

Constraint on Reproductive Output in Brachyuran Crabs: Pinnotherids Test the Rule¹

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SYNOPSIS. Brood weight and number of eggs per brood are primarily determined by female body size in brachyuran crabs. Brood weight exhibits an isometric relationship spanning more than four orders of magnitude in body weight among 33 non-pinnotherid species, with brood size being constrained to about 10% of female body weight by the space available for yolk accumulation within the cephalothorax. In contrast, two pinnotherids (*Pinnotheres ostreum*, *Fabia subquadrata*) have relative brood sizes which are 66% and 97%, respectively, of body weight. The allometric constraint is circumvented in these extraordinarily large brood sizes by two pinnotherid features which allow more space for yolk accumulation. Unlike other brachyurans, their ovaries extend out of the cephalothorax into the abdomen, and calcification of their exoskeleton is greatly reduced, potentially allowing distension of the body. As in crabs, pinnotherid egg size is highly variable among species, which tends to increase the variance among species in fecundity per brood, making pinnotherid fecundities not extraordinary. The number of broods produced per year in these two species is limited by short reproductive seasons, which tends to bring their annual reproductive output in line with other brachyurans. The trade-offs among reproductive variables in pinnotherids is adaptive for the small body size and parasitic niche of these species.

INTRODUCTION

Physical limits and phylogenetic history sometimes impose constraints upon evolutionary solutions to ecological problems (Stearns, 1977). Surface-to-volume ratios and effects of fluid viscosity are examples of physical properties which can constrain scaling patterns in such physiological problems as metabolism, movement in water, and circulation. As a phylogenetic example, evolution of an external skeleton imposes limits on growth patterns in arthropods. These kinds of constraints set limits for variation in certain traits, and suites of traits may evolve in patterns of trade-offs as a consequence of these constraints.

Brood size and fecundity are primarily determined by female body size in brachyuran crabs (Hines, 1982, 1988, 1991). Brood weight in brachyuran crabs is generally con-

strained to about 10% of female body weight by space available for yolk accumulation within the calcified cephalothorax (Hines, 1982). Egg size is a major reproductive trait which is highly variable among brachyuran species (Hines, 1982, 1986, 1988, 1991). As a consequence of the constraint in brood size relative to body size, the high interspecific variability in egg size results in much greater interspecific variation in fecundity (many small *versus* few large eggs) than in brood mass for equivalently sized crabs (Hines, 1982). Recent analysis of covariation in these reproductive traits within two families of crabs (Geryonidae and Cancridae) suggests, however, that the range in relative brood size of some species may be as much as about twice the 10% average among a wide array of species (Hines, 1988, 1991).

In this paper, I provide a further test of the hypothesis that reproductive output per brood in brachyurans is constrained by space available in the cephalothorax, resulting in limited variation in brood weight relative

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TABLE 1. *Collecting information for crab species.*

Species	No. of females	Collecting site	Depth (m)	Collecting method	Date
<i>Pinnotheres ostreum</i>	10	Indian River, FL	0-1	Hand	Jul, 1983
<i>Fabia subquadrata</i>	12	Bodega Head, CA	0	Hand	Dec, 1987
<i>Neopanope sayi</i>	8	Chesapeake Bay, VA	2-4	Dredge	Jul, 1984
<i>Portunus spinicarpus</i>	9	Fort Pierce, FL	17	Trawl	Mar, 1981
<i>Menippe nodifrons</i>	12	Indian River, FL	2	Hand, SCUBA	Jul, 1983
<i>Loxorhynchus grandis</i>	13	Santa Barbara, CA	30-60	Trap	Oct, 1983

to female body weight. Because parasitic species often have higher reproductive outputs than free-living species, I measured the brood size, egg size, and fecundity relative to female body size in two species of pinnotherid crabs which live obligatorily within the mantle cavities of bivalve molluscs. *Pinnotheres ostreum* occurs within the oyster *Crassostrea virginica* (also some species of scallops and mussels) along the east coast of North America, throughout the Gulf of Mexico, Caribbean, and to Brazil (Christensen and McDermott, 1958; Williams, 1984). *Fabia subquadrata* inhabits the mussel *Mytilus californianus* (also other mussel species and some clams) along the west coast of North America from Alaska to southern California (Pearce, 1966; Garth and Abbott, 1980). Both crab species consume food particles and mucus on the gills of their host, sometimes inflicting significant damage to one ctenidium. The life histories of both species are similar. After post-larval megalopae infect the bivalve host from the plankton, the crabs begin juvenile growth. Mating occurs outside the host, however, when the female leaves the host and re-enters the water column temporarily. Inseminated females return to a bivalve host and continue to grow and produce eggs, which are brooded in the usual brachyuran way. Males are dwarf and are also found within the bivalve host part of the time, though usually not with a female.

MATERIALS AND METHODS

Samples of 12-16 ovigerous females of *Pinnotheres ostreum* and *Fabia subquadrata* were collected from *Crassostrea virginica* and *Mytilus californianus*, respectively, at locations shown in Table 1. For compara-

tive purposes, samples of 7-15 ovigerous females of four non-pinnotherid species of crabs (*Neopanope sayi*, *Portunus spinicarpus*, *Menippe nodifrons*, *Loxorhynchus grandis*) were also collected from locations listed in Table 1. The samples for analysis were selected to span the size range of ovigerous females collected 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 collectors selected crabs with brooding embryos in developmental stages from late blastula to early gastrula to avoid confounding effects of egg 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. The following variables were measured for each crab: maximum (spine-to-spine) carapace width (mm) of the female; female dry body weight (g); dry weight (g) of the brooded egg mass; average diameter (μm), including the chorionic membrane adhering tightly 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 2,000 eggs (Hines, 1982, 1988, 1991). All broods were examined under a dissecting microscope for the presence of nemertean worms or other potential infections by egg predators. Data on numbers of broods produced per year in the pinnotherids were extracted from Christiansen and McDermott (1958) and Pearce (1966).

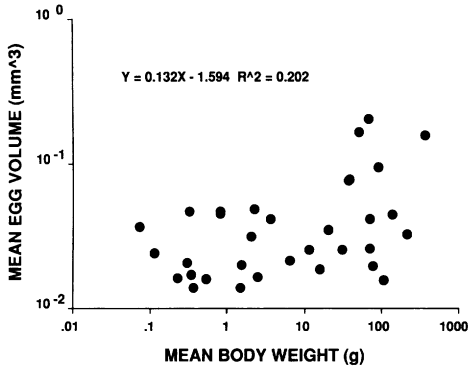


FIG. 1. Egg size as a function of body size for 35 species of brachyuran crabs. Mean values of measured egg volume and dry body weight are plotted on logarithmic scales. Equation for the linear regression and R^2 value are given.

Comparative data on fecundity and reproductive output for other species of non-pinnotherid crabs were taken as complete sets from Hines (1981, 1988, 1991).

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. I compared reproductive variables among different sized crabs using ANCOVA with female body weight as the covariate after testing for homogeneity of variances with Fmax tests (Sokal and Rohlf, 1981) and equality of slopes, as discussed in Hines (1982).

RESULTS

Body size (dry weight) of ovigerous females in the four non-pinnotherid species ranged up to an order of magnitude within each species and ranged over four orders of magnitude among species, from 0.07 g in the smallest individual of *Neopanope sayi* (mean = 0.227 g) to 517 g in the largest individual of *Loxorhynchus grandis* (mean = 370 g). For the two pinnotherid species, mean body size was very small but also spanned nearly an order of magnitude within species (*Pinnotheres ostreum* = 0.0357 g, range 0.0112 to 0.0786 g); *Fabia subquadrata* = 0.0721 g, range 0.0414 to 0.101 g), which overlapped the range of the non-pinnotherid species. These size ranges were judged to be adequate samples of variation within species, because analyses of size dependence in reproductive variables

TABLE 2. Size and reproductive regressions for six crab species.*

Species	Log bod. wt. = b(log carap. width) + c	R^2	Log brood b(log bod. wt.) + c	R^2	Log egg no. = b(log bod. wt.) + c	R^2
<i>Pinnotheres ostreum</i>	$Y = 2.180X - 3.486$	0.637	$Y = 0.967X - 0.234$	0.763	$Y = 1.002X + 5.189$	0.732
<i>Fabia subquadrata</i>	$Y = 2.567X - 3.694$	0.726	$Y = 1.306X + 0.326$	0.922	$Y = 1.423X + 5.490$	0.951
<i>Neopanope sayi</i>	$Y = 3.136X - 4.062$	0.997	$Y = 0.743X - 1.095$	0.923	$Y = 0.700X + 4.083$	0.923
<i>Portunus spinicarpus</i>	$Y = 2.967X - 4.837$	0.929	$Y = 1.787X - 1.663$	0.918	$Y = 1.913X + 4.100$	0.904
<i>Menippe nodifrons</i>	$Y = 2.410X - 2.794$	0.962	$Y = 1.106X - 1.452$	0.600	$Y = 1.016X + 3.617$	0.634
<i>Loxorhynchus grandis</i>	$Y = 1.940X - 1.520$	0.749	$Y = 0.767X - 0.705$	0.501	$Y = 0.850X + 3.467$	0.499

*For each species, the following linear regressions are estimated by least squares method of fit to the data: log body weight in g = (slope)(log carapace width in mm) + constant; log brood weight in g = (slope)(log body weight in g) + constant; log number of eggs per brood = (slope)(log body weight) + constant. For each regression, the R^2 value is listed.

yielded significant regression coefficients in all species, which is an important component of the subsequent regression analyses and allometric considerations (Table 2). They are also a good indicator of the range in body size among species (see Hines 1982, 1988, 1991, and below).

Nemertean worms (*Carcinonemertes* spp.) or other potential egg predators were not observed in the egg masses of any of the samples.

Mean egg sizes (diameter and volume, respectively) varied considerably among the four non-pinnotherid species: *Neopanope sayi* 314 μm , 0.0164 mm^3 ; *Portunus spinicarpus* 336 μm , 0.0201 mm^3 ; *Menippe nodifrons* 365 μm , 0.0258 mm^3 ; and *Loxorhynchus grandis* 666 μm , 0.159 mm^3 . Egg sizes (diameter and volume, respectively) varied widely between the two pinnotherid species: *Pinnotheres ostreum* 260 μm , 0.0092 mm^3 ; *Fabia subquadrata* 414 μm , 0.0372 mm^3 . Egg size did not vary significantly within species (ANOVA, $P > 0.05$). Egg size did vary significantly among the six pinnotherid and non-pinnotherid species (ANOVA on Log Egg Diameter: $F_{(5,64)} = 221.95$, $P > 0.001$). Although the largest species, *Loxorhynchus grandis*, had the largest egg, and *Pinnotheres ostreum* (the smallest species) had the smallest egg, mean egg size was not correlated with female body size among the six species (ANCOVA of Log Egg Volume on Log Body Weight, $F_{(5,64)} = 0.36$, $P > 0.55$). However, egg size was significantly correlated with female body size among the 35 species in the larger data set (Fig. 1; ANOVA of Log Egg Volume on Log Body Weight, $F_{(1,34)} = 8.328$, $P < 0.01$), but variation in body size only explained a small portion of the variation in egg size ($R^2 = 0.201$) (Hines, 1982, 1988, 1991; see also Hines, 1986). Along with *Callinectes sapidus*, *P. ostreum* had the smallest egg of the 35 species, and had an egg which was smaller than the 95% confidence limits of the mean for the group (mean \pm 95% confidence limits: Egg Diameter $406 \pm 20 \mu\text{m}$; Egg Volume $0.045 \pm 0.008 \text{mm}^3$). *Fabia subquadrata*, on the other hand, had an egg size which was near the mean for the group.

Brood weight for the four non-pinnotherid species increased significantly with

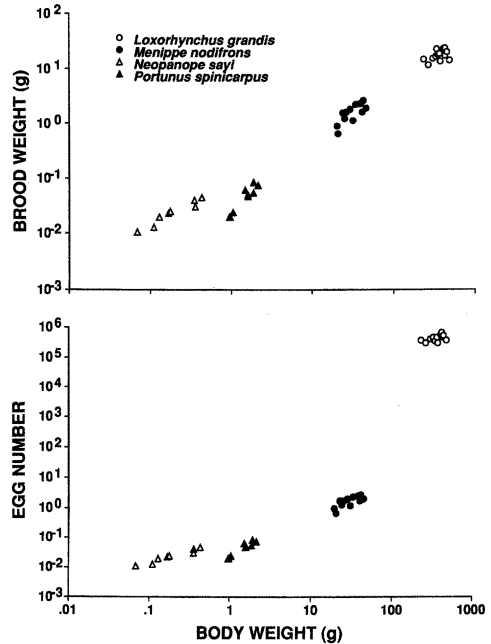


FIG. 2. Brood weight (top) and number of eggs per brood (bottom) versus body size in samples of four non-pinnotherid species of crabs spanning four orders of magnitude in dry body weight. Note log-log scales. Regression equations are given in Table 2.

female body weight both within and among species (Table 2, Fig. 2, ANOVA of Log Brood Weight on Log Body Weight, $P < 0.05$); and mean dry brood weight ranged from 0.0259 g in *Neopanope sayi* to over 18.2 g in *Loxorhynchus grandis*. Similarly, brood weight for the pinnotherid species increased significantly with female body weight within species (Fig. 3; ANOVA on Log Brood Weight on Log Body Weight, $P < 0.001$); and mean brood weight of the pinnotherid species overlapped that of the smallest non-pinnotherid species: *Pinnotheres ostreum* 0.0237 g; *Fabia subquadrata* 0.0697 g. Because regression slopes differed significantly among the 6 species (ANCOVA of Log Brood Weight on Log Body Weight with significant interaction of Log Brood Weight \times Log Body Weight, $F_{(5,64)} = 3.06$, $P < 0.02$), further contrasts of reproductive effort using ANCOVA were not possible. To compare brood size of the pinnotherids with an array of other non-pinnotherid species, mean log brood weight was regressed on mean log body weight for each of the 6 spe-

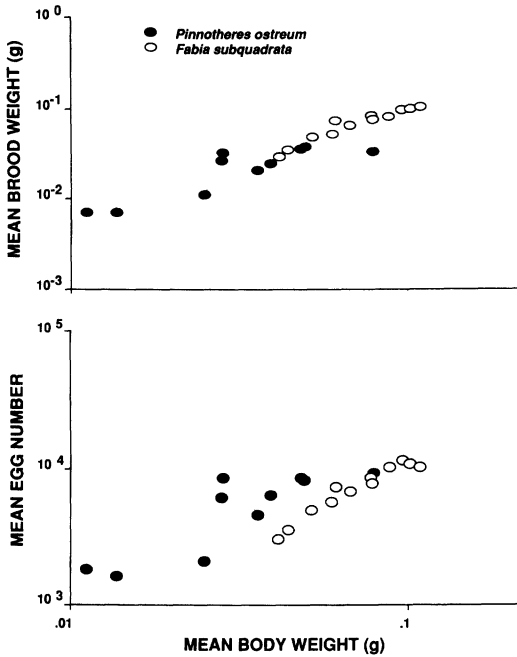


FIG. 3. Brood weight (top) and number of eggs per brood (bottom) versus dry body weight in samples of two species of pinnotherid crabs. Note log-log scales. Regression equations are given in Table 2.

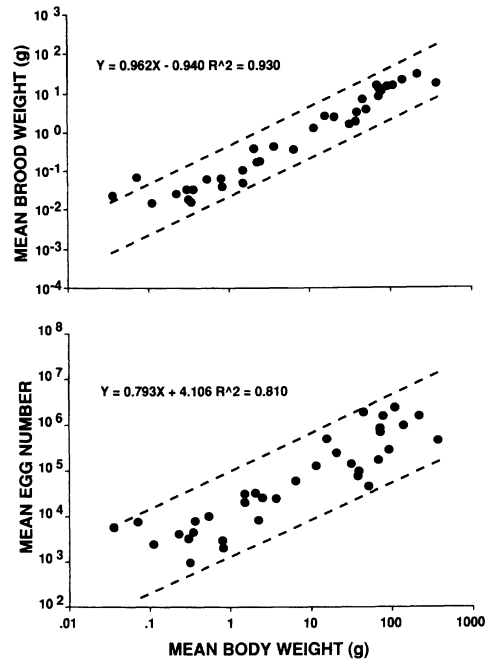


FIG. 4. Mean brood weight (top) and mean number of eggs per brood (bottom) versus mean body weight in 35 species of crabs from this paper and Hines (1982, 1988, 1991). Regression equations and R^2 values are indicated. Dashed lines indicate the 95% confidence belts of the data in the regressions. Note that only the mean brood weights for the two pinnotherid species fall outside the confidence limits. Note log-log scales.

cies along with comparable data for 29 other species extracted from earlier publications (Hines, 1982, 1988, 1991). Whereas mean brood weights for all 33 non-pinnotherid species lie within the 95% confidence limits of the regression, brood weights of the two pinnotherid species were significantly larger and fell outside the confidence belt (Fig. 4). Based on a *a posteriori* chance alone for a 95% confidence limit for a sample size of 35, 1.9 species might be expected to lie outside the confidence belt of the regression; but the *a priori* chance of both pinnotherids being those species is only 1 in 400 (0.25%).

Mean brood weight as a fraction of mean body weight for the 33 non-pinnotherid species averaged 10.7% and ranged from as low as 3.2% in *Portunus spinicarpus* to as high as 23.0% in *Chaceon quinquedens* (Fig. 5). In contrast, mean brood weight for the two pinnotherids was very much larger at 66.2% for *Pinnotheres ostreum* and 96.7% for *Fabia subquadrata* (Fig. 5).

Fecundity per brood also increased significantly with body weight within and

among non-pinnotherid species, ranging from 1,790 eggs per brood in the smallest *Neopanope sayi* to 634,000 eggs per brood in the largest *Loxorhynchus grandis* (Fig. 2; Table 2). However, variance in size-specific fecundity among species was greater than for brood weight, and it is not initially clear for this limited number of species whether the increase in fecundity with body size among species is best described by a linear or curvilinear regression of log egg number versus log body weight (Fig. 2, but see below). For the two pinnotherid species, log egg number per brood was also a linear function of log body weight, with mean fecundities overlapping the small non-pinnotherid species: *Pinnotheres ostreum* 5,680 eggs per brood; *Fabia subquadrata* 7,560 eggs per brood (Fig. 3). Again, because regression slopes differed significantly among the 6 species (ANCOVA of Log Brood Weight on Log Body Weight with significant interac-

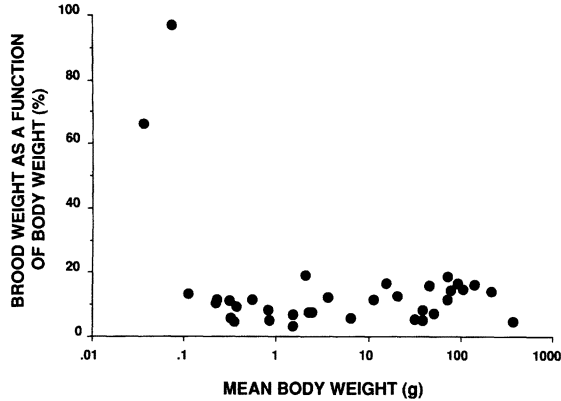


FIG. 5. Brood weight in proportion to female body size for 35 species of crabs from this paper and Hines (1982, 1988, 1991) spanning over four orders of magnitude in dry body weight. Note that brood weight in non-pinnotherid species averaged about 10% (minimum = 3%, maximum = 22%) of female body weight, but brood sizes in the two pinnotherid species were 66% (*Pinnotheres ostreum*) and 97% (*Fabia subquadrata*). Note log scale on the X-axis.

tion of Log Egg Number \times Log Body Weight, $F_{(5,64)} = 3.85$, $P < 0.01$), further comparison of fecundities using ANCOVA was not possible. Regression of mean log egg number per brood on mean log body weight for each of the 35 species reported here and in earlier papers (Hines, 1982, 1988, 1991) showed that the two pinnotherid species had relatively high fecundities for their body size (Fig. 4). However, while the fecundity of *P. ostreum* fell on the upper 95% confidence limit, that for *F. subquadrata* was within the belt at a deviation from the mean similar to that for *Callinectes sapidus* (Fig. 4).

Mean numbers of broods per year produced by the four non-pinnotherid species are: 1.5 in *Neopanope sayi* (Swartz 1972); 2.0 in *Portunus spinicarpus* (Camp and Whiting, 1991), 2.0 in *Menippe nodifrons* (Wilber, 1989; Hines, personal observation); and 3.5 in *Loxorhynchus grandis* (Hines, unpublished). Similarly, the two pinnotherid species each produce a mean of 1.5 broods (range 1–2 broods) per year over a distinct reproductive season from June through August in *Pinnotheres ostreum* (Christensen and McDermott, 1958) or December through March in *Fabia subquadrata* (Pearce, 1966). Considering the total of 35 species reported in this and earlier publications (Hines, 1982, 1988, 1991), the pinnotherids produce somewhat fewer broods per year than the overall average of 2.4 broods (range 1.0 to 8.0 broods), but

they lie within the 95% confidence limits of the mean.

The mean brood weight per year and the mean fecundity per year produced by each species was estimated by multiplying the mean brood weight or the mean number of eggs per brood, respectively, by the mean number of broods per year. Mean annual reproductive output (brood weight) is a linear function of body weight (Fig. 6; ANOVA, $F_{(1,34)} = 426.1$, $P < 0.001$). The pinnotherid species had large reproductive outputs, but outputs of none of the 35 species fell outside the 95% confidence belt of the regression. Mean annual fecundity is also a linear function of body weight (Fig. 6; ANOVA, $F_{(1,34)} = 190.3$, $P < 0.001$). Annual fecundities of the pinnotherids were high, but only *Callinectes sapidus* had a reproductive output outside the 95% confidence belt for the regression. Again, by definition, there is an *a posteriori* probability of 1.9 species falling outside the 95% confidence belt.

DISCUSSION

Comparison of reproductive variables between pinnotherid species and other families provides insight into the evolutionary patterns of life history strategies in the Brachyura. Body size is the principal determinant of reproductive output and fecundity in brachyuran species ranging over 4 orders of magnitude in body weight (Hines, 1982, 1988, 1991). Although pinnotherids

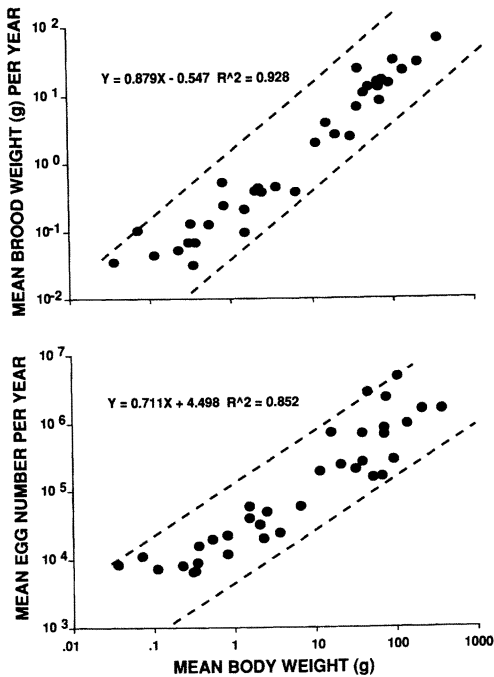


FIG. 6. Mean brood weight produced per year (top) and mean number of eggs produced per year (bottom) versus mean body weight in 35 species of crabs from this paper and Hines (1982, 1988, 1991). Regression equations and R^2 values are shown. Dashed lines indicate the 95% confidence belts of the data in the regressions. Only the number of eggs per year for *Callinectes sapidus* lies outside the confidence limits. Note log-log scales.

are small, brood weight and fecundity also increase markedly with body size in *Pinnotheres ostreum* and *Fabia subquadrata*. For all non-pinnotherid species sampled here and in earlier papers (Hines, 1982, 1988, 1991), brood mass is limited to about 10% of the female body weight, within a range from 3 to 22%. In contrast, brood masses of these two pinnotherid crabs are extraordinarily large (66% and 97% of body weight) in relation to female body size. If brood size in brachyurans is constrained allometrically by space available within the cephalothorax by yolk accumulation (Hines, 1982, 1988), what accounts for the huge relative brood size in the two pinnotherid species? Two factors appear to allow these species to escape the constraint. First, the ovaries in *P. ostreum* and *F. subquadrata* extend out of the cephalothorax and into the abdomen (Fig. 7), providing extra space for yolk accumulation that is apparently not

available in any of the non-pinnotherid species, which have ovaries confined to the cephalothorax. Second, unlike well-calcified, non-pinnotherid species, females (but not males) of these pinnotherids have very little calcium carbonate deposited in their exoskeleton (Christiansen and McDermott, 1958; Pearce, 1966; Hines, personal observation), which makes their exoskeleton flexible, and which provides the possibility that the body is distensible during yolk accumulation.

Just as egg size is a major variable of reproductive strategies in non-pinnotherid brachyurans (Hines, 1982, 1986, 1988, 1991; Fig. 1), egg size is highly variable between the two pinnotherids from very small to nearly average in size. Two consequences of this variation in egg size are evident in fecundities of the pinnotherids relative to the other species. First, the large interspecific variation in egg size among all crabs results in a much greater variance in the relation between number of eggs per brood and body size than in the relatively "tight" regression for brood weight on body weight. Compared to brood weight, this increased variance tends to reduce the size-specific difference in pinnotherid fecundities relative to the other species. Second, variation in egg size between the two pinnotherid species altered the ranking of their relative fecundity. Whereas *Fabia subquadrata* had a relative brood size nearly equal to female weight, and *Pinnotheres ostreum* had a brood size of about two thirds of female weight, fecundity of the former species with an average sized egg was lower than the latter with a very small sized egg. Thus, while fecundities per brood in the pinnotherids are high, they are not extraordinary to the extent that reproductive mass is for these two species.

The large reproductive output of the pinnotherids may be adaptive to the parasitic niche of these species. Their larvae may suffer greater mortality during their search for a more specific settlement site (the bivalve host) than do larvae of free-living crabs. Greater reproductive output would help to compensate for higher larval mortality. In addition, extra reproductive effort may be required to compensate for the allometric limits of small body size inherent for inter-

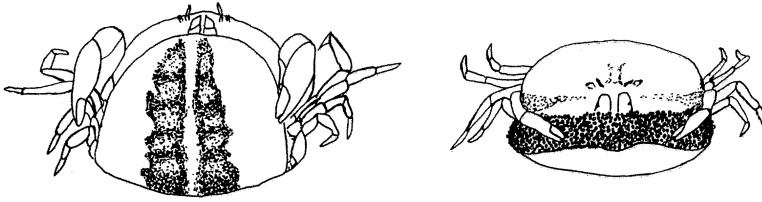


FIG. 7. (Left) Camera lucida drawing of ventral view of female *Pinnotheres ostreum* with ripe ovaries extending into abdomen prior to egg extrusion. (Right) Camera lucida drawing of frontal view of brooding female *Fabia subquadrata*. In specimens newly preserved in formalin, the ovaries and newly extruded eggs appear light orange and the crabs are light yellow. Note very large abdominal flap, which aids in incubation of extraordinarily large brood mass relative to body size in both species.

nal parasites. Just as many invertebrates face "evolutionary difficulties" imposed by small body size upon reproductive tactics (Menge, 1975; Strathmann and Strathmann, 1982), a crab the size of a pinnotherid is markedly limited in its absolute reproductive output. In species which brood, there are only three options for increasing fecundity: reducing egg size (more but smaller eggs); increasing the number of broods per year; and/or increasing brood mass. Because the cumulative data indicates that 250 μm appears to be approaching the lower limit of egg size for brachyurans (Fig. 1; Hines, 1982, 1988, 1991; Hines and Morgan, unpublished), and since eggs of *Pinnotheres ostreum* are near that size limit, reducing egg size alone would not appear to increase fecundity "enough." Both of these species also appear to be restricted in the number of broods produced by relatively short reproductive seasons. Since this seasonal limit applies to both winter and summer cycling species, it is not clear whether ecological (e.g., timing of larval settlement) or energetic (plankton production for the host's food) considerations pertain. Clearly, the parasitic habitat of the adult females of these species minimizes the disadvantages of reduced calcification in the exoskeleton, because the host bivalve both restricts movement and provides protection from predators, thus negating two of the major functions of a rigid, non-distensible exoskeleton. Thus, these pinnotherids provide a test of the rule that brood size is constrained to about 10% of female body weight by space available for yolk accumulation in the cephalothorax. Pinnotherids are able to produce broods which are proportionately much larger than in other

crabs only by evolving two mechanisms (extension of ovaries into the abdomen and distensible exoskeleton) that circumvent this allometric constraint.

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