

## Allometric Constraints and Variables of Reproductive Effort in Brachyuran Crabs

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### Abstract

Allometric relationships of reproductive output were compared in 20 species from 7 families of brachyuran crabs from the east and west coasts of North America, using regression analysis of log reproductive parameters versus log body weight. Comparisons of crabs spanning 4 orders of magnitude in body weight indicated that female body size was the principal determinant of reproductive output: 95% of the variance in brood weight, 79% of the variance in the number of eggs per brood, 63% of the variance in annual brood weight, and 74% of the variance in annual fecundity were explained by body weight. Brood weight exhibited an isometric constraint to about 10% of body weight. Allometric limitations on space available for yolk accumulation in the body cavity appeared to be the main constraint on brood size. Ovum size increased significantly, but only slightly, with increasing body size. There was a significant trade-off between ovum size and the number of eggs per brood. There was no significant relationship between the number of broods per year and body size. The number of eggs per brood was significantly better than brood weight as a predictor of the number of broods produced per year by a species, indicating that demographic pressure on fecundity rather than energetic considerations is the primary selective mechanism influencing annual reproductive effort. Each of the 7 families of crabs exhibited trends toward distinct patterns for the suite of co-adapted reproductive traits. However, no interspecific reproductive patterns were apparent with respect to the variables of feeding type, salinity tolerance, habitat, and geographic range represented by the 20 species.

### Introduction

Inter-specific comparisons of reproductive effort provide much of the basis for theoretical considerations of life-

history tactics (Giesel, 1976; Stearns, 1976, 1977). Although current models of life-history tactics assume that reproductive parameters are free to co-evolve (Stearns, 1976), Stearns (1980) points out that many taxa exhibit strong allometric constraints which restrict the possible range of variability in reproductive effort relative to body size. Examples of allometric constraints in reproductive effort occur in some primates (Leutenegger, 1979), ungulates and subungulates (Robbins and Robbins, 1979), salamanders (Kaplan and Salthe, 1979), and some frogs (Kuramoto, 1978). Patterns of reproductive effort in Crustacea have been examined in varying detail in amphipods (Nelson, 1980; Van Dolah and Bird, 1980), anostracans (fairy shrimp) (Belk, 1977), barnacles (Barnes and Barnes, 1968; Hines, 1978, 1979), copepods (McLaren, 1966; McLaren *et al.*, 1969; Palmer, 1980), cumaceans (Corey, 1981), hermit crabs (Bertness, 1981), hippid anomuran crabs (Diaz, 1980), isopods (Lawlor, 1976), lobsters (Morizur *et al.*, 1981), mysids (Mauchline, 1973), and stomatopods (Reaka, 1979). These studies demonstrated a strong correlation between reproductive output and body size, as measured by the weight or volume of the brood and fecundity. Clearly, comparisons of individuals or groups of different body size should include allometric analysis (e.g. log reproductive parameters versus log body weight) in order to determine the relative independence of reproductive parameters (e.g. fecundity, brood, and egg size) from body size (Kaplan and Salthe, 1979; Sweet, 1980). Allometric analysis allows formulation of precise null hypotheses against which sample observations of very different-sized animals can be tested (Gould, 1966, 1971, 1975).

In the present paper, I examine allometric relationships of reproductive effort in 20 species of brachyuran crabs representing 7 families from the east and west coasts of North America. The purpose of the study was to examine the relationships of 6 principal components of reproductive effort (brood size, egg size, number of eggs per brood, number of broods per year, brood weight per

**Table 1.** Regressions of reproductive output for 20 species from 7 families of crabs. For each species, the following sequence of information is presented for the sample analyzed: collection site; no. of individuals; size range of female dry body wt; regression of log dry body wt (g) versus carapace width (mm); regression of log dry brood wt (g) versus log dry body wt (g) plus correlation coefficient (*r*); regression of log number of eggs per brood versus log dry body wt (g) plus correlation coefficient (*r*); season of females brooding eggs; and range and average number of broods produced per female per year. The literature sources for the brooding data are also given

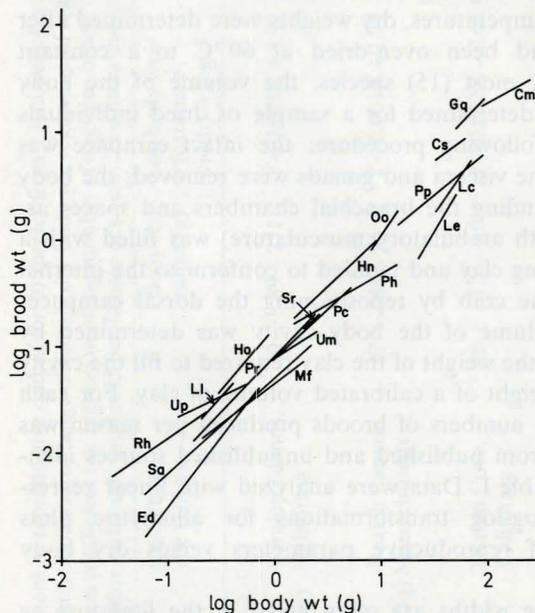
Species	Collection site (USA)	<i>N</i>	Body size range (g)	Log body wt = $b$ (carapace width) + log $c$	Log brood wt = $b$ (log body wt) + log $c$	( <i>r</i> )	Log no. eggs = $b$ (log body wt) + log $c$	( <i>r</i> )	Brood season	Broods yr <sup>-1</sup>	Source
Cancridae											
<i>Cancer magister</i> (Cm)	Farallon Islands, California	10	89 – 251	$Y = 0.001X + 1.97$	$Y = 0.527X + 0.23$	(0.802)	$Y = 0.611X + 4.68$	(0.793)	Oct. – Feb.	1 $\bar{X} = 1$	Butler (1961)
Geryonidae											
<i>Geryon quinquidens</i> (Gq)	Veatch Canyon, Massachusetts	17	48 – 91	$Y = 0.001X + 1.70$	$Y = 0.954X - 0.57$	(0.744)	$Y = 0.714X + 3.90$	(0.720)	Oct. – Feb.	1 $\bar{X} = 1$	Haefner (1977, 1978)
Grapsidae											
<i>Hemigrapsus nudus</i> (Hn)	Diablo Cove, California	20	1.5 – 9.0	$Y = 0.042X - 0.66$	$Y = 0.934X - 0.90$	(0.952)	$Y = 0.839X + 3.90$	(0.951)	Dec. – Mar.	1 $\bar{X} = 1$	Knudsen (1960), Boolootian <i>et al.</i> (1959)
<i>Hemigrapsus oregonensis</i> (Ho)	Moss Landing, California	21	0.3 – 1.2	$Y = 0.073X - 1.45$	$Y = 0.887X - 0.97$	(0.847)	$Y = 0.924X + 4.23$	(0.906)	Mar. – July	2 $\bar{X} = 2$	Knudsen (1960)
<i>Pachygrapsus crassipes</i> (Pc)	Moss Landing, California	19	0.9 – 5.2	$Y = 0.045X - 0.82$	$Y = 0.905X - 1.10$	(0.864)	$Y = 0.792X + 4.08$	(0.855)	Jan. – Aug.	2 $\bar{X} = 2$	Hiatt (1948)
<i>Sesarma reticulatum</i> (Sr)	Lewes, Delaware	6	1.8 – 2.6	$Y = 0.044X - 0.66$	$Y = 0.907X - 1.08$	(0.822)	$Y = 1.123X + 3.52$	(0.867)	Apr. – Aug.	2 – 3 $\bar{X} = 2.5$	Seiple (1979)
Majidae											
<i>Libinia emarginata</i> (Le)	Lewes, Delaware	8	22 – 48	$Y = 0.013X + 0.74$	$Y = 1.782X - 2.55$	(0.931)	$Y = 1.761X + 2.09$	(0.906)	June – Sep.	3 – 4 $\bar{X} = 3.5$	Hinsch (1968)
<i>Loxorhynchus crispatus</i> (Lc)	Pacific Grove, California	12	32 – 69	$Y = 0.021X + 0.39$	$Y = 1.420X - 1.88$	(0.753)	$Y = 1.333X + 2.35$	(0.760)	Continuous	3 – 4 $\bar{X} = 3.5$	Hines (1982, and unpublished data)
<i>Mimulus foliatus</i> (Mf)	Pacific Grove, California	11	0.21 – 1.8	$Y = 0.059X - 1.33$	$Y = 0.773X - 1.34$	(0.879)	$Y = 0.770X + 3.36$	(0.886)	Continuous	4 – 8 $\bar{X} = 6$	Hines (1982, and unpublished data)
<i>Pugettia producta</i> (Pp)	Pacific Grove, California	23	14 – 79	$Y = 0.019X + 0.24$	$Y = 0.873X - 0.87$	(0.931)	$Y = 0.862X + 3.60$	(0.937)	Continuous	5 – 10 $\bar{X} = 7.5$	Boolootian <i>et al.</i> (1959), Hines, (1982, and unpublished data)
<i>Pugettia richii</i> (Pr)	Pacific Grove, California	28	0.17 – 2.3	$Y = 0.072X - 1.36$	$Y = 1.030X - 1.09$	(0.943)	$Y = 1.007X + 3.54$	(0.939)	Continuous	6 – 10 $\bar{X} = 8$	Hines (1982, and unpublished data)
<i>Scyra acutifrons</i> (Sa)	Pacific Grove, California	18	0.06 – 2.1	$Y = 0.116X - 1.76$	$Y = 0.895X - 1.29$	(0.828)	$Y = 0.977X + 3.45$	(0.863)	Continuous	4 – 10 $\bar{X} = 7$	Knudsen (1960), Hines (1982, and unpublished data)
Ocypodidae											
<i>Uca minax</i> (Um)	Deal Island, Maryland	6	0.8 – 2.4	$Y = 0.091X - 1.87$	$Y = 0.647X - 1.10$	(0.841)	$Y = 0.647X + 4.19$	(0.841)	Apr. – Sep.	2 $\bar{X} = 2$	Williams (1965), Sandifer (1973)
<i>Uca pugnax</i> (Up)	Lewes, Delaware	11	0.12 – 0.54	$Y = 0.088X - 1.80$	$Y = 0.436Y - 1.26$	(0.962)	$Y = 0.571X + 4.16$	(0.922)	Apr. – Sep.	2 $\bar{X} = 2$	Williams (1965), Sandifer (1973)



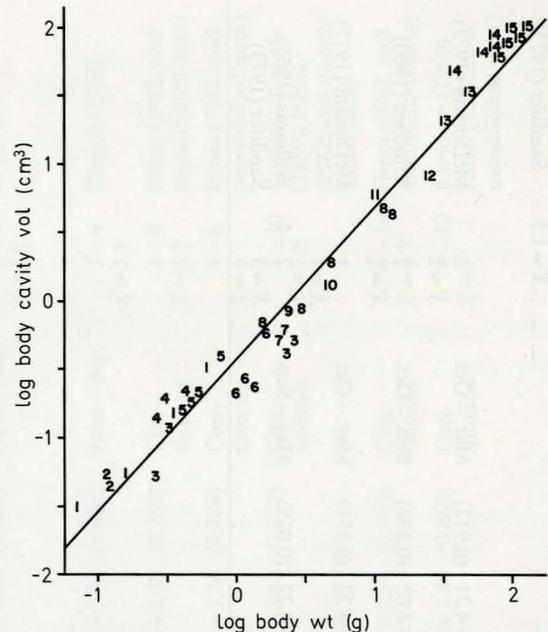
dards of measure. For example, body weight can be converted to carapace width; brood volume can be derived from egg volume and egg number; egg weight can be derived from brood weight and egg number; and egg volume can be converted to egg diameter with the formula for the volume of a sphere.

## Results

Female dry body weights for most (14 of 20) of the species of crabs examined spanned about one order of magnitude (Table 1), and the size range from the smallest individual of *Rhithropanopeus harrissii* to the largest individual of *Cancer magister* encompassed over 4 orders of magnitude in body weight (0.03 to 251, respectively). Brood weights ranged from about 0.002 g for the smallest individual of *Eurypanopeus depressus* to about 30 g for the largest individual of *C. magister*. Brood weight was strongly and positively correlated with body size in each of the 20 species (Student's *t*-tests of  $r \neq 0$ ;  $P < 0.05$  for each species), and log brood weight was a linear allometric function of log body weight for each species (Table 1). The slopes of the allometric relationships for brood weight varied considerably around the isometric value of 1.0. For each species, allometric regression slopes greater than, less than, or equal to 1.0 indicate that large individuals had proportionately larger, smaller, or equal-sized broods, respectively, compared to smaller crabs of the same species. Although the scaling of brood size for each species often was not isometric, brood weight exhibited an ap-



**Fig. 1.** Log brood weight versus log body weight for 20 species of crabs. Relationship for pooled samples is approximately isometric:  $\log \text{ brood wt} = 1.041 \log \text{ body wt} - 1.057$ ;  $r = 0.978$ . Brood weight is approximately constant at 10% of female body weight. Regressions for individual species are indicated by initials corresponding to species listed in Table 1



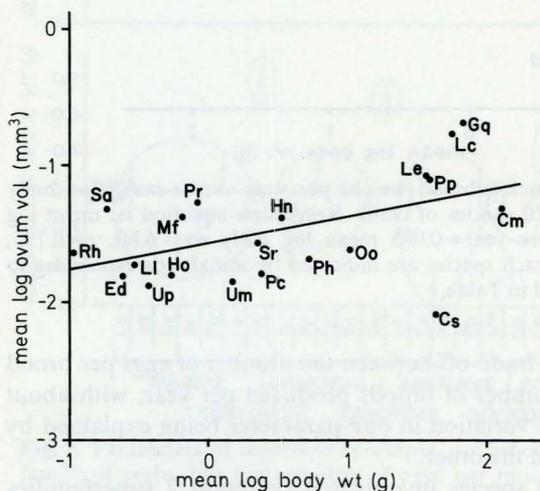
**Fig. 2.** Log volume of the body cavity versus log body weight for 15 species of crabs. The relationship is approximately isometric:  $\log \text{ body vol} = 1.13 \log \text{ body wt} - 0.489$ ;  $r = 0.989$ . Numbers indicate value for individual crabs: 1 = *Eurypanopeus depressus*; 2 = *Rhithropanopeus harrissii*; 3 = *Mimulus foliatus*; 4 = *Uca pugnax*; 5 = *Hemigrapsus oregonensis*; 6 = *Pugettia richii*; 7 = *Scyra acutifrons*; 8 = *Panopeus herbstii*; 9 = *Sesarma reticulatum*; 10 = *Hemigrapsus nudus*; 11 = *Ovalipes ocellatus*; 12 = *Libinia emarginata*; 13 = *Callinectes sapidus*; 14 = *Geryon quinquidens*; 15 = *Cancer magister*

proximately isometric relationship to body weight for the pooled sample of all 20 species of crabs (Fig. 1; Table 2: Eq. 1). After statistically controlling for variation in body size, brood weights proved significantly different between species (ANCOVA of log brood wt by species controlling for log body wt;  $N = 282$ ;  $P < 0.001$ ). Nevertheless, the very high correlation of log brood wt with log body wt, as well as the tightness of the overall isometric relationship compared to the variation in other parameters of reproductive effort (see below), indicate that brood weight was generally constrained to about 10% of the body weight in these brachyurans (Fig. 1).

Similarly, brood volume (brood vol = mean ovum vol  $\times$  mean no. of eggs per brood) exhibited an approximately isometric relationship to body weight (Table 2: Eq. 2). The general isometric relationships of brood weight and brood volume to body weight suggests that a constant scalar relationship of volume to weight limits brood size. To test this hypothesis, the volume of the body cavity was compared to body weight for 15 of the 20 species. Like brood volume, the volume of the body cavity proved to be approximately isometric with respect to body weight (Fig. 2; Table 2: Eq. 3). In general, species with larger or smaller brood weights than predicted by the pooled regression (i.e., Table 2: Eq. 1) had larger or smaller body cavity volumes, respectively (Fig. 2).

**Table 2.** Summary of allometric regressions for 20 species of crabs. SE: standard error of slope;  $N$ : sample size (when  $N=20$ , data were calculated means for each species; when  $N>20$ , data were pooled for all individuals among species);  $r$ : correlation coefficient;  $P$ : significance level of Student's  $t$ -tests for  $r \neq 0$

Regression equation	SE	$N$	$r$	$P$
(1) $\log$ brood wt = 1.041 $\log$ body wt - 1.057	0.013	282	0.978	0.001
(2) $\log \bar{X}$ brood vol = 1.020 $\log \bar{X}$ body wt - 0.659	0.018	20	0.982	0.001
(3) $\log$ body vol = 1.130 $\log$ body wt - 0.489	0.025	43	0.989	0.001
(4) $\log \bar{X}$ ovum vol = 0.187 $\log \bar{X}$ body wt - 1.57	0.008	20	0.490	0.05
(5) $\log$ egg no. = 0.822 $\log$ body wt + 3.889	0.025	279	0.893	0.001
(6) $\log$ yearly $\bar{X}$ brood wt = 0.985 $\log \bar{X}$ body wt - 6.60	0.062	20	0.795	0.001
(7) $\log$ yearly $\bar{X}$ no. eggs = 0.750 $\log \bar{X}$ body wt + 4.24	0.105	20	0.860	0.001

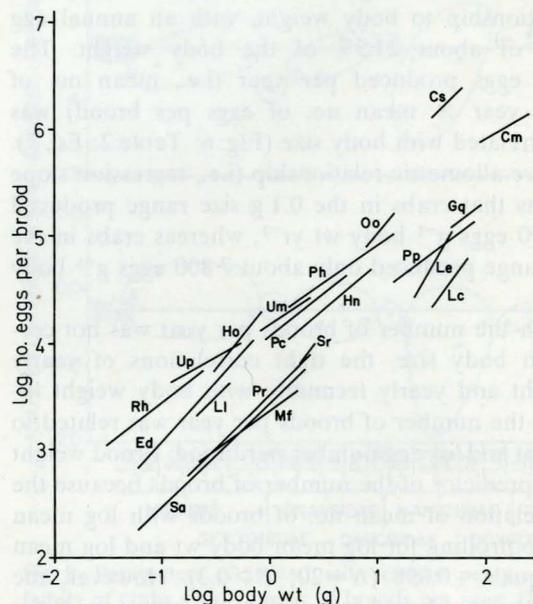


**Fig. 3.** Mean log ovum volume versus mean log body weight for 20 species of crabs. Egg size increased significantly with body size, but with negative allometry:  $\log$  ovum vol = 0.187  $\log$  body wt - 1.57;  $r=0.490$ . Values for each species are indicated by initials corresponding to species listed in Table 1

Within a species, egg size at a given developmental stage showed little variation within or among individuals; standard deviations were less than 5% of mean egg diameters. Mean ovum diameter ranged from 251  $\mu\text{m}$  for *Callinectes sapidus* to 731  $\mu\text{m}$  for *Geyon quinquidens*, encompassing a range of more than one order of magnitude in mean ovum volume. Mean log ovum volume increased slightly but significantly with log body weight for the 20 species of crabs (Fig. 3; Table 2: Eq. 4). *C. sapidus* had an extremely small egg compared to other crabs of its size range. When *C. sapidus* was excluded, the correlation between ovum size to body size increased to  $r=0.671$  ( $N=19$ ,  $P<0.01$ ), with body size accounting for 45% of the variation in egg size between the remaining species.

Numbers of eggs per brood ranged from about 150 for small *Scyra acutifrons* to about 2 750 000 for large *Callinectes sapidus*. The number of eggs per brood was positively correlated with body size in each of the 20 species of crabs (Student's  $t$ -tests of  $r \neq 0$ ;  $P<0.05$ ), and

$\log$  egg number was a linear allometric function of  $\log$  body weight for each species (Table 1). As with brood weight, regression slopes greater than, less than, or equal to 1.0 indicate that large individuals had proportionately larger, smaller, or equal numbers of eggs per brood, respectively, compared to smaller crabs within the same species. Egg number was also strongly correlated with body weight for pooled samples of all species (Fig. 4; Table 2: Eq. 5). This negative allometric relationship means that small crabs in the 0.1 g size range produced about 11 700 eggs  $\text{g}^{-1}$  body wt, whereas large crabs in the 100 g size range produced about 3 400 eggs  $\text{g}^{-1}$  body wt. After statistically controlling for variation in body size, there were highly significant differences in egg numbers per brood between species of crabs (ANCOVA of  $\log$  egg no. by species controlling for  $\log$  body wt;  $N=279$ ;  $P<0.001$ ). The correlation of  $\log$  egg number with  $\log$



**Fig. 4.** Log number of eggs per brood versus log body weight for 20 species of crabs. Overall relationship for pooled samples has significant negative allometry:  $\log$  egg no. = 0.822  $\log$  body wt + 3.889;  $r=0.893$ . Regressions for individual species are indicated by initials corresponding to species listed in Table 1

body weight was significantly lower than the correlation of log brood weight with log body weight (Student's *t*-tests;  $P < 0.05$ ). Variation in egg numbers per brood was largely accounted for by variation in egg size between species because, given the general constraint of brood size, there was a significant trade-off between the components of reproductive output. That is, increased egg size was tightly correlated with decreased egg number per brood: the partial correlation coefficient of log ovum volume with log egg number per brood for crabs of a given size was  $-0.846$  ( $N=279$ ;  $P < 0.001$ ). Thus, about 72% of the variation in one parameter was explained by variation in the other parameter.

The number of broods per year produced by each species ranged from 1 to 10 (Table 1). These estimates reported in the literature are the number of broods per year produced by a typical female, usually based on deductions from the seasonal cycles of the incidence of brooding in mature females, and occasionally based on laboratory observations of the time between successive broods produced by individual females. These estimates are not based on statistically independent observations of brood production per year by individual crabs. Therefore, analyses of the relationship of the number of broods to other reproductive parameters were based on comparisons of modal values of the number of broods reported in the literature and the mean values of other parameters measured in the present study for each species. The numbers of broods per year were not correlated with body weight for the 20 species ( $r = -0.17$ ;  $P > 0.2$ ). However, the brood weight produced per year (i.e., mean no. of broods per year  $\times$  mean brood wt) was significantly correlated with body weight (Fig. 5; Table 2: Eq. 6). The annual production of brood weight had an approximately isometric relationship to body weight, with an annual egg production of about 21.5% of the body weight. The number of eggs produced per year (i.e., mean no. of broods per year  $\times$  mean no. of eggs per brood) was strongly correlated with body size (Fig. 6; Table 2: Eq. 7). This negative allometric relationship (i.e., regression slope  $< 1.0$ ) means that crabs in the 0.1 g size range produced about 43 500 eggs  $g^{-1}$  body wt  $yr^{-1}$ , whereas crabs in the 100 g size range produced only about 7 800 eggs  $g^{-1}$  body wt  $yr^{-1}$ .

Although the number of broods per year was not correlated with body size, the tight correlations of yearly brood weight and yearly fecundity with body weight indicates that the number of broods per year was related to brood weight and/or egg number per brood. Brood weight was a poor predictor of the number of broods because the partial correlation of mean no. of broods with log mean brood wt, controlling for log mean body wt and log mean egg no., equals  $-0.098$  ( $N=20$ ;  $P > 0.3$ ). However, the number of eggs per brood was clearly the better predictor of the number of broods per year because the partial correlation of mean no. of broods with log mean egg no., controlling for log mean body wt and log mean brood wt, equals  $-0.608$  ( $N=20$ ;  $P < 0.001$ ). Thus, there was a

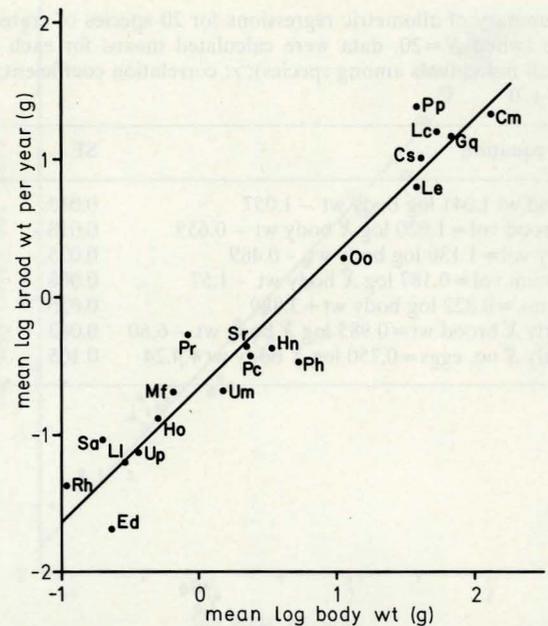


Fig. 5. Mean log brood weight per year versus mean log body weight for 20 species of crabs. Regression equation is: mean log brood wt per year =  $0.985$  mean log body wt  $- 6.60$ ;  $r = 0.795$ . Values for each species are indicated by initials corresponding to species listed in Table 1

significant trade-off between the number of eggs per brood and the number of broods produced per year, with about 36% of the variation in one parameter being explained by variation in the other.

The 20 species investigated represent 2 superfamilies and 7 phylogenetically diverse families within the division

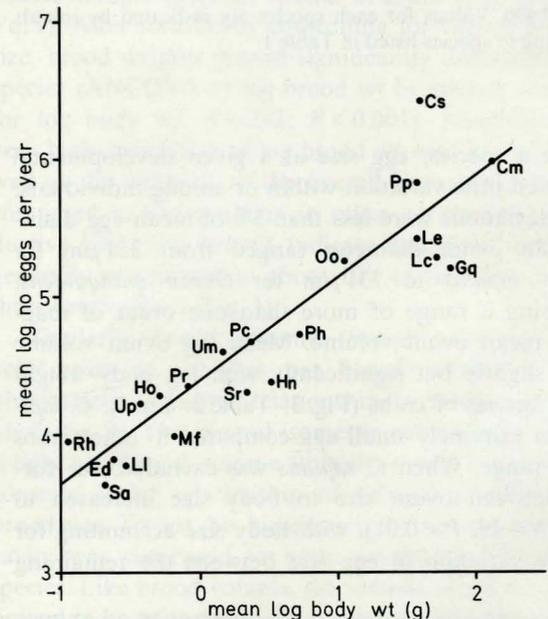


Fig. 6. Mean log number of eggs per year versus mean log body weight for 20 species of crabs. Regression equation is: mean log no. eggs per year =  $0.750$  mean log body wt  $+ 4.24$ ;  $r = 0.860$ . Values for each species are indicated by initials corresponding to species listed in Table 1

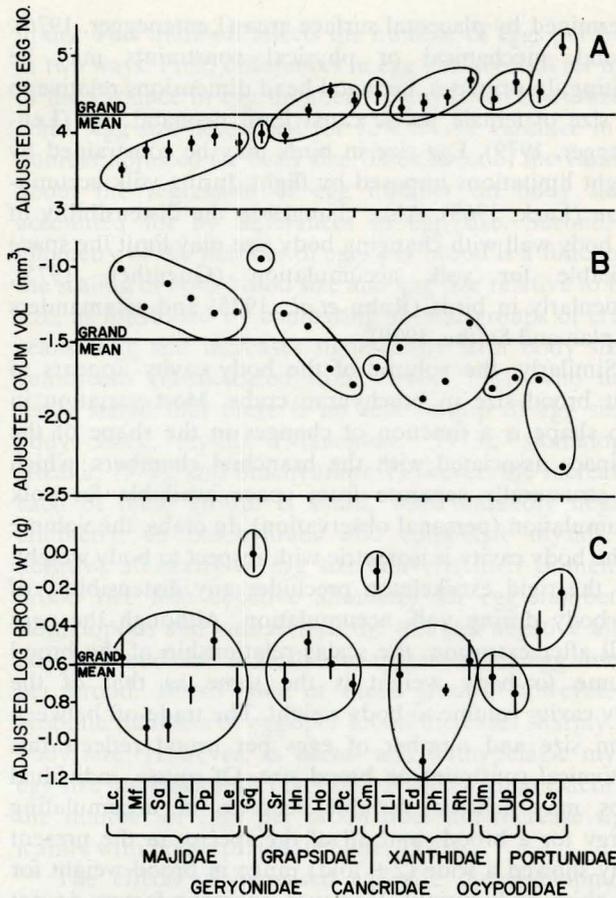


Fig. 7. Parameters of reproductive output per brood grouped by family of crabs. (A) Log number of eggs per brood; (B) ovum volume; (C) log brood wt. Means ( $\pm 2$  SE) adjusted by ANCOVA for body weight of each species are plotted for each parameter. Grand means for pooled samples are indicated by horizontal lines for each parameter. Species initials correspond to species listed in Table 1

Brachyrrhyncha. The limited number of species that were studied from any one family made it difficult to compare patterns of reproductive effort between families, even after controlling for differences in body size. However, after statistically controlling for variation in body size (ANCOVA), all 6 species of the Majidae had significantly lower numbers of eggs per brood than the grand mean of all 20 species (Fig. 7A) (Student's *t*-tests of log mean egg no. adjusted for log body wt;  $P < 0.01$ ). The majids also had larger than average eggs (Fig. 7B), but they had approximately average brood weight (Fig. 7C). The majid's lower number of eggs per brood was compensated by a greater than average number of broods per year (Fig. 8A), resulting in approximately average fecundity per year (Fig. 8B). However, the greater number of broods did not result in unusually large brood weight per year for the family (Fig. 8C). The single species in the Geryonidae had large eggs, larger brood weight adjusted for body size, and lower numbers of eggs per brood than average (Fig. 7). *Geryon quinquidens* also produced fewer broods and had lower annual fecundity adjusted for body size than average, but

it displayed about average yearly brood weight (Fig. 8). The Grapsidae, represented by 4 species, had about average number of eggs per brood, egg size, adjusted brood weight, number of broods per year, yearly fecundity, and yearly brood weight production (Figs. 7 and 8). The Cancridae, represented by *Cancer magister*, had a greater adjusted number of eggs per brood, smaller egg size, and larger adjusted brood weight, than average (Fig. 7), but its lower than average number of broods resulted in average adjusted yearly fecundity and average adjusted yearly brood weight (Fig. 8). Variability between the 4 species in the Xanthidae made it difficult to discern a pattern of reproductive effort which is characteristic of the group. Three of the 4 species were characterized by approximately average values for the 6 reproductive parameters (Figs. 7 and 8). However, *Eurypanopeus depressus* had a very low adjusted egg size, brood weight, yearly fecundity, and brood weight per year, but had a mean adjusted number of eggs per brood and number of broods per year which were similar to the other 3 species of xanthids (Figs. 7 and 8). The 2 species of fiddler crabs in the Ocypodidae were characterized by approximately average adjusted brood weights, but they had small eggs and greater than average numbers of eggs per brood (Fig. 7).

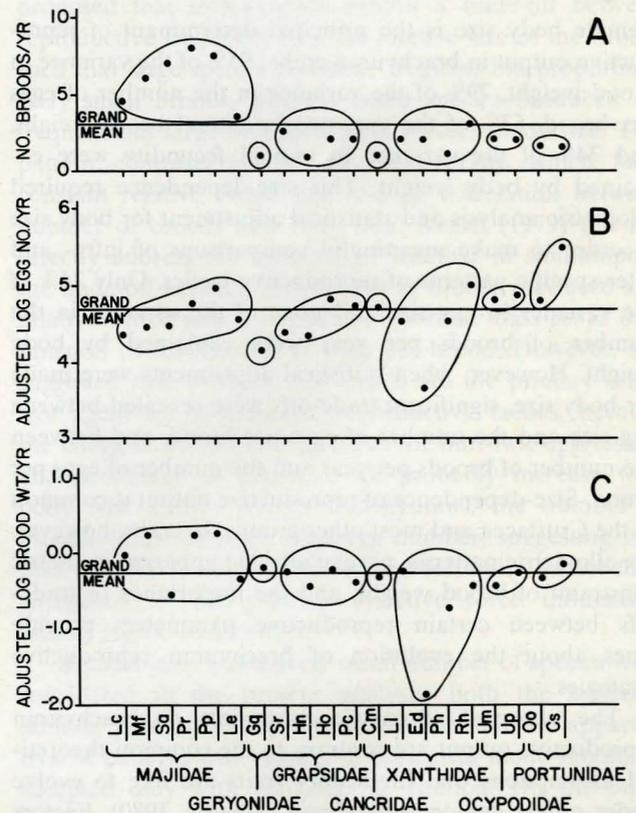


Fig. 8. Parameters of reproductive output per year grouped by family of crabs. (A) Number of broods per year; (B) log number of eggs per year; (C) log brood wt per year. Means are plotted for each parameter. Parameters B and C are adjusted by ANCOVA for body weight of each species. Grand means for pooled samples are indicated by horizontal lines for each parameter. Species initials correspond to species listed in Table 1

Approximately average numbers of broods per year resulted in average adjusted yearly production of eggs and brood weight for the 2 *Uca* spp. (Fig. 8). In the 2 species of Portunidae, the combination small eggs and larger than average adjusted brood weights resulted in higher than average adjusted number of eggs per brood (Fig. 7). The small number of broods produced by the 2 portunids resulted in about average production of brood weight per year (Fig. 8). *Ovalipes ocellatus* also had about average yearly fecundity, but for *Callinectes sapidus* the extremely small egg and concomitantly large number of eggs per brood (Fig. 7) resulted in the highest adjusted yearly fecundity of the 20 species (Fig. 8).

The 20 species represented a diverse array of feeding types (carnivores, herbivores, omnivores), salinity tolerances (dilute euryhaline to stenohaline marine), habitats (estuaries, marshes, kelp forests, intertidal zone to deep-water continental shelf, hard and soft substrates), and geographic ranges (cold temperate to tropical). However, no apparent patterns or changes of reproductive effort with respect to these ecological variables were detected within the present data.

## Discussion

Female body size is the principal determinant of reproductive output in brachyuran crabs: 95% of the variance in brood weight, 79% of the variance in the number of eggs per brood, 63% of the variance in annual brood weight, and 74% of the variance in annual fecundity were explained by body weight. This size-dependence required allometric analysis and statistical adjustment for body size in order to make meaningful comparisons of intra- and inter-specific patterns of reproductive tactics. Only 24% of the variance in egg size and none of the variance in the number of broods per year were explained by body weight. However, when statistical adjustments were made for body size, significant trade-offs were revealed between egg size and the number of eggs per brood, and between the number of broods per year and the number of eggs per brood. Size-dependence of reproductive output is common in the Crustacea and most other groups. In crabs, however, the allometric patterns, particularly the apparent isometric constraint of brood weight, and the importance of trade-offs between certain reproductive parameters provide clues about the evolution of brachyuran reproductive strategies.

The observed allometric constraints on brachyuran reproductive output are contrary to the common theoretical assumptions that life-history traits are free to evolve under purely demographic forces (Stearns, 1980). Factors which may place allometric constraints on the mass or volume of reproductive output fall into two general categories. First, energetic constraints may limit reproductive output. For example, the surface area of the gut may limit variability in clutch size of a teleost fish (Hubbs *et al.*, 1968). Birth size in eutherian mammals is apparently

determined by placental surface area (Leutenegger, 1976). Second, mechanical or physical constraints may be limiting. In primates, neonatal head dimensions relative to the size of female pelvic canal limit neonatal size (Leutenegger, 1979). Egg size in birds may be constrained by weight limitations imposed by flight during yolk accumulation (Lack, 1968). Also, changes in the distensibility of the body wall with changing body size may limit the space available for yolk accumulation (Guenther, 1975), particularly in birds (Rahn *et al.*, 1975) and salamanders (Kaplan and Salthe, 1979).

Similarly, the volume of the body cavity appears to limit brood size in brachyuran crabs. Most variation in crab shape is a function of changes in the shape of the carapace associated with the branchial chambers, which are structurally separate from space available for yolk accumulation (personal observation). In crabs, the volume of the body cavity is isometric with respect to body weight, and the rigid exoskeleton precludes any distensibility of the body during yolk accumulation. Although the eggs swell after extrusion, the scalar relationship of the brood volume to body weight is the same as that of the body cavity volume to body weight. The trade-off between ovum size and number of eggs per brood reflects this anatomical constraint on brood size. Of course, individual crabs may achieve variable success in accumulating energy for a brood; and all of the species in the present study showed a wide (2+ fold) range in brood weight for any given body weight. However, energetic factors do not appear to be the primary constraints limiting brood size at the species level, as indicated both by the tightness of the overall isometric relationship of brood weight to body weight among species, and by the close correspondence of this relationship with the allometry of the volume of the body cavity. The trade-off between the number of broods per year and the number of eggs per brood indicates that annual reproductive output also is not generally limited by energetic constraints. If energetic factors were the primary constraints limiting reproductive output, then brood weight, not egg number, should be the best predictor of the number of broods produced per year.

The isometric scaling of brood size in the brachyurans is similar to that in mysid shrimp, which also produce broods equal to approximately 10% of the parental body volume (Mauchline, 1973). In stomatopods, however, clutch volume is negatively allometric, with large species having relatively smaller clutch volumes than small species (Reaka, 1979). Reaka also proposed that the capacity to store eggs in the body cavity limited the size of the brood, although she did not determine whether the volume of the body cavity is negatively allometric in stomatopods. Clutch volume also exhibits negative allometry in cumaceans (Corey, 1981) and amphipods (Nelson, 1980).

A trade-off between egg size and the number of eggs per brood occurs in amphipods (calculated from Nelson, 1980), cumaceans (calculated from Corey, 1981), mysids (Mauchline, 1973), fairy shrimps (Belk, 1977), and stomatopods (Reaka, 1979), as well as in the present brachy-

urans. This trade-off affects the number of eggs per brood in two ways. First, differences in egg size account for much of the variance in egg number for any given body size. In crabs, egg size accounted for 72% of the variance in egg number adjusted for body size. Thus, most of the variation about the regression of egg number on body size is accounted for by differences in egg size. Second, the allometry of the number of eggs per brood is a function of the scaling of both brood size and egg size relative to body size, as illustrated by comparing several groups of crustaceans. Egg size increases significantly with body size in cumaceans (recalculated from Corey, 1981, who incorrectly stated that there is no relationship of egg size to body size), mysids (Mauchline, 1973), stomatopods (Reaka, 1979), and brachyurans. However, the increase in each of these groups is small, with markedly negative allometry. In brachyurans and epipelagic mysids, the negative allometry of egg size converts their isometry of brood size into negative allometry for egg number. In stomatopods and cumaceans, the marked negative allometry of brood size is further exaggerated for egg number per brood. In all four of these groups, however, the absolute numbers of eggs per brood increases sharply with body size. However, in meso- and bathypelagic mysids, egg size increases with body size to such a great extent that the number of eggs per brood does not increase significantly with body size (Mauchline, 1973).

The effects of increased egg size on developmental time and larval ecology differ from group to group among invertebrates. In many groups (e.g., echinoderms, molluscs, polychaetes), increased egg size is generally correlated with longer pre-feeding period, shorter planktonic period, and shorter total developmental time to metamorphosis (Thorson, 1950; Mileikovsky, 1971; Vance, 1973). However, Underwood (1974) argued that there is no general relationship between egg size and developmental period (but see Steele, 1977). Increased egg size correlates with longer development time in many crustacean groups (Steele and Steele, 1975 a), including barnacles (Patel and Crisp, 1960), copepods (McLaren *et al.*, 1969), amphipods (Steele and Steele, 1973), decapods (Wear, 1974), and isopods, mysids, and cumaceans (summarized in Steele and Steele, 1975 a). However, Strathmann (1977) showed that pre-feeding and pelagic feeding intervals in larvae of some barnacles and hermit crabs are not correlated with egg size; rather larger eggs simply produce larger larvae and juveniles at metamorphosis. Similarly, egg size of stomatopods does not appear to influence benthic pre-feeding time or length of pelagic feeding and dispersal period, but larger egg size results in larger size at settlement (Reaka, 1979, 1980). Egg size is also correlated with increased larval and settlement size in fairy shrimp (Belk, 1977) and mysids (Mauchline, 1973). Euphausiids and the major groups of decapod crustaceans may be ranked in the following evolutionary series of increasing egg size, declining number of larval instars, and decreasing variability in the length of larval period and rate of larval growth: Euphausiacea, Penaeidea, Caridea, Anomura,

Macrura, and Brachyura (Knowlton, 1974). In brachyurans, the effect of increased egg size probably is partly dependent on the family of crabs, because the number of larval instars varies from family to family, but is relatively constant within a given family (Rice, 1980). The adjusted number of eggs per brood (Fig. 7A) tends to increase, and the size of eggs (Fig. 7B) tends to decrease, relative to increasing number of zoeal stages for each family (Rice, 1980). Within the Majidae, egg size is directly correlated both with the length of larval period at equivalent temperature and with size of the first crab (Hines, 1981 and unpublished data). In crustaceans, larger size at settlement may improve the ability to obtain a larger array of food, to reduce competition, and to avoid predators (Mauchline, 1973; Belk, 1977; Reaka, 1979). Other growth factors being equal, larger size at settlement will also result in shorter time to sexual maturity (Hines, 1981).

For most other groups of crustaceans, data on the number of broods produced per year are inadequate to make detailed comparisons with brachyurans. Nelson (1980) showed for amphipods that production of only a single brood occurs in species of all sizes and that brood size is larger in single-brooded versus multiple-brooded species, but there is inadequate quantification of multiple broods to permit further generalizations. Reaka (1979) proposed that stomatopods exhibit a trade-off between reproductive frequency and the relative size of the brood, such that large species produced frequent but proportionately small broods, whereas small species produced infrequent but large broods relative to their body size. This pattern contrasts to that of brachyurans, which have constant relative brood size and no correlation between number of broods and body size. Reaka (1979) did not directly address the question of whether in stomatopods the trade-off between the number of broods produced and relative brood size is a function of brood mass *per se* or a function of the number of eggs per brood. However, she suggested that energetic constraints are the primary selective agent for stomatopod reproductive tactics, because the energetic costs of competition for burrows, aggression, and avoidance of predators all probably increase with body size. In the present brachyurans, the number of broods varies inversely with egg number, suggesting that demographic pressure for increased fecundity, rather than energetics, is the primary selective force influencing annual reproductive effort.

Because only a relatively small number of species were considered in the present analysis, both the apparent familial patterns of reproductive effort and the apparent lack of patterns with respect to ecological mode should be accepted only with considerable caution. On the other hand, my survey of the scattered literature (e.g. see Williams, 1965; Powers, 1977; Garth and Abbott, 1980) revealed only minor exceptions to the general trends advanced here. For example, *Uca subcylindrica*, a semi-terrestrial fiddler crab occurring in the unusual habitat of semi-arid environments of southwest North America, produces few ( $\bar{x}=522$ ), very large (1.1 mm diam) eggs per

brood compared to other ocypodids (Rabalais and Cameron, 1981; Thurman and Thurman, 1981). However, the familial patterns of coadapted reproductive traits are consistent with the allometric constraints and trade-offs that generally characterize brachyurans. Amphipods and stomatopods also exhibit significant differences in reproductive patterns between families (Reaka, 1979; Nelson, 1980). However, other groups of crustaceans apparently have not been analyzed in this way. Although the present species of crabs did not reveal any consistent relationship between reproductive pattern and major ecological mode, several other groups of crustaceans do exhibit such a relationship. For example, consistent reproductive differences have been documented for: epifaunal versus infaunal, and brackish-water versus freshwater and marine amphipods (Nelson, 1980; Van Dolah and Bird, 1980); arctic, temperate, littoral, and deep water cumaceans (Corey, 1981); and epipelagic versus meso- and bathypelagic mysids (Mauchline, 1973).

The present study focuses on interspecific comparisons of reproductive effort, and intraspecific variability has not been addressed. However, other crustacean groups exhibit significant intraspecific variation in the components of reproductive effort with respect to (1) geographic location, especially latitude: mole crabs (Hippidae) (Efford, 1969), stomatopods (Reaka, 1979), barnacles (e.g. Barnes and Barnes, 1965, 1968), copepods (McLaren *et al.*, 1969), mysids (Lasenby and Langford, 1972), lobsters (Morizur *et al.*, 1981), and amphipods (Steele and Steele, 1975b); (2) season: mole crabs (Diaz, 1980) and cumaceans (Corey, 1981); (3) tidal height: barnacles (e.g. Barnes and Barnes, 1968) and copepods (Palmer, 1980); and (4) limiting resources: hermit crabs (Bertness, 1981). I am unaware of any similar analysis of intraspecific variation in reproductive parameters for brachyurans. However, the interspecific patterns of allometric constraints, variables, and trade-offs in the present study suggest predictive hypotheses concerning intraspecific variability. For example, selection for increased fecundity in populations at higher latitudes is likely to result in increased numbers of eggs per brood and, concomitantly, decreased egg size, because strong seasonality presumably would preclude increases in the number of broods per year. This predicted decrease in egg size at higher latitudes is contrary to the observed interspecific pattern of increasing egg size at high latitudes in other groups (Thorson, 1950). Intraspecific selection for increased fecundity at low latitudes could be realized either by reductions in egg size, or by increases in numbers of broods per season, or both. It is theoretically possible to "fine tune" fecundity by adjusting egg size as a continuous variable (e.g. Perron and Carrier, 1981); whereas the number of broods is a discrete variable, producing incremental adjustments in fecundity. However, any selective advantage derived from precise adjustments in fecundity by means of changes in egg size may be counterbalanced by the disadvantages of altering sizes of later life stages. If adjustments in egg size or number of broods were prohibited by disadvantages for later life

stages or by seasonal limitations, respectively, then changes in mean size of reproductive females could alter fecundity. The balance of trade-offs between female size and fecundity will depend on the allometric constraints exhibited by each species.

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