Fecundity and Reproductive Output in Nine Species of *Cancer* crabs (Crustacea, Brachyura, Cancridae)[1]

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The major variables of reproductive output and fecundity were compared among brooding females of nine species of *Cancer* from the North Pacific and North Atlantic: *C. oregonensis, C. gracilis, C. irroratus, C. antennarius, C. productus, C. borealis, C. anthonyi, C. magister,* and *C. pagurus.* Female body size is the principal determinant of reproductive output, with dry body weights spanning two orders of magnitude from 1.2 to 199.5 g among species and often one order of magnitude within species. Mean dry brood weights ranged from 0.21 to 26.7 g among species, with relative brood size varying from 11 to 19% of female weight. The brood mass is partitioned into eggs ranging among species from 311 to 442 μm, resulting in mean fecundities ranging among species from 18 200 to 2 208 000 eggs per brood. Most species produce one or two broods per year over the winter–spring season over a reproductive span averaging 6.6 yr (range 4–10 yr). Cumulative reproductive output and cumulative fecundity over the maximum estimated life span exhibited approximately isometric functions of maximum body size, and they ranged among species from 1.88 to 316 g brood weight and 158 000 to 22 300 000 eggs per lifetime, respectively. The pattern of covariation of reproductive traits in the Cancridae corresponds well with the overall pattern previously determined for a diverse array of brachyurans from seven families.

Les paramètres principaux de la production d'oeufs et de la fécondité ont été comparés chez les femelles oeuvées de neuf espèces de *Cancer* du Pacifique Nord et de l'Atlantique Nord : *C. oregonensis, C. gracilis, C. irrotatus, C. antennarius, C. productus, C. borealis, C. anthonyi, C. magister* et *C. pagurus.* La taille des femelles est le facteur le plus fortement corrélé à la production d'oeufs; le poids corporel sec mesuré variait de deux ordres de grandeur dans l'ensemble des espèces, allant de 1,2 à 199,5 g, et différait souvent d'un ordre de grandeur entre les individus d'une même espèce. Le poids moyen de la ponte variait de 0,21 à 26,7 g pour l'ensemble des espèces, et le poids de la ponte d'une femelle représentait entre 11 et 19 % de son poids. Pour l'ensemble des espèces, la taille des oeufs variait de 311 à 442 μm et le nombre d'oeufs par ponte (fécondité), de 18 200 à 2 208 000. La plupart des espèces produisent une ou deux pontes par année durant l'hiver et le printemps sur une période de 6,6 ans en moyenne (4 à 10 ans). La production pondérale d'oeufs et la fécondité cumulatives pour la durée de vie maximale estimée montrent une relation approximativement isométrique avec la taille corporelle maximale et varient parmi les espèces de 1,88 à 316 g (poids total des oeufs) et de 158 000 à 22 300 000 oeufs, respectivement, pour toute la durée de la vie des femelles. Les rapports de covariance des paramètres caractérisant la reproduction chez les Cancridae correspondent avec les relations générales établies antérieurement chez divers brachyoures de sept familles.

The principal determinant of fecundity per brood and reproductive output (brood mass) in female brachyuran crabs is body size, such that brood weight is generally constrained to about 10% of female body weight by the space available for yolk accumulation in the cephalothorax (Hines 1982). Egg size is the major reproductive trait which is highly variable among brachyuran species (Hines 1982, 1986a). This high interspecific variability in how the relatively constrained brood mass is partitioned (many small or few large eggs) results in much greater interspecific variation in fecundity than in brood mass for equivalent-sized crabs (Hines 1982). Because of the relative constraint on brood mass, the number of broods produced per year is probably the other key reproductive trait which exhibits high interspecific variability in brachyuran life history strategies (Hines 1982). In combination with these size-specific reproductive variables, age and size of mature instars determine

the schedules of reproductive output and fecundity (the m_x schedule of life tables; Deevey 1947) throughout the reproductive life of a brachyuran species.

The ecological and evolutionary consequences of these apparent covariations of reproductive traits have not been studied extensively in any group of closely related brachyuran species in similar habitats (Hines 1986a). However, I recently compared their covariation in two species of large deep-sea crabs in the family Geryonidae (Hines 1988). As in other crab species, body size was the primary determinant of reproductive output in the deep-sea species; however, their brood masses at 16 and 22% of body weight are considerably larger than the 10% average for other crab species and are near the upper extreme of apparently typical interspecific variation. They also had very large eggs and relatively low fecundity per brood compared with many species of similar size. Comparison of covariation in reproductive traits between the two species showed that one (*Geryon quinquedens*) had a 50% larger volume of the body

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cavity, resulting in a 50% larger brood mass, than the other (*G. fenneri*). Despite its larger brood mass, egg size in *G. quinquedens* was about twice as large as in *G. fenneri*, resulting in about equal size-specific fecundity per brood in the two species. There are no other published comparisons of reproductive traits among an array of closely related brachyuran species which span a broad size range.

The brachyuran genus *Cancer* comprises 23 extant species distributed throughout the cold temperate and boreal zones of the Pacific and Atlantic oceans (Mackay 1943; Nations 1975, 1979). Species in the genus span a wide range of body size at maturity. Because several of the larger species are conspicuous and form the basis of historically lucrative or of currently developing fisheries, the biology of several important commercial species is well studied: *C. magister* (e.g. Poole 1966; Wild and Tasto 1983; Melteff 1985), *C. pagurus* (e.g. Hancock and Edwards 1967; Ingle 1981), *C. anthonyi* (Anderson and Ford 1976; Shields 1987), *C. antennarius* (Carroll 1982), *C. productus* (Trask 1970), and *C. borealis* (Haefner 1977; Sastry 1977; Carpenter 1978). Although not commercially important, *C. irroratus* is also relatively well studied (e.g. Krouse 1976; Haefner 1976; Reilly and Saila 1978) because of its ecological importance in shallow subtidal communities of the North Atlantic and also apparently because of its proximity to concentrations of marine biologists in northeastern North America. The biology of the nine species which occur along the west coast of North America has been reviewed (Garth and Abbott 1980), and Orensanz and Gallucci (1988) recently provided valuable new information on the growth and life histories of *C. oregonensis*, *C. gracilis*, and *C. productus*. Thus, data on the rate of brood production, as well as size and age of reproductive instars, can be extracted from the literature for at least eight species of *Cancer*. However, there has been no detailed analysis of the group's reproductive patterns employing appropriate allometric, statistical, and demographic methods for interspecific comparisons. Moreover, most of these key reproductive variables have been inadequately quantified, even though they comprise demographic traits which should be considered for sound fisheries management of commercially important species.

This study compares brood weight, fecundity per brood, and egg size as a function of female body size in nine species of *Cancer* from the north-temperate and boreal and zones of the eastern Pacific and Atlantic oceans. In combination with data on age, size, and brood production rates extracted from the literature, these size-specific reproductive variables are used to estimate the schedules of brood production and fecundity over the maximum life span of eight of the species. I also compare the pattern of covariation in reproductive traits in the genus with the apparently general pattern for brachyurans determined from species representing a diverse array of families (Hines 1982).

Methods

Samples of 5–15 ovigerous females of each of nine species of *Cancer* were obtained from locations and sources listed in Table 1. The samples selected females which spanned the size range of ovigerous females collected from populations at the sites. Although the size range of sampled crabs did not necessarily span the range reported in the literature for reproductive females, the range of sampled crabs was in all cases more than adequate to determine the size-dependent regressions for reproductive variables (see Results). The collections selected crabs with brooded embryos in developmental stages from late blastula to early gastrula to avoid confounding effects of embryonic diameters swelling during late stages of development or of egg loss from the brood during incubation. The samples were frozen and then fixed in 10% formalin–seawater and stored in 70% ethanol until they were processed. Processing followed the method of Hines (1982, 1988), in which the following variables were measured for each crab: maximum (spine-to-spine) carapace width (millimetres) of the female, female dry body weight (grams), dry weight (grams) of the brooded egg mass, average volume (cubic millimetres) of an egg, calculated for a sphere

TABLE 1. Collecting information for nine species of *Cancer*.

Species	No. of females	Collecting site	Depth (m)	Collecting method	Date
C. oregonensis	14	Puget Sound, Washington	0–10	Hand, dredges	April 1985
C. gracilis	12	Puget Sound, Washington	36	Trawl, dredges	April 1985
C. irroratus	10	Boothbay Harbor, Maine	3–10	Lobster trap	July 1984
C. antennarius	10	Humboldt Bay, California	30	Crab pot	December 1980
C. productus	6	Humboldt Bay, California	30	Crab pot	February 1984
C. borealis	11	Boothbay Harbor, Maine	3–10	Lobster trap	July 1984
C. anthonyi	8	Santa Barbara, California	15–70	Crab pot	September 1982
C. magister	10	Gulf of Farallones, California	35–75	Crab pot	December 1980
C. pagurus	5	Scotland	12–45	Crab pot, dredge	December 1985, March 1986

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TABLE 2. Size and reproductive regressions for nine species of *Cancer* (ns = not significant).

	log body wt. = b(log carapace width) + c	R^2	log brood wt. = b(log body wt.) + c	R^2	log no. of eggs = b(log body wt.) + c	R^2
C. oregonensis	y = 3.041x − 4.089	0.995	y = 1.075x − 0.757	0.978	y = 1.026x + 4.188	0.965
C. gracilis	y = 2.896x − 4.134	0.904	y = 1.049x − 0.851	0.812	y = 1.081x + 4.392	0.946
C. irroratus	y = 2.612x − 3.656	0.736	y = 1.393x − 1.472	0.725	y = 1.187x + 3.781	0.703
C. antennarius	y = 2.745x − 3.663	0.945	y = 1.349x − 1.530	0.922	y = 1.518x + 3.285	0.929
C. productus	y = 2.523x − 3.379	0.983	y = 0.838x − 0.429	0.965	y = 0.711x + 4.462	0.854
C. borealis	y = 2.547x − 3.443	0.722	y = 1.282x − 1.476	0.698	y = 1.137x + 3.711	0.621
C. anthonyi	y = 2.896x − 4.093	0.973	y = 1.011x − 0.855	0.948	y = 0.995x + 4.354	0.960
C. magister	y = 0.378x + 1.292	0.004 ns	y = 0.527x + 0.229	0.644	y = 0.611x + 4.677	0.629
C. pagurus	y = 4.119x − 6.813	0.959	y = 1.246x − 1.440	0.956	y = 1.152x + 3.499	0.955

TABLE 3. Means and ranges of body size and reproductive variables for nine species of *Cancer*. "Observed min.–max." indicates range of observations for a variable in the sample for each species. "Predicted min.–max." indicates range predicted by the regressions in Table 2 for the smallest and largest individuals sampled for each species.

	Body size		Egg size	Brood size		Fecundity
	$\bar{x}$ carapace width (mm) (observed min.–max.)	$\bar{x}$ dry wt. (g) (observed min.–max.)	$\bar{x}$ diameter (μm) (observed min.–max.)	$\bar{x}$ dry wt. (g) (observed min.–max.) (predicted min.–max.)	$\bar{x}$ % of body wt.	$\bar{x}$ no. of eggs/brood (observed min.–max.) (predicted min.–max.)
C. oregonensis	23 (8–27)	1.2 (0.05–5.1)	383 (296–489)	0.21 (0.007–0.085) (0.007–1.008)	17.5	18 200 (780 to 82 500) (713 to 82 000)
C. gracilis	68 (52–81)	14.7 (6.7–23)	329 (294–352)	2.36 (0.3–5.5) (1.0–3.8)	16.1	453 700 (189 300 to 789 400) (192 700 to 731 200)
C. irroratus	78 (66–89)	19.5 (13–31)	406 (332–441)	2.11 (1.2–4.3) (1.2–4.0)	10.8	205 200 (101 600 to 356 400) (126 800 to 355 800)
C. antennarius	100 (65–120)	67.6 (20–118)	333 (306–374)	8.68 (1.6–24.0) (1.7–18.4)	12.8	1 156 000 (198 500 to 3 004 000) (182 000 to 2 692 000)
C. productus	116 (92–142)	67.6 (39–107)	367 (340–401)	12.7 (7.6–18.9) (8.0–18.7)	18.8	877 300 (559 000 to 1 036 000) (593 300 to 1 216 000)
C. borealis	120 (105–135)	70.8 (46–95)	428 (353–470)	7.87 (3.7–12.4) (4.5–11.5)	11.1	652 300 (311 400 to 1 045 000) (399 500 to 1 802 000)
C. anthonyi	127 (86–153)	100.0 (33–173)	311 (278–331)	14.7 (4.1–23.5) (4.8–25.6)	14.7	2 208 000 (680 100 to 3 849 000) (732 700 to 3 809 000)
C. magister	155 (145–170)	131.8 (89–251)	442 (412–462)	22.2 (15.5–32.6) (18.0–31.1)	16.8	938 300 (658 600 to 1 342 000) (738 000 to 1 391 000)
C. pagurus	163 (140–184)	199.5 (108–332)	396 (383–414)	26.7 (10.9–45.5) (12.4–50.3)	13.4	1 408 000 (605 600 to 2 310 000) (694 200 to 2 531 000)

with the mean measured diameter (micrometres) including the chorionic membrane tightly adhering to the embryonic surface of a subsample of seven eggs before drying, and the number of eggs per brood, extrapolated from the dry weights of the total brood and a counted subsample of about 2000 eggs. At the time of egg measuring and counting, all broods were examined under a dissecting microscope for the presence of nemertean worms or other potential infections by egg predators.

Published data on the number, age, size, and brood production rates of mature instars were extracted from the literature for females of eight of the nine species sampled. These data were combined with the size-specific reproductive output determined empirically from the sampled crabs to estimate schedules of brood mass production and fecundity over the maximum life span of the species and to estimate the cumulative maximum lifetime brood weight and cumulative maximum lifetime fecundity for the species.

Data were analyzed with regressions of log–log transformations for allometric plots ($y = cX^b$; $\log y = b \log X + c$) of the reproductive variables versus dry weight. Comparisons

of different-sized crabs utilized ANCOVA with female body weight as the covariate after testing for homogeneity of variances with F_{max} tests (Sokal and Rohlf 1981) and equality of slopes, as discussed in Hines (1982).

Results

Mature females sampled within most of the nine species varied widely in body size. The sample of *C. oregonensis* had the largest range in size, with the largest individual being 4.6 times the carapace width and 102 times the dry body weight of the smallest individual (Tables 2 and 3). In contrast, the sample of *C. magister* ranged only 1.2-fold in carapace width and that of *C. borealis* ranged only 2.1-fold in dry body weight from the smallest to largest individuals (Tables 2 and 3). These size ranges were judged to be adequate samples of variation within species for three main reasons: (1) analyses of size dependence in reproductive variables yielded significant regression coefficients in all nine species, which is an important component of the subsequent allometric considerations (Table 2); (2) with careful consideration of exceptions, the ranges of most of the samples closely matched the size range of reproductive females reported in the literature (see below, Tables 3 and 4); and (3) the mean sizes of sampled females closely matched the average size of reproductive females reported in the literature for each of the nine species (see below, Tables 3 and 4). Mean body size of the females among the species ranged over sixfold in carapace width and about two orders of magnitude in dry body weight from 23 mm and 1.2 g, respectively, in *C. oregonensis* to 163 mm and 200 g, respectively, in *C. pagurus* (Tables 2 and 3; Fig. 1). Log body weight differed significantly among species (ANOVA, $F_{(8,81)} = 66.04$, $P < 0.001$). However, all of the species except the smallest (*C. oregonensis*) overlapped considerably in body size, and even *C. oregonensis* represented a clear continuum in body size of the group (Table 3; Fig. 2 and 3).

Nemertean worms (*Carcinonemertes* spp.) were observed in the egg masses of only one species (*C. magister*), but these infections were in their earliest stages and judged not to have impacted the egg masses significantly (Wickham 1979a, 1979b, 1980, pers. comm.).

Mean egg size ranged from 311 μm in diameter and 0.0157 mm³ in volume for *C. anthonyi* to 442 μm and 0.0452 mm³ for *C. magister* (Table 2; Fig. 1). Egg size did not vary significantly within species (ANOVA, $P > 0.05$). Mean egg size also was not correlated with female body size among species (Fig. 1; Table 2; ANCOVA, $F_{(8,81)} = 0.40$, $P > 0.05$).

Brood weight increased significantly with female body weight for all species (Fig. 2; Table 2; ANCOVA, $P < 0.05$); however, regression slopes did not differ significantly among species (ANCOVA, $F_{(8,81)} = 1.28$, $P > 0.2$). As a result of the size differences among species, brood size differed significantly among species, with mean dry brood weights ranging from only 0.21 g in *C. oregonensis* to over 26 g in *C. pagurus* (Fig. 1; Table 3; ANOVA on log brood weight, $F_{(8,81)} = 94.32$, $P < 0.001$). When adjusted for differences in female body size, least squares mean brood weights were similiar but still differed significantly and ranged from about 2.6 g in *C. pagurus* to 10.28 g in *C. magister* (Fig. 1; ANCOVA on log brood weight with log body weight as a covariate, $F_{(8,81)} = 2.17$, $P < 0.05$). Brood weight as a proportion of female
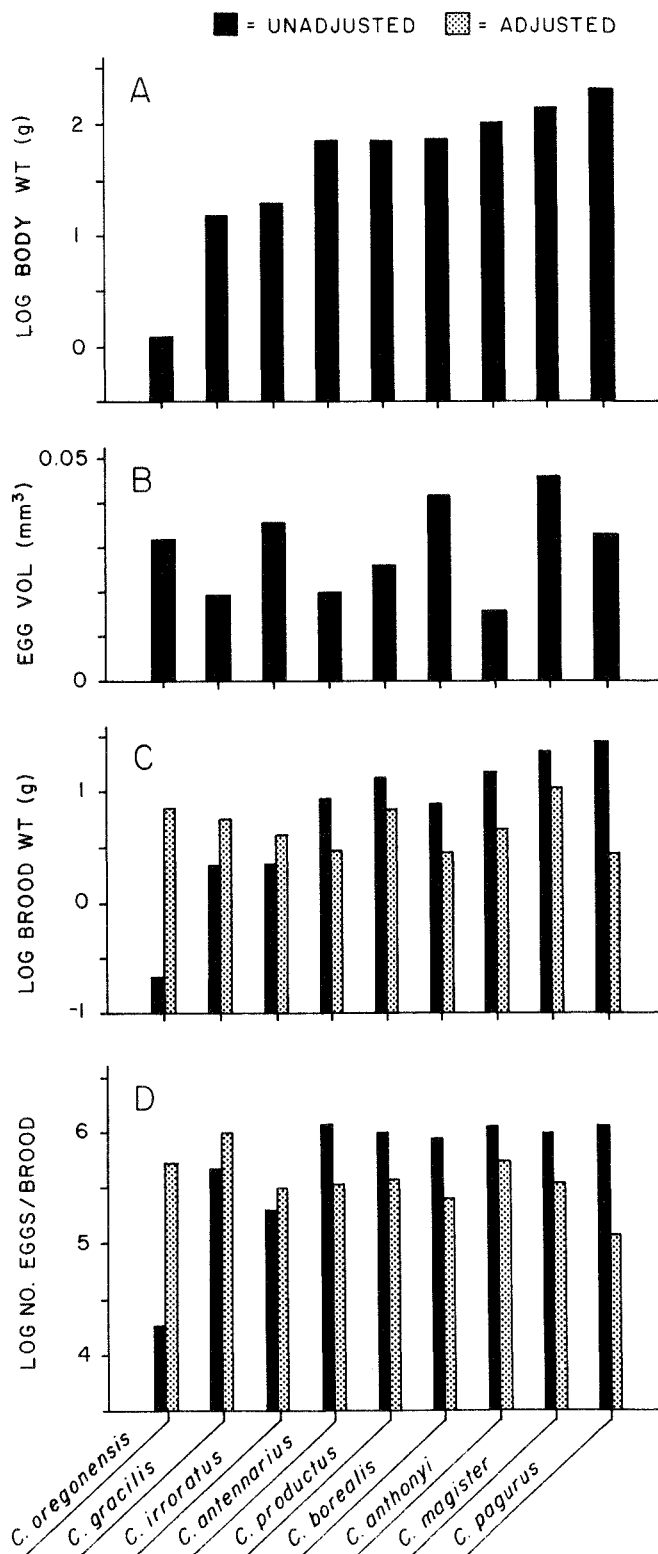

FIG. 1. Comparison of body size and reproductive variables for nine species of *Cancer* listed in Table 1. (A) Dry body weight; (B) egg volume; (C) dry brood weight; (D) number of eggs per brood. Plotted values are either arithmetic means (unadjusted for variation in body size) or least squares means (adjusted for variation in body size) from ANCOVA with log body weight as the covariate. Note log scale of Fig. 1A, 1C, and 1D.

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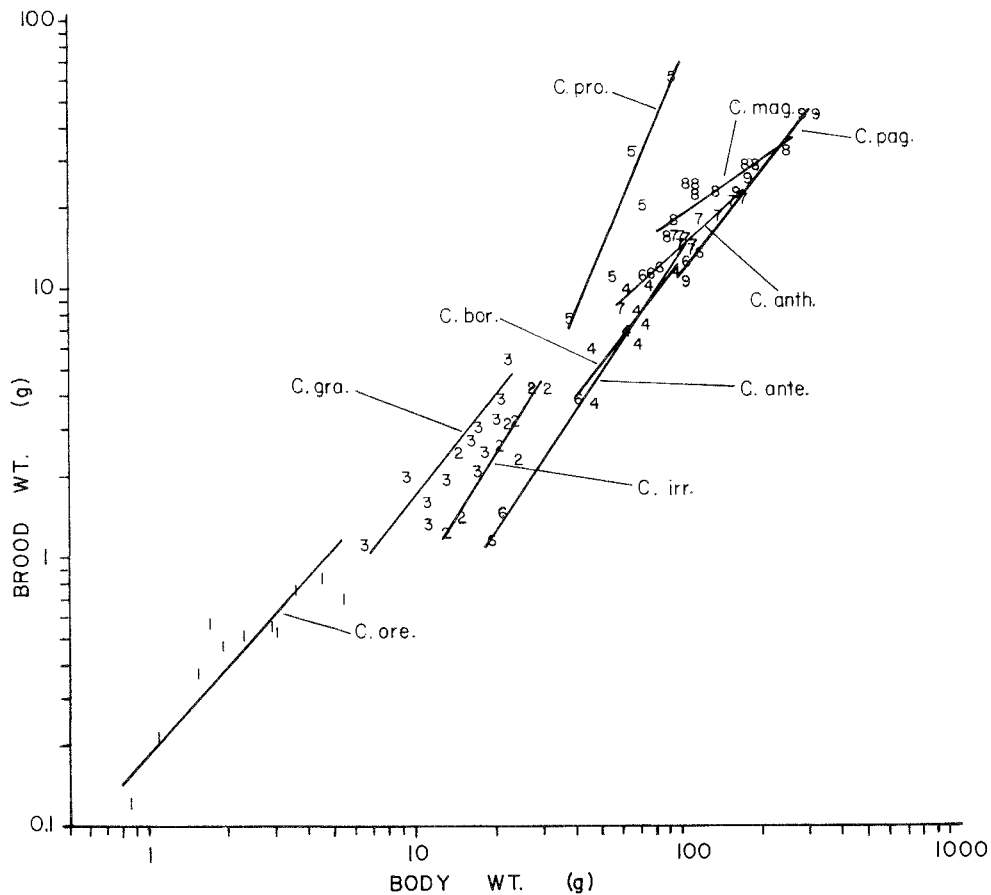
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FIG. 2. Comparison of dry brood weight as a function of dry body weight for nine species of *Cancer* listed in Table 1. Regression equations are given in Table 2. Numbers coded for each species plot the points for each brood. Note log scales.

body weight ranged from 10.8% in *C. irroratus* to 18.8% in *C. productus*.

Fecundity per brood increased significantly with female body size in all nine species (Fig. 3; Table 2; ANOVA, $F = 197.98$, $P < 0.001$), and only *C. magister* differed significantly (lower) in regression slope for log egg number versus log body weight (Table 2; ANCOVA, $P < 0.05$). As a result of the differences in female body size, fecundities per brood differed significantly among species, with mean fecundities ranging from only about 18 000 eggs per brood in *C. oregonensis* to over 2 200 000 eggs in *C. anthonyi* (Fig. 1 and 3; Table 3; ANOVA, $F_{(8,81)} = 133.45$, $P < 0.001$). When adjusted for differences in female body size, least squares mean log numbers of eggs per brood were similar but still differed significantly among species and ranged from about 158 000 eggs per brood in *C. pagurus* to about 977 000 eggs in *C. gracilis* (Fig. 1; ANCOVA on log number of eggs with log body weight as a covariate, $F_{(8,81)} = 2.39$, $P < 0.05$).

Estimates of the instar number, age, and size of mature females extracted from the literature corresponded well with the size range of ovigerous crabs in my samples of the nine species, although the minimum and maximum sizes reported for some species exceeded the sampled range in a few species (Table 4). No data are available for growth in *C. borealis*, so data on instar number, size, and age could not be extracted from the literature, and cumulative maximum lifetime brood production and fecundity could not be estimated for this species. Most species produce a single brood each winter, although up

to two or three broods per year have been reported for *C. gracilis*, *C. antennarius*, *C. productus*, and *C. anthonyi* (Table 4). Females of most other species mated and molted to a new instar each year, although larger individuals of the largest species (especially *C. magister* and *C. pagurus*) and perhaps *C. irroratus* are reported to skip molting in some years (e.g. Butler 1961; Hancock and Edwards 1967; Bennett 1974; Haefner and Van Engel 1975; Hankin et al. 1985). Age at maturity ranged from as young as 0.5 yr in *C. oregonensis* to as old as 4 yr in *C. pagurus*, although most species apparently mature at 1–2 yr old. The reproductive life span in the group ranged from about 4 yr in *C. gracilis*, *C. productus*, and *C. magister* to about 7 yr or more in *C. antennarius* and *C. pagurus*, with an average of 5 yr for the group (Table 4). The cumulative number of broods produced over the maximum life span of each species ranged from about 4 broods in *C. productus* and *C. magister* to about 10 in *C. antennarius* and *C. anthonyi*, with an average of 6.6 for the group. Although the smallest species (*C. oregonensis*) had the earliest age at maturation, neither the reproductive life span nor the cumulative number of broods produced was dependent on body size. Cumulative maximum lifetime brood weight (Table 4) ranged from 1.88 g in *C. oregonensis* to 316 g in *C. pagurus*; and it is a linear, isometric function of maximum body size, with very little variation among the species (Fig. 4A; log Cumbroodwt = 1.078 log Maxbodwt − 0.457; ANOVA, $F_{(1,6)} = 498.73$, $P < 0.0001$, $R^2 = 0.99$). Cumulative maximum lifetime fecundity (Table 4) ranged from 158 000 eggs in *C. oregonensis* to about 22 300 000 in *C. anthonyi*. Cumu-
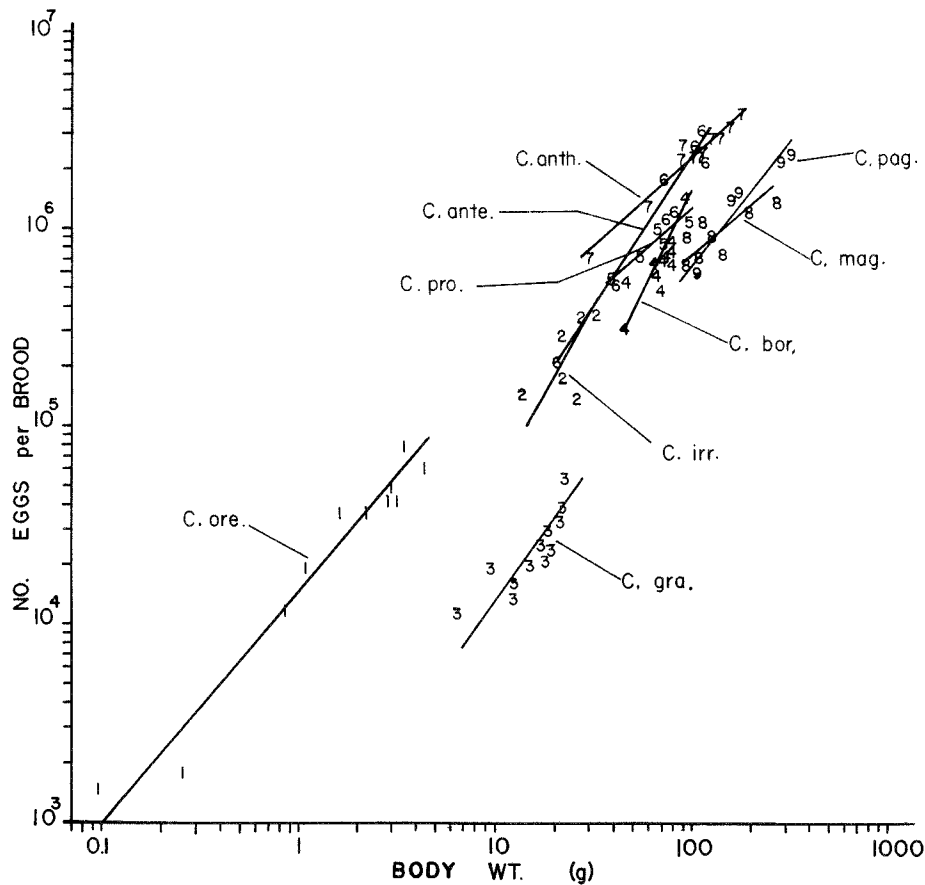
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FIG. 3. Comparison of number of eggs per brood as a function of dry body weight for nine species of *Cancer* listed in Table 1. Regression equations are given in Table 2. Numbers coded for each species plot the points for each brood. Note log scales.

lative fecundity also is an approximately linear, isometric function of maximum body size, but variation among species about the regression is considerably greater than for brood weight (Fig. 4B; log Cumfecund = 1.003 log Maxbodwt + 4.621; ANOVA, $F_{(1,6)} = 49.82$, $P < 0.001$, $R^2 = 0.89$).

Discussion

The basic patterns of reproductive variables and constraints in the Cancridae conform generally well with those determined earlier for a broad array of brachyuran species (Hines 1982). Female body size is clearly the principal determinant of reproductive output and fecundity in the nine cancrid species, which spanned two orders of magnitude in mean body weight among species and often ranged an order of magnitude in body weight among ovigerous individuals within species. As a result of variation in body size, reproductive output and fecundity per brood also ranged about two orders of magnitude among species and one order of magnitude among individuals within species. Although the species differed significantly in brood weight and fecundity per brood after adjusting statistically for variation in body size, variation among species is relatively small. It is evident that brood size and fecundity are similar among equivalent-sized females (Fig. 1), with all species exhibiting a similar allometric relationship (Fig. 2 and 3). These cancrid species apparently produce a small number of broods per year, typically only about one or two over the winter season. Cumulative reproductive output and fecundity over the predicted life spans of each species exhibit nearly isometric relationships for the

group, although cumulative fecundity is more variable than cumulative brood weight (Fig. 4). In contrast with reproductive output and fecundity, egg size did not vary with female size within or among species, but egg volume varied about threefold among species (Fig. 1). Thus, female body size and egg size appear to be the major variables of reproduction in the Cancridae, while brood weight adjusted for body size and the number of broods per season are relatively constant. Fecundity per brood and fecundity per life span appear to follow as direct consequences of female size limits on reproductive output, albeit with increased variance.

The comparative data reported for reproductive variables of the nine cancrids in this paper are generally corroborated by the literature on individual species. For some species, the size range of reproductive females is wider than those of my relatively limited samples, especially for *C. borealis*, *C. antennarius*, *C. productus*, *C. magister*, and *C. pagurus* (compare sizes in Tables 3 and 4). Both maximum and minimum size at maturity vary geographically within some species, especially *C. irroratus* (Scaratt and Lowe 1972; Krouse 1976; Haefner 1976; Reilly and Saila 1978; Bigford 1979; Campbell and Eagle 1983). However, the size-dependent regressions provided from my samples allow comparative estimates of reproductive variables for all sizes of females within each species. There are essentially no other published measures for brood weight in cancrids, except by Hankin et al. (1985) for *C. magister* with somewhat smaller brood weights for equivalent-sized females (about 16–26 g versus about 16–32 g in my samples). Fecundities per brood in species with published estimates correspond

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TABLE 4. Schedules of brood production and fecundity for nine species of *Cancer*. Data for instar, age, carapace width, and no. of broods are extracted from references. Dry brood wt., cumulative brood wt., no. of eggs per brood, and cumulative fecundity are derived from regressions in Table 2. "Cumulative brood wt." and "cumulative fecundity" are cumulative schedules for $\bar{x}$ no. of broods times the brood wt. or no. of eggs per brood for each age interval.

Species (references)	Instar (no.)	Age (yr)	Carapace width (mm)	Dry body wt. (g)	No. of broods $\bar{x}$ (min.-max.)	Brood wt. (g)	Cumulative brood wt. (g)	No. of eggs per brood	Cumulative fecundity
C. oregonensis	5	0.5	12	0.156	1 (1-2)	0.024	0.024	2 290	2 290
(Orensanz and	6	1	16	0.374	1 (1-2)	0.061	0.085	5 620	7 910
Gallucci 1988)	7	2	21	0.855	1 (1-2)	0.148	0.233	13 200	21 100
	8	3	27	1.84	1 (1-2)	0.337	0.570	28 800	49 900
	9	4	31	2.79	1 (1-2)	0.527	1.10	43 700	93 600
	10	5	35	4.04	1 (1-2)	0.785	1.88	64 600	158 200
C. gracilis	9	1.5	47	5.11	1 (1)	0.780	0.780	143 800	143 800
(Orensanz and	10	2	62	11.4	1.5 (1-2)	1.81	2.59	342 400	486 200
Gallucci 1988)	11	3	77	21.3	1.5 (1-2)	3.49	6.08	672 900	1 159 100
	12	4	86	29.4	1 (1-2)	4.89	11.0	953 400	2 112 500
C. irroratus	9	3	51	6.37	1 (1)	0.445	0.445	54 400	54 400
(Reilly and Saila	10	4	61	10.2	1 (1)	0.857	1.30	95 100	149 500
1978; Haefner and	11	5	71	15.1	1 (1)	1.48	2.78	151 500	301 000
Van Engel 1975;	12	6	80	20.6	1 (1)	2.28	4.98	219 100	520 100
Krouse 1976)	13	7	89	27.3	1 (1)	3.38	8.36	306 000	826 100
	14	8	97	34.2	1 (1)	4.62	13.0	399 800	1 225 900
C. antennarius	10	1.5	62	18.1	1 (1)	1.47	1.47	156 400	156 400
(Carroll 1982)	11	2	71	26.2	1.5 (1-2)	2.42	3.89	274 100	430 500
	12	3	83	40.3	1.5 (1-2)	4.32	8.21	527 100	957 600
	13	4	97	61.8	1.5 (1-2)	7.69	15.9	988 900	1 946 600
	14	5	112	91.6	1.5 (1-2)	13.1	29.0	1 833 000	3 779 500
	15	6	128	132.0	1.5 (1-2)	21.4	50.4	3 192 000	6 971 500
	16	7	145	186.0	1.5 (1-2)	34.0	84.4	5 372 000	12 343 500
C. productus	10	1	59	12.3	1 (1-2)	3.05	3.05	172 600	172 600
(Orensanz and	11	2	78	24.8	1 (1-2)	5.49	8.54	284 100	456 700
Gallucci 1988)	12	3	107	55.1	1 (1-2)	10.7	19.2	501 100	957 800
	13	4	118	70.5	1 (1-2)	13.2	32.4	597 100	1 554 900
C. borealis	?	?	90	34.2	1 (1)	3.09	3.09	285 200	285 200
(Haefner 1977;	?	?	?	?	1 (1)	?	?	?	?
Carpenter 1978)	?	?	140	106.0	1 (1)	13.2	?	1 032 000	?
C. anthonyi	12	1	90	36.9	2 (1-3)	5.36	10.7	818 800	1 638 000
(Anderson and Ford	13	2	105	57.6	2 (1-3)	8.41	27.5	1 275 000	4 188 000
1976; Shields	14	3	120	84.8	2 (1-3)	12.4	52.3	1 569 000	7 326 000
1987)	15	4	150	130.0	2 (1-3)	19.2	90.7	2 359 000	12 044 000
	16	5	170	233.0	2 (1-3)	34.5	159.7	5 123 000	22 290 000
C. magister	10	2	108	115.0	1 (1)	20.7	20.7	886 200	886 200
Mackay and Weymouth	11	3	131	124.0	1 (1)	21.5	42.2	903 800	1 790 000
1935; Cleaver 1949;	12	4	161	134.0	1 (1)	22.4	64.6	947 800	2 737 800
Butler 1961;	13	5	182	140.0	1 (1)	22.9	87.5	973 400	3 711 200
Collier 1983; Hankin et al. 1985)									
C. pagurus	14	4	118	52.6	1 (1)	5.06	5.06	303 100	303 100
(Mackay 1942;	15	5	146	126.0	1 (1)	15.0	20.1	829 100	1 132 200
Edwards 1979;		6			1 (1)		35.1		1 961 300
Hancock and Edwards	16	7	177	280.0	1 (1)	40.7	75.8	2 080 000	4 041 300
1967; Bennett 1974)		8			1 (1)		116.0		6 121 300
	17	9	211	576.0	1 (1)	99.9	216.0	4 775 000	10 896 300
		10			1 (1)		316.0		15 671 300

closely with my samples. For example, numbers of eggs per brood in my samples for *C. magister* are virtually identical to estimates by Hankin et al. (1985) for equivalent-sized crabs. My size-dependent estimates of fecundity per brood are also similar to fecundity ranges reported by others for *C. oregonensis* (Knudsen 1964; Orensanz and Gallucci 1988), *C. gracilis* (Orensanz and Gallucci 1988), *C. irroratus* (Reilly and Saila 1978; Campbell and Eagle 1983), *C. antennarius* (Carroll 1982), *C. borealis* (Haefner 1977), *C. anthonyi* (Shields 1987; Shields 1991), and *C. pagurus* (Edwards 1979). *Cancer setosus*, another cancrid in the same size range as *C. magister*, produces 600 000 to 1 700 000 eggs per brood in females 83–

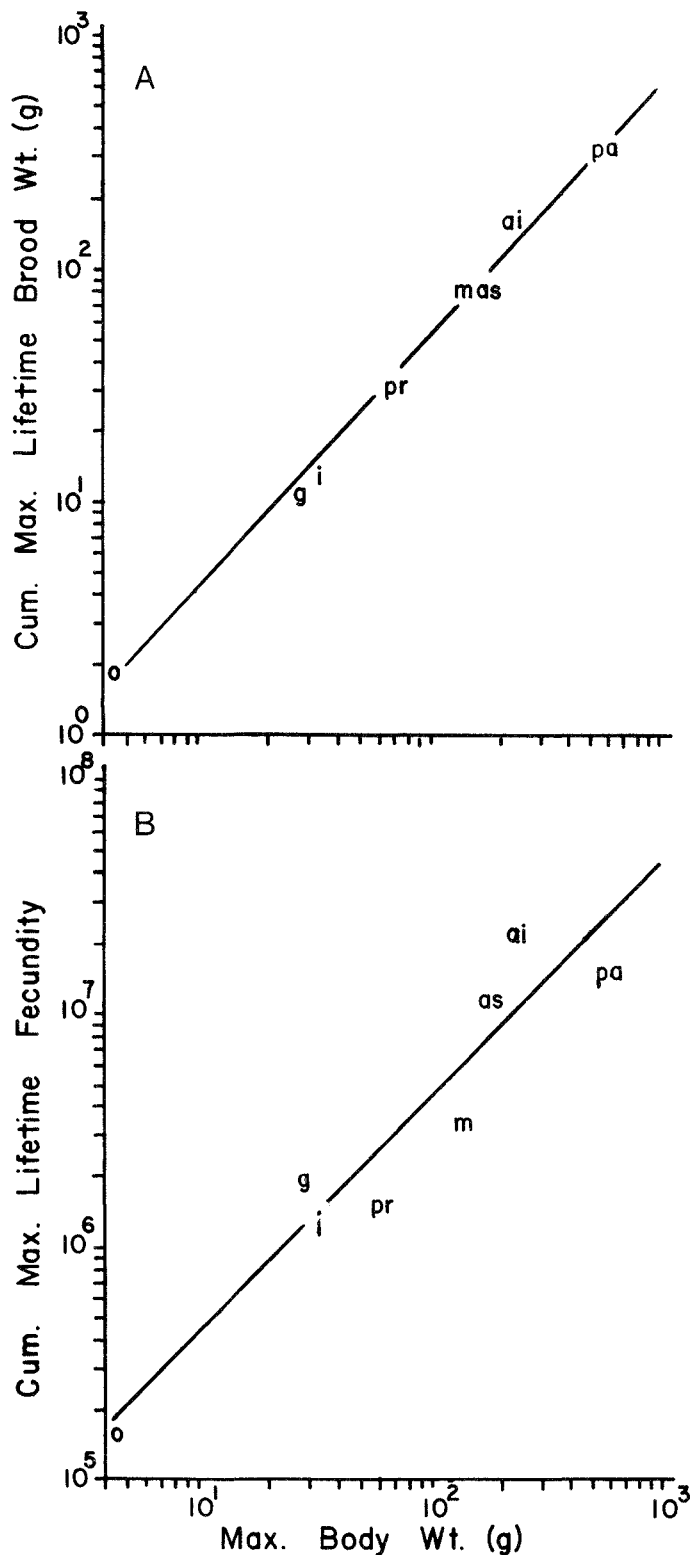*Can. J. Fish. Aquat. Sci., Vol. 48, 1991*

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FIG. 4. Comparison of (A) cumulative brood weight and (B) cumulative fecundity over the maximum predicted life span of eight species of *Cancer*, as calculated in Table 4. Regression equations are given in text. Note log scales. Species codes: ai = *C. anthonyi*; as = *C. antennarius*; g = *C. gracilis*; i = *C. irroratus*; m = *C. magister*; o = *C. oregonensis*; pa = *C. pagurus*; pr = *C. productus*.

151 mm carapace width, respectively (Gutierez and Zuniga 1976), which is also about the fecundity of *C. magister*. The occurrence of "skip molting" in some larger females of some species may reduce fecundities per brood, perhaps because females lack adequate stored sperm without copulation between each brood, as suggested by Hankin et al. (1985) for *C. magister*. Extrapolated numbers of eggs per brood for the largest instars of *C. antennarius*, *C. anthonyi*, and *C. pagurus* (Table 4) are about 1.5 times higher than values directly estimated for any sampled crab. However, rigorous quantitative tests of this hypothesis are lacking in most species.

The pattern of covariation in reproductive traits in the Cancridae contrasts with that in the Geryonidae (Hines 1988). Relative brood size was somewhat smaller in the cancrids (11–19% of female body weight) than in the geryonids (16–22%). However, egg size in the cancrids is much smaller than in the geryonids (by nearly an order of magnitude in volume, about 0.03 mm³ in cancrids versus about 0.15 mm³ in geryonids), which have among the largest eggs of the Brachyura with planktotrophic larvae (Hines 1986a, 1988). As a result of this difference in egg size, cancrids have much higher fecundity per brood than geryonids of comparable body size (by nearly an order of magnitude, about 1 000 000 eggs in cancrids versus about 225 000 eggs in geryonids). Cancrid eggs, however, are not unusually small, and many species in other families have eggs which are of similar size (e.g. Grapsidae, Ocypodidae, and Xanthidae) or smaller (e.g. Portunidae and Pinnotheridae) (Hines 1986a). Although the fecundities of several cancrids (e.g. *C. antennarius*, *C. anthonyi*, and *C. pagurus*) are among the highest reported for a brachyuran species, much of the high fecundity results from their large body size. Some other species of crabs (e.g. *Callinectes sapidus* with 1–2 million eggs; Hines 1982) produce comparable numbers of eggs per brood at smaller body size.

Thus, reproductive strategies in the Cancridae appear to have evolved in direct covariation with body size, which is in turn related to variation in growth patterns in the life histories of the species (see Orensanz and Gallucci 1988). The biogeographic restriction of cancrids to cold temperate and boreal zones (Mackay 1943; Nations 1975, 1979) apparently restricts the brooding activity in most species to a winter–spring season that results both in larval release during the spring peak of plankton production and in settlement during warm summer temperatures optimal for growth. This seasonal restriction may limit the rate of brood production, and the allometric constraint on brood size by body space for yolk accumulation (Hines 1982, 1988) further restricts variation in reproductive output. Variation in fecundity is inherently constrained by a trade-off with egg size (Hines 1982, 1986b). Because the Cancridae apparently have evolved a pattern of covariation in reproductive traits which differs from the Geryonidae, detailed analyses of reproductive patterns in other families radiating into other ecological zones will be necessary to understand fully the evolutionary constraints and variables of brachyuran reproductive strategies.

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