Reproductive Migrations and Patterns of Habitat Utilization.—Patterns of adult reproductive migration reported in the literature can be divided in the following broad groups:

- (A) Both sexes remain in the same area year-round: *C. gracilis* and *C. oregonensis* (this study); *C. antennarius* (Carroll, 1982; personal observation in Baja California); *C. irroratus* from Massachusetts, Maine, and Canada (Krouse, 1972).
- (B) Males do not show seasonal migrations, but females do: (1) Females move offshore following the molting/mating season; larval hatching takes place offshore: *C. productus* (Knudsen, 1964; this study), *C. pagurus* (Edwards, 1979; Le Foll, 1986), *C. borealis* (Krouse, 1980). (2) Females move inshore following the molting/mating season; larval hatching takes place inshore: *C. irroratus* from Narragansett Bay (Jones, 1973, p. 56).
- (C) Females do not show seasonal migrations, but males do: *C. irroratus* from New Jersey, Delaware, and Virginia (Shotton, 1973; Haefner and van Engel, 1975; Haefner, 1976; Winget *et al.*, 1974). Here, males move inshore following the mating season, and molt (during the winter) while in shallow waters.
- (D) Both sexes have seasonal migrations: *C. magister* (Gotshall, 1978; PFMC, 1978; Diamond and Hankin, 1985). Here both sexes move offshore following the mating season; males seem more motile than females; hatching takes place offshore with respect to the mating grounds. ("Offshore"

is used here in a relative sense. The offshore emigration may take crabs to deeper but not necessarily distant waters.)

Three hypotheses have been proposed to explain these migrations:

- (a) Crabs migrate following their thermo-preferenda. This has been proposed for the winter inshore migration of *C. irroratus* (Bigford, 1979; Haefner and van Engel, 1975).
- (b) Female crabs migrate following mating so that larvae are released in areas where hydrography facilitates their transport to adequate settlement habitats. This was hypothesized for the postmating offshore emigration of *C. pagurus* (Edwards, 1979).
- (c) Female crabs migrate inshore because they require the type of sandy bottoms found in shallow areas for the adequate extrusion of the egg masses; proposed by Diamond and Hankin (1985) to explain the inshore spring migration of female *C. magister*.

To these we add two more:

- (d) Both sexes converge during the mating season, a behavior selected to facilitate mating encounters. We suggest this hypothesis for female *C. productus*, returning to shallow areas where males overwinter, and for the late winter/spring aggregation of *C. magister*.
- (e) The emigration away from estuaries of gravid female *C. productus* (Knudsen, 1964; this study) and *C. magister* (Cleaver, 1949; Stevens and Armstrong, 1984, 1985; this study) may avoid the exposure of eggs to osmotic stress. There are no records of *Cancer* hatching in brackish waters. A similar emigration has been observed in *C. irroratus*, estuarine portunids (Tagatz, 1968a), and some grapsids.

Prehatching female offshore emigration, whatever its origin, may facilitate the utilization of estuarine environments by *C. magister* and *C. productus*. A comparison of the latter with *C. antennarius* is interesting. The two species are similar to each other in microhabitat utilization pattern, and convergent in size and shape, but differ in migratory behavior and ability to utilize estuaries. Strictly marine *C. antennarius* does not osmoregulate in brackish water (Jones, 1941). Evolution of osmotolerance in *C.*

productus may have been facilitated by a preexisting female migratory behavior. In fact, none of the three species known to lack reproductive migrations (group A, above) is a successful inhabitant of estuarine areas. This reasoning implies that estuaries were secondarily invaded by species of *Cancer*, originally marine. Studies on osmoregulation support this hypothesis: *C. pagurus* and *C. antennarius* are osmoconformers over the entire salinity range (Jones, 1941; Krogh, 1939). *Cancer magister* and *C. irroratus*, which are able to survive in estuarine areas, hyperosmoregulate in brackish water and are partial osmoconformers in sea water (Engelhardt and Dehnelt, 1973; Hunter and Rudy, 1975; Robinson and Potts, 1979; Haefner and van Engel, 1975).

Mating Systems.—Mating in species of *Cancer* has been discussed by Hartnoll (1969), Ridley (1983), and Elner *et al.* (1985). Knudsen (1964) described pairing in *C. gracilis*, *C. productus*, and *C. oregonensis*, and several other authors in *C. magister* (Cleaver, 1949; Butler, 1960; Snow and Neilsen, 1966). Males of all species of *Cancer* have at least the potential for being polygynous (Cleaver, 1949; Butler, 1960; Snow and Neilsen, 1966; personal observation). Emlen and Oring (1977) assembled polygynic mating systems into a model which takes into account ecological correlates. Environmental Potential for Polygyny (EPP) increases as the temporal availability of mates (females in this case) becomes asynchronous, or as critical resources become unevenly distributed in space. We argue that three of the species studied here (*C. magister*, *C. gracilis*, and *C. oregonensis*) diverge in their mating systems in directions that parallel the three types of polygyny recognized by those authors: resource defense, female defense, and male dominance (explosive breeding assemblage). These are discussed below.

Resource defense polygyny.—Males control access to females indirectly, by monopolizing critical resources. Males of *C. oregonensis* are apparently able to control small "refuge" areas, more or less discrete spatial segments in structurally complex substrates. Distribution of crabs in the field, sex ratio in the natural population, and laboratory observations give credit to this hypothesis. A similar mating system has been reported

for crab species in other families showing a convergent type of habitat utilization. These include the porcellanids *Petrolisthes cinctipes* and *P. cabrilloi* (Molenock, 1975), and the xanthid *Pilumnus sayi* (Lindberg, 1980).

Female defense polygyny.—Males control access to females *directly*, usually by virtue of female gregariousness. Such a mating system seems to be represented in the reproductive clusters reported here for *C. gracilis* (Results, Mating and Sex Ratio). Within these aggregates males are more active than females; they are involved in contests with other males, searching for females approaching molting, or are mating. Many of the females are still ovigerous, suggesting that they may "sit and wait" for their molting/mating turn. Males that stay in the clusters during the protracted mating season may increase their chances of multiple copulas; females within an aggregate minimize the risk of not having a partner available during the short receptive period, and may have the opportunity to mate with the "best" males (i.e., those who manage to outcompete, or "cheat," other males and remain in the cluster). The mechanism for the generation of the aggregates is uncertain. Males were never seen "herding" females. Sites of aggregation are not associated with any observable peculiarity of the substrate. Because males are more mobile (and have a presumably more transient affiliation), females might be expected to play the most important role in generating and holding together the clusters. How crabs assess the proximity of other individuals is difficult to explain. Pheromones have been often advocated in crustacean communication but, while gradients of pheromonal concentration play a role in male orientation towards females approaching a molt, a certain concentration cannot be maintained in the water flowing above a congregation site. One possibility is the "conditioning" of the substrate by chemicals released with the feces, as has been reported in terrestrial isopods (Takeda, 1984).

"Heaps" of the majid *Maja squinado* (Carlisle, 1957; Stěvčič, 1971) may be interpreted as an extreme case of this type of mating system. Heaps (which in laboratory experiments were initiated by females) form in shallow water during the reproductive season and are integrated by females ap-

proaching their puberty molt (the most abundant group), males in their terminal anecdysis, and prepuberty males. Females mate, as they molt, with one of the available males. Large males position themselves in the periphery of the heap. Crabs not participating in the heaps are mostly large males. Both Stěvčíc and Carlisle hypothesized that the main function of heaps was protection of "subordinates" (prepuberty males and females) by "dominants" (large males) during the molting season. Mating was assigned subsidiary importance. Their interpretation reflects the group-selectionist mood prevailing at that time. Heaps of *Maja* may reflect a female defense polygynic mating system, analogous to the one we describe here for *C. gracilis*. Prepuberty males within the heap might be getting protection, as suggested by Stěvčíc, but, their maleness masked, they might also be cheaters. Hartnoll (1965, p. 8) found sexually mature but morphologically prepuberty males in other majids.

Explosive breeding assemblages (a subtype of "male dominance polygyny.")—Both sexes converge for a relatively short-lived, synchronized mating period; synchrony pushes the OSR towards unity, monopoly of mates becomes less economically feasible, and sexual selection decreases. As a result, ability to search becomes proportionally more important. Several authors have reported a seasonal inshore migration before the mating season in *C. magister* (Discussion, *Reproductive Migrations and Patterns of Habitat Utilization*). In this species the period of maximum mating activity is relatively short, and its timing predictable as compared with other congeners.

Sexual Selection.—Pattern of sexual dimorphism is consistent with inference on mating systems. Dimorphism in the size of the chelae among decapod crustaceans is associated with sexual selection. From the preceding discussion of mating systems it should be expected to be minimal in *C. magister*; in fact, there seems to be little dimorphism, if any at all, in this species (Results, *Males: Carapace-Chela Allometry*). This is also consistent with a lack of special action patterns related to mating in adult males (Jacoby, 1983). *Cancer magister* may be the only species of its kind in the genus;

judging from the systematic literature, most (if not all) others are dimorphic.

In *C. oregonensis*, on the opposite end, strong dimorphism is expressed early in life history (Results, *Males: Carapace-Chela Allometry*). This seems to be the most sedentary of the species studied. Early development of large chelae in males may be related to the defense of territories that, once gained (sometimes by a young crab), will be held for a long period (eventually for the whole life-span).

In *C. gracilis* and *C. productus* there are two clear phases. Chelae of young males are similar in development to those of the females, but become proportionally larger after the puberty molt. Males of these two species do not hold refuge space for long periods. At least in *C. gracilis* access to females is not related to "resource (refuge) defense" at all. We hypothesize that secondary sexual characters become expressed later in life, because it is only then (cheating aside) that they become a requisite for success in the "female defense" polygynic mating system.

Intraspecific Variation in *Cancer magister*

Postlarval life history of *C. magister* is the best known in the genus. Schedules have been assembled for several shallow water environments: Queen Charlotte Islands in northern British Columbia (Butler, 1961), Boundary Bay in the southern Strait of Georgia (Mackay and Weymouth, 1935), Garrison Bay in northern Puget Sound (this study), Grays Harbor in Washington (Cleaver, 1949), and San Francisco and Bodega Bays in California (Poole, 1967; Collier, 1983; Tasto, 1983).

Comparison of our results with previous studies provides the best possible picture of intraspecific variability in the genus, and some insights in the factors behind it. It also helps to put interspecific comparisons in context.

Bimodal Recruitment in Garrison Bay.—Settlement of megalopae peaks earlier at lower latitudes, ranging from April in Central California (Reilly, 1983) to September in the Queen Charlotte Islands (Butler, 1960, 1961). The bimodal recruitment pattern that we report for Garrison Bay cannot be accommodated into this gradient. Cohort A (late spring, large megalopae) fits well within

Table 22. Size-at-instar schedules in natural populations of *Cancer magister*.

Instar		San Francisco Bay (Collier, 1983) (*)	Bodega Bay (Poole, 1967) (*)	Grays Harbor (Cleaver, 1949) (*)	Garrison Bay (this study)		Boundary Bay (Mackay and Weymouth, 1935)		Queen Charlotte Islands (Butler, 1961)				
J	1	7.8	7.6	(6.4)	7.9		5.2		6.9				
	2	11.4	12.2	9.6	12.6		7.4		<u>10.0</u>				
	3	15.2	16.9	12.8	17.6		9.7		<u>13.8</u>				
	4	<u>19.7</u>	22.5	17.1	25.8		13.4		18.5				
	5	25.2	30.3	24.0	34.8		18.2		24.2				
	6	32.0	39.6	30.8	43.8		24.0		31.1				
	7	40.2	50.9	37.7	57.6		31.5		39.6				
	8	50.3	67.9	47.7	72.0		41.0		49.9				
	9	62.8	91.1	60.4	90.5		52.5		62.5				
	10	77.8		73.2			65.7		77.9				
	11	96.4		90.9			80.5		96.6				
	12						95.8						
A	1	119.1	114.5	114.0	109.3	107.5	112.6		119.5	117.5			
	2	146.2	—	135.9	—	131.2	131.4	130.0	127.3	146.9	136.6		
	3	174.6	—	162.8	—	165.5	160.5	149.6	141.3	176.2	152.5		
	4	204.5	—	182.0	—			170.8	153.5	207.5	167.6		
Maximum CW		—	—	240.0	—	254(+)	170.0	186.0	182.0	170.0	165.0	218.0	171.0

(*) Original values transformed to include the tenth anterolateral spines, when these were excluded from CW measurements.

(+) A single, exceptional individual.

Underlined figures indicate anchors, when utilized by the author. When sexes were discriminated, males appear on the left, females on the right.

the outer coast cline, while cohort B (late summer, small megalopae) resembles the pattern reported for the Strait of Georgia (Mackay and Weymouth, 1935). This dichotomy suggests the existence of two stocks, distributed respectively along the outer coast (Central California to Alaska), and in the Strait of Georgia. According to this hypothesis, Garrison Bay (midway between the Strait and the outer coast) would be receiving recruits from both stocks. Soule and Tasto (1983) found homogeneity in a study of genetic variation over a wide latitudinal range (California to Alaska), but they did not study samples from the Puget Sound-Strait of Georgia. The stock structure hypothesized here is similar to that reported for the Pacific hake *Merluccius productus* (McFarlane and Beamish, 1985).

Recruitment to Coastal Nurseries — Crabs enter bays and estuaries reported as "nurs-

ery grounds" at varying ontogenetic stages: as megalopae in Garrison Bay and Grays Harbor (Stevens and Armstrong, 1984, 1985; this study), at early postlarval instars in San Francisco Bay (Tasto, 1983), and at advanced juvenile instars (~J8) in the Columbia River estuary (Emmett and Durkin, 1986). Use of bays and estuaries as nursery grounds seems to be contingent upon local conditions. There is great variation even within relatively small geographic areas, as is the case in Washington.

Growth and Environmental Conditions. — Reaching adulthood (instar A-1, 109–119 mm on average) may take 1–4 years following settlement, and 9–12 J-instars (Table 22; Figs. 7, 8). Size-at-instar may be influenced by a number of factors, among them:

(1) Size-at-settlement: Differences between the schedules of the 1982 and 1984 year

Table 23. *Cancer magister*, different juvenile populations. Reported total time and number of instars required to reach a carapace width of 100 mm.

Area	Time	Instars	Winter anecdyis	Author
San Francisco Bay	early winter, year 2	11	no evidence	Collier, 1983
Bodega Bay	summer, year 2	9	no evidence	Poole, 1967
Grays Harbor	late spring, year 3	11	October–April	Cleaver, 1949
Garrison Bay (Cohort B)	spring, year 2	9–10	December–March	This study
Boundary Bay	summer, year 4	12	November–May	Mackay and Weymouth, 1935
Queen Charlotte Islands	spring/summer, year 3	11	no data	Butler, 1961

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classes in Garrison Bay (Table 9) are attributable to variation in average size at settlement (7.9 mm in 1982 versus 7.1 in 1984). Ebert *et al.* (1983) found similar levels and effects of year-to-year variation in size of the megalopae. Very small size at settlement underlies the large number of J-instars (12) in the Strait of Georgia stock.

(2) Temperature: Growth rate (reflected in average age at instar A-1) and duration of the winter anecydyses vary clinally along the outer coast, most likely in relation to temperature (Table 23). Stevens and Armstrong (1984, 1985) found growth rates reported for San Francisco too high, suggesting that Tasto (1983) and Collier (1983) misinterpreted the San Francisco Bay data. Our study, and preliminary experimental results by Kondzela and Shirley (1985, fig. 21), however, suggest that environmental variability can account for the large differences reported. Strong inshore-offshore growth-rate gradients (Tasto, 1983; Carrasco *et al.*, 1985) are also attributable to temperature.

(3) Salinity: Reported average number of J-instars is 9-10 in Garrison Bay (cohort A) and Bodega Bay, both marine environments, and 11 in Grays Harbor and San Francisco Bay (Table 23, Fig. 7). The last two are estuaries where salinity decreases in winter to 10-20‰ (Tasto, 1983; Loehr and Collias, 1981). Experimental results on other crustaceans (Newell, 1979) indicate that osmotic stress increases metabolic expenditure, competing with growth in the energy budget when animals live off their osmopreferenda. Behavioral (Sugarman *et al.*, 1983), physiological (Robinson and Potts, 1979), and field (Cleaver, 1949) studies suggest that seasonal salinity minima in the two estuaries are below the preferendum for *C. magister*. Reduced size increments in crabs reared off their osmopreferenda have been reported for *Callinectes* (Tagatz, 1968b), *Carcinus* (Breteler, 1975), and *Reginoponopeus* (Hartnoll, 1978a). We hypothesize that the larger number of J-instars required to reach adulthood in estuaries, as compared to shallow marine environments, reflects the cost of osmoregulation. It should be noted that even if the instar-specific reductions in size increment are small, their accumulation can easily result in additional instars to reach a given size.

(4) Shadow of an exceptional year?: Growth

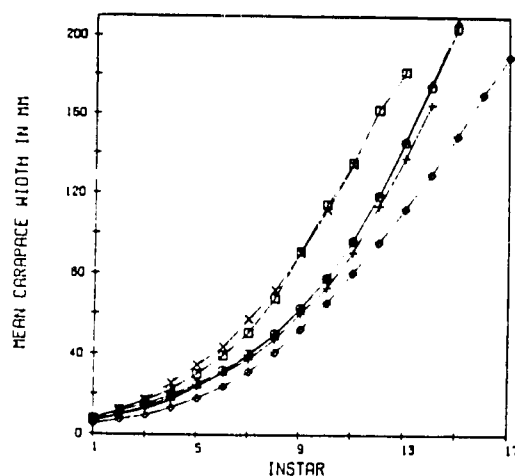


Fig. 7. *Cancer magister*, comparison of published size-at-instar schedules. (x) Garrison Bay, (□) Bodega Bay, (Δ) Queen Charlotte Island, (O) San Francisco Bay, (τ) Grays Harbor, (◇) Boundary Bay.

rate of the 1982 year class in Garrison Bay is similar to that reported for Bodega Bay (Poole, 1967), in spite of the latitudinal separation of the two sites. Latitudinal clines may be obscured because Bodega Bay is an open area seasonally cooled by upwelling, while water above Garrison Bay flats is warmed during the summer. It may be also that the 1982 year class was exceptional. A strong El Niño anomaly became evident in the Northeast Pacific by the fall of 1982 (Huyer and Smith, 1985; Tabata, 1985). The growth rate of the 1982 year class may have been higher than average, this being reflected in shorter-than-expected winter anecydyses.

Sexual Maturity.—In Garrison Bay females mate while molting from instar A1 to A2 (Year 2); males mate for the first time in instar A2 (Year 3). Observations from other areas indicate some plasticity. At least some females mature in the transition between instars J+ and A1, judging from published data on MOS (Hankin *et al.*, 1985), MPS (Cleaver, 1949; Butler, 1961), MCS in males (Cleaver, 1949), and sexual maturity in males (Butler, 1961; Poole, 1967). However, effective sexual maturity seems to be reached by males at instar A-2 in, at least, Garrison Bay (observed MCS = 135 mm) and Queen Charlotte Islands (observed MCS = 141 mm). Females leave the bay after mating, and males do not stay beyond instar A3. A comparison with Grays Harbor

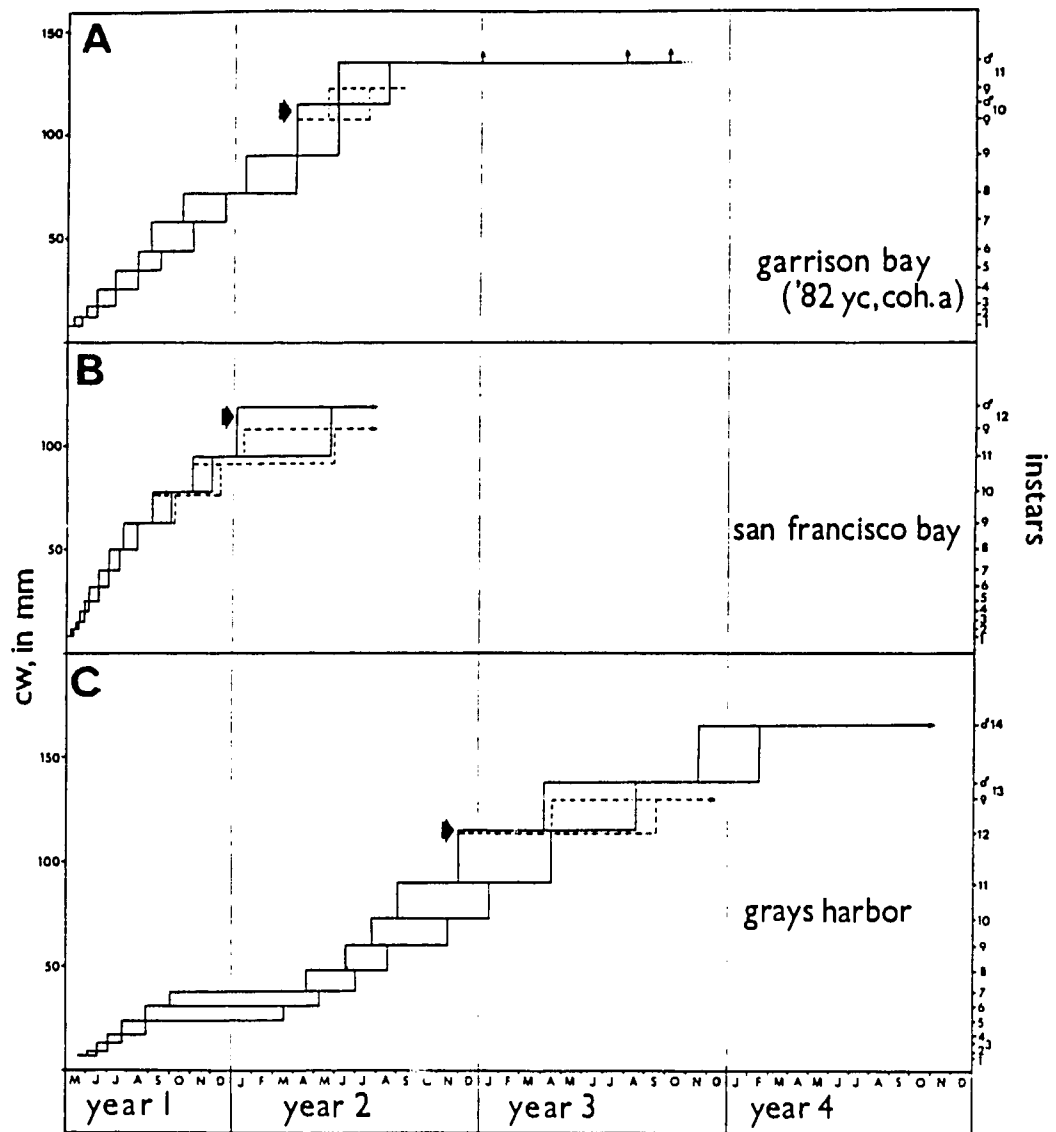


Fig. 8. *Cancer magister*. schematic representation of growth in three "nursery areas." A. Garrison Bay (this study); B. San Francisco Bay (from Collier, 1983, and Tasto, 1983); C. Grays Harbor (from Cleaver, 1949). Solid lines = juveniles and males; dashed lines = females; arrows = instar A1.

(Cleaver's data) suggests a similar pattern, although delayed one year. In San Francisco Bay, in contrast, males and females leave the bay simultaneously, by late summer of Year 2 (Collier, 1983), leaving the possibility that crabs mate before emigrating.

Corollary.—Genetic homogeneity can be expected to be favored in this species by the dispersal capability of the adult males and the long duration of pelagic larval devel-

opment, as shown by results from electrophoretic studies. A separate stock may inhabit the Strait of Georgia/North Puget Sound area. Phenotypic plasticity, contingently determined by local/yearly environmental conditions, allows parsimonious explanations of variability in settlement, growth, and utilization of coastal nurseries from Central California to the outer coast of Washington and British Columbia.

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Diversity Among the Cancridae

Comparisons of life-history schedules, mating systems, and sexual selection converge on one common theme: a number of morphological and ecological traits of species of *Cancer* can be associated with habitat or microhabitat. Other authors came to similar conclusions for other aspects, including activity patterns (Jeffries, 1966) and shape (Blake, 1985). Abele (1974) assigned to microhabitat (substrate) diversity a primary role as a determinant of decapod species richness. Our results on a cancrid guild support his view. Further, they led us to propose that habitat selection is the template in the assembly of alternative evolutionary strategies in *Cancer*.

Lawton and Elner (1985) advocated a different viewpoint, in which several morphological characters were related to feeding. The discrepancy between the two conceptual models is best seen in the interpretation of patterns of relative chela size. Species of *Cancer* can be ranked according to the way in which they perceive their habitats, from *C. magister*, fine-grain extreme, to *C. oregonensis*, coarse-grain extreme. Chelae are proportionally smaller (less powerful) in species living in open sandy areas (fine-grain environment), and tend to be larger (more powerful) in species occupying complexly structured substrates (coarse-grain environment). Lawton and Elner interpreted the relatively small chelae of *C. magister* and *C. gracilis* as well suited to feed on the soft-bodied, more mobile prey available on sandy areas, and the more robust chelae of *C. pagurus*, *C. productus*, and other species as an adaptation to feed on hard-shelled, sedentary prey. We suggest, alternatively, that habitat modulated the mating systems of species of *Cancer*. Resource defense polygyny is prevalent towards the coarse-grain extreme of the gradient, and explosive breeding assemblages towards the fine-grain extreme. Different mating systems resulted in varying degrees of sexual selection, determining observed patterns of relative chela size.

While Lawton and Elner did not speculate on the process leading to feeding specialization in cancrids, Vermeij (1977) suggested that "competition provides the ecological mechanism that controls the size and

sturdiness of prey items available to crabs." He observed that chela size in *Cancer* (among other genera) "increases as the number of sympatric congeners or the total number of brachyuran species in a given region rises," and hypothesized that geographic patterns of relative chela size result in part from diffuse and intrageneric competition. His conclusions were not supported by a subsequent reexamination of the data (Abele *et al.*, 1981).

We propose the following conceptual model for the diversification of the genus *Cancer*: (a) Species of *Cancer* diverge primarily in their utilization of different habitats; predation and limited availability of refuge space may have played an important role in shaping alternative strategies. (b) Natural diets are largely determined by availability at the selected habitats or microhabitats. (c) Habitat modulated mating systems, and these governed by sexual selection. (d) As a corollary, the main selective pressures that determined observed patterns of size and shape include habitat selection, predation, and sexual selection, with feeding adaptations playing a minor role, if any at all. Figure 9 summarizes the two alternative conceptual models of diversification in the genus *Cancer*. In what follows we briefly consider their main building blocks.

Predation, Size, and Refuges.—Size and habitat are intimately related to predation. Predators impose a heavy toll on the survival of epibenthic Crustacea, and may have driven the evolution of nocturnal foraging, protective coloration, manipulation of epibionts, and the use of refuges. All species of *Cancer* make use of structural refuges when small. Although frequency distributions of refuge size are difficult to obtain, "large" refuges are unavailable or scarce (Caddy, 1986, p. 2338). An alternative to the use of structural refuges is large size, implying a strong energetic allocation to growth until a "refuge in size" is reached, at the expense of other competing allocations. Thus, two (extreme) sets of alternative strategies are (a) refuge in size, strong commitment to growth over a relatively large number of instars, delayed reproductive maturity, or (b) use of structural refuges, modest commitment to growth over a relatively small

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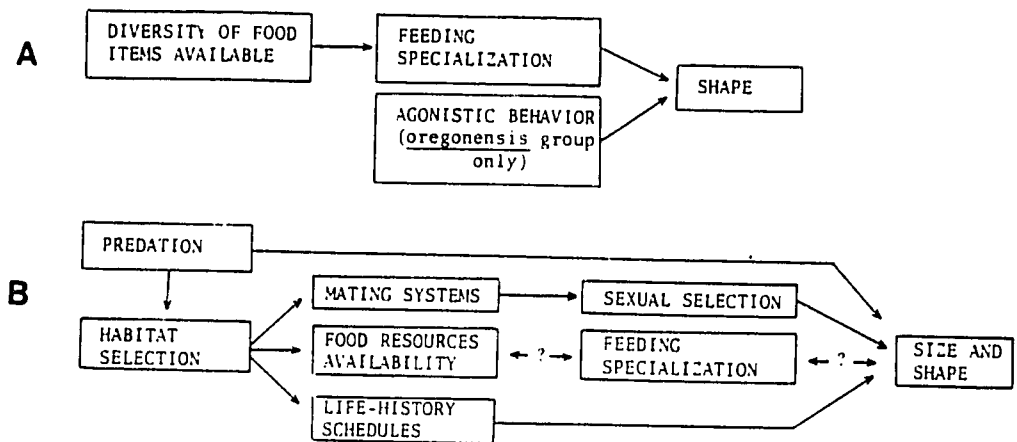


Fig. 9. Schematic representation of conceptual models of diversification in the genus *Cancer*. A, Lawton and Elner (1985) hypothesis; B, alternative model proposed in this study.

number of instars, early reproductive maturity. These are exemplified, respectively, by *C. magister* and *C. oregonensis* (Fig. 6).

Interference Competition for Microhabitat.—We and others found that locally coexisting species of *Cancer* from the Northeast Pacific tend to be segregated by microhabitat, as Jeffries (1966) did for the two species that coexist in Narragansett Bay. Several experimental studies (Fogarty, 1976; Wang, 1982) support the hypothesis that there is interference competition for microhabitat among the two Atlantic coast species and lobsters. Daly (1981) showed similar results for *C. productus* and two grapsids. There is good evidence of refuge space being a resource in limited supply in many environments.

Exploitative Competition for Food.—All species of *Cancer* are opportunistic carnivores and scavengers; their catholic diet depends on availability more than preference (Palmisano, unpublished data; personal observation). Coexisting species tend to overlap widely in their diet (Bernard, 1979; Lawton and Elner, 1985; personal observation), and the same species will exploit diverse resources in different areas (see Butler, 1954; Gotshall, 1977; Bernard, 1979; and Stevens *et al.*, 1982, for *C. magister*). Within patchy environments (such as many shallow bays) interspecific differences in diet can be explained from patterns of habitat use, but the opposite is not true. While there is good

evidence of interference competition for microhabitat, there is no convincing evidence of exploitative competition for food in decapod guilds which include cancrids.

Mating Systems and Secondary Sexual Characters.—Lawton and Elner (1985) used the ratio CHSIZE (ChW/CW) to assess relative chela size, this being "the template upon which feeding habits and prey preferences are determined." While it is obvious that chela size will influence the range of prey available, CHSIZE may have been determined by selective pressures other than foraging. The ratio is higher in *C. oregonensis*, which paradoxically has the mechanically weakest chela. The authors did not include it in their comparisons under suspicion of its role in agonistic behavior. For similar reasons *C. gracilis*, *C. productus*, and other species should also be eliminated, perhaps leaving *C. magister* alone in the foraging-related gradient. Lawton and Elner indicated that several species show sexual dimorphism for morphometric ratios (including CHSIZE), but found "no consistent intrageneric pattern." We suggest that there is a consistent intrageneric pattern, related to mating systems.

Lawton and Elner's consideration of CHSIZE requires further comments. There are good reasons to expect that differences in relative chela size may be influenced by sexual selection in males (Stein, 1976). Therefore, foraging-related evolutionary

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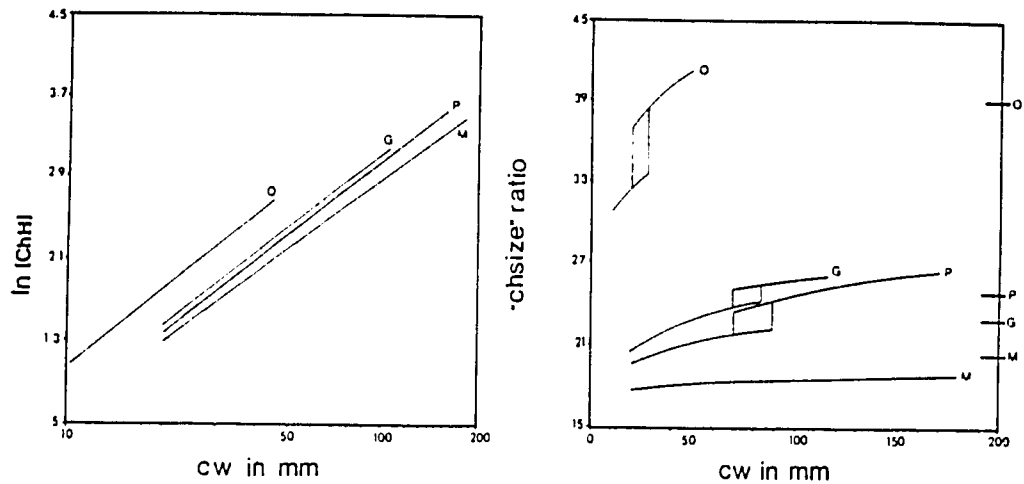


Fig. 10. Allometric relation between carapace width (CW) and chela height (ChH). Left, lines fitted to female log-transformed data (range of lines corresponds to range of measurements). Right, "CHSIZE" (ChH/CW) as a function of CW in males. Phases represented when appropriate. Marks on right indicate "CHSIZE" values given by Lawton and Elner (1985). G = *Cancer gracilis*, M = *C. magister*, O = *C. oregonensis*, P = *C. productus*.

considerations should be better addressed with female measurements. Lawton and Elner, however, compared males. Relative female chela sizes of the four species studied here are compared in Fig. 10 (left). The chela is proportionally higher in *C. gracilis* than in *C. productus*. The same relationship holds for pre- and postpuberty males (Fig. 10, right). Lawton and Elner (their table 4) concluded, however, that CHSIZE is proportionally higher in *C. productus*. The average CW of the specimens measured by them were 75.8 mm ($N = 7$) for *C. gracilis*, and 141.0 mm ($N = 3$) for *C. productus*. Their analysis apparently involved postpuberty *C. productus* and mostly prepuberty *C. gracilis*. Figure 10 (right, based on several hundreds of measurements) illustrates this point. As Abele *et al.* (1981) mentioned in their discussion of Vermeij's (1977) results, caution is advised in the analysis of crab morphometric relationships for the following reasons: (a) slopes of linear relationships between log-transformed measurements frequently differ among species or sexes, (b) ratio values are often size-dependent and nonlinearly related to size, and (c) allometric phases are of frequent occurrence.

Shape.—Several morphological traits and their physiological correlates have habitat-related adaptive significance, including the "straining device" of *C. magister* (Wey-

mouth, 1915), relatively long legs of "motile" species (Lawton and Elner, 1985), and hydrodynamics of carapaces (Blake, 1985). Two alternative explanations have been proposed for the relatively long legs of crabs living in open grounds: feeding on fast moving epifaunal prey (Lawton and Elner, 1985), and avoidance of predators (Jeffries, 1966, p. 480). The first is questionable, the second is reasonable. Crabs are mostly nocturnal foragers and localize/assess prey mostly by chemoreception (Pearson *et al.*, 1979), tactile cues, and vision playing complementary roles. They are fine searchers, even fast catchers at short range (Spencer, 1932, p. 16; Mackay, 1943, p. 262), but poor pursuers. The diet of *C. gracilis*, a species which because of its relatively long legs was predicted to feed on motile prey, is composed mostly of bivalves and polychaetes, at least in Garrison Bay.

The model proposed is compatible with the apparent diversification of the genus within a single biogeographic domain during the Miocene (Nations, 1975, 1979). Given the dispersal capability of species of *Cancer*, Nations' scheme is difficult to accommodate without advocating parapatric or sympatric speciation, which may have involved habitat selection, assortative mating for habitat, and divergence favored by sexual selection.

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