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LARVAL PATTERNS IN THE LIFE HISTORIES OF BRACHYURAN CRABS (CRUSTACEA, DECAPODA, BRACHYURA)

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ABSTRACT

Developmental and larval patterns of brachyuran crabs are compared using data extracted from the literature for complete larval descriptions of 47 species and partial larval descriptions of 154 species. Focus was on four areas of interest: (1) Relationship between egg size, larval growth and size of first crab at settlement. Species with direct or abbreviated development had large eggs. Megalopal size and first crab size were positively correlated with adult size; egg size and zoeal size were not. Zoeal growth increased significantly with number of zoeal instars. There were no significant effects of egg size or adult size on incubation and larval periods. Species which produced only one brood per year had significantly longer brood incubation times, longer zoeal and total larval periods, and larger sizes of last zoea, first crab and adult size than multiple brood species. (2) Patterns indicating evolutionary constraints by lineage (family) on larval biology. Among the seven families with data for the most species (Cancridae, Grapsidae, Majidae, Ocypodidae, Portunidae, Pinnotheridae, and Xanthidae), there were significant differences in: adult size, incidence of species with single broods per year, brood incubation period, egg size, first zoea size, number of zoeal instars, first crab size, zoeal period, and total larval period. However, there were no significant differences in last zoeal size or megalopal size, except for large megalopas of *Ocypode* spp. (3) Patterns of larval biology with respect to adult habitat and climatic zone. Cold-water species (polar, cold-temperate, and deep water) had significantly longer brood incubation times, longer zoeal and total larval periods, and larger adult size than warm-water species (tropical, subtropical, and warm-temperate species dwelling shallower than 100 m). Species with life cycles restricted entirely to freshwater/terrestrial habitats had significantly larger eggs than marine species. *Ocypode* spp. on sandy beaches had large megalopas, and intertidal species had significantly smaller eggs and adult size than subtidal species. (4) Relationship between species geographic range and length larval period as a measure of dispersal potential. Species with greatly reduced or no larval duration in terrestrial or freshwater habitats had very small ranges. However, among marine species there was no significant relationship between extent of the range and duration of the larval dispersal period.

The patterns described in this paper should be accepted with caution, because larvae have been described for only a small proportion of species in any habitat, family, or the Brachyura as a whole. However, this analysis provides a preliminary synthesis of patterns in the context of brachyuran life histories based on a more extensive data set than available for most groups of invertebrates.

Larval development in brachyuran crabs has been studied extensively for systematic purposes (Rice, 1980; Williamson, 1982; Martin, 1984), for analyses of physiological ecology (Anger and Dawirs, 1982; Dawirs, 1984; Costlow, 1976), for bioassays of chemical pollutants (Epifanio, 1971; 1979; Cucci and Epifanio, 1979), and for analyses of larval behavior (Forward and Costlow, 1974; Cronin and Forward, 1983; Sulkin, 1984). Juvenile growth and adult ecology of crabs have also been studied extensively because of their commercial importance in fisheries and their trophic importance in nearshore communities (Millikan and Williams, 1984). However, there has been no attempt to integrate data on larval and post-settlement biology in the context of brachyuran life history strategies. Focusing on four primary relationships, the purpose of this paper is to present an initial synthesis of these data extracted from the literature so that broad interspecific patterns can be determined.

First, the relationship between egg size, larval growth, and size of the first crab at settlement will be examined. Strathmann (1977) showed that in some crustacean groups egg size is not a good indicator of developmental mode (sensu Thorson, 1950), but rather that larger eggs result in larger size of juveniles at settlement. Hines (1982) discussed the importance of egg size in several crustacean groups and showed that egg size is positively correlated with adult size in 21 species of brachyurans. In addition, Hines (in press) compared the life histories of five species of spider crabs and showed that increased egg size resulted in increased size of the first crab instar, fewer juvenile molts, and shorter time to sexual maturity. In several groups of crustaceans, larger size at settlement may improve the ability of juveniles to obtain a larger array of food, to reduce competition, and to avoid predators (Mauchline, 1973; Belk, 1977; Reaka, 1979). Therefore, it is of interest to determine whether egg size, larval size, size at settlement, and adult size are positively correlated across the complete range of brachyuran life histories.

Second, the data will be tested for patterns indicating evolutionary constraints by lineage (family) on larval biology. Stearns (1983; 1984) showed that vertebrates exhibit significant design constraints on life-history evolution by order and family when effects of body size are removed statistically (see Vitt and Seigel, 1985; Hedges, 1985; Dunham and Miles, 1985). Evolutionary constraints by lineage have been observed and proposed for reproductive strategies of several groups of crustaceans (Reaka, 1979; 1980; Nelson, 1980; Phillips and Sastry, 1980; Hines, 1982; Reaka and Manning, in press). Knowlton (1974) ranked the major groups of euphausiids and decapod crustaceans along an evolutionary series of increasing egg size, declining number and variability in the number of larval instars, and decreasing variability in the length of larval period and rate of larval growth. Although the number of zoeal instars in the Brachyura ranges from two to eight, the number of larval instars is relatively constant within a given family and varies among families (Rice, 1980). Thus, larval patterns may exhibit constraints by family in the life histories of crabs.

Third, patterns of larval biology with respect to adult habitat and climatic zones will be examined. Patterns of developmental mode along latitudinal and depth gradients have been observed for many groups of invertebrates (Thorson, 1950; Mileikovsky, 1971), including amphipods (Nelson, 1980), cumaceans (Corey, 1981), copepods (McLaren et al., 1969), and mysids (Mauchline, 1973). In addition, consistent reproductive differences have been documented among habitats for amphipods (Nelson, 1980; Van Dolah and Bird, 1980) and stomatopods (Reaka, 1980; Reaka and Manning, in press). However, the life histories of brachyurans have not been analyzed with respect to habitat and climate.

Fourth, the relationship between length of the larval phase as a measure of dispersal potential and species range will be investigated. Scheltema (1978; 1979; 1981), has shown a positive correlation between larval dispersal (developmental mode and length of larval life), species range, species duration, and rates of speciation in molluscs. Jablonski (1982) and Jablonski and Lutz (1983) have argued that similar patterns occur in fossil assemblages of gastropods. In addition, Reaka (1980) and Reaka and Manning (in press) showed in stomatopods that short larval periods and low dispersal abilities are significantly related to smaller species ranges (endemism) and greater rates of speciation. Despite scholarly zoogeographic analyses of brachyurans (Rathbun, 1918; 1925; 1930; Williams, 1974; 1984; Garth, 1958; Stephenson, 1962; Crane, 1975; Manning and Holthius, 1981; Powers, 1977), the relationship between larval dispersal and zoogeography of this group has not been examined.

This synthesis is neither an exhaustive review of the brachyuran literature, nor

Table 1. Regressions for sizes of consecutive developmental stages

Dependent variable	Independent variable	Slope	Intercept	r
First zoea carap. length	Log egg diameter	1.64	1.28	0.93
Last zoea carap. length	First zoea carap. length	0.575	0.814	0.41
Megalopa carap. width	Last zoea carap. length	1.26	−0.194	0.90
First crab carap. width	Megalopa carap. width	1.73	−0.264	0.88

a definitive analysis of brachyuran life history patterns. Rather, by extracting and distilling a large and representative proportion of the extant data from the literature, I provide a preliminary analysis of larval patterns in the life history strategies of brachyurans and identify major data gaps and fruitful directions for additional research.

Materials and Methods

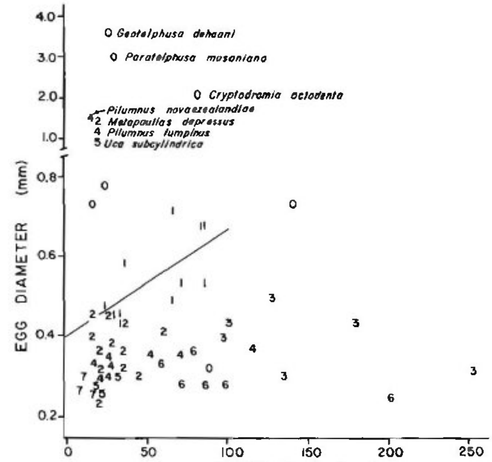
Data on several variables of the embryonic, larval, juvenile, and mature stages of 201 species of crabs were extracted from the literature and supplemented with my own unpublished data (Appendix 1). The variables were: egg diameter, incubation time of the brood, sizes (carapace length) of the first and last zoeae, the number of zoeal instars, megalopa size (carapace width), durations of the zoeal and total larval periods (in days), size (carapace width) of the first crab, adult size (maximum carapace width of mature females), and whether one or more broods were produced per year. In addition, the following variables on habitat and geographic range were recorded for many of these species: primary habitat type (six categories, e.g., estuarine, coral reef), substrate (eight categories), depth (five cagetories from terrestrial to deep water), latitudinal zone (five categories from tropical to polar), range size (measured linearly in kilometers on a globe to eliminate map distortion), range in degrees latitude, and range in degrees longitude. Data on habitats and ranges were taken from the references in the Appendix and from Stephenson (1962), Nations (1975), Powers (1977), Garth and Abbott (1980), and Williams (1984). Ranges resulting from known introductions (e.g., *Carcinus maenas, Rhithropanopeus harrisii*) were excluded.

The data have several major problems. Only 47 species had data for all parameters. Most species lacked data for several, often most, variables, so that statistical analyses utilized different subsets of data for each question tested. I analyzed only species for which at least one larval and one additional variable were available. In several cases, species were not included because accurate measurements of larval size were not possible due to inadequate scale documentation in drawings (e.g., much of the classical work by Lebour, 1928).

Statistical treatments utilized computer programs for SAS (Statistical Analysis System) of SAS Institute, Inc. Individual statistical tests are presented in the results.

Results

Size Relationships between Developmental Stages.—Sizes of consecutive developmental stages had significant positive regressions, although the correlation of size of the last zoea with the first zoea was low as a result of growth through variable numbers of instars among species (see below) (Table 1). Egg size ranged enormously among species from diameters of 0.252 mm for *Callinectes sapidus* to 3.6 mm for *Geotelphusa dehaani.* However, there was no significant effect of adult body size on egg size among species (ANOVA, $P > 0.1$), even when unusual species with direct or abbreviated development (Potamidae, Dromiidae, *Metopaulias depressus, Uca subaylindrica, Heterozius rotundifrons, Pilumnus lumpinus, P. novaezealandiae, P. vestitus*) were excluded from the analysis (ANOVA, $P > 0.1$; Fig. 1). Similarly, size of the first zoea did not change significantly with adult body size among species (ANOVA, $P > 0.1$). However, size of the last zoea increased significantly with adult body size when unusual species with direct or abbreviated development were excluded from the analysis (ANOVA, $P < 0.001$), although the relationship was not tightly correlated ($r = 0.46$). Although the growth



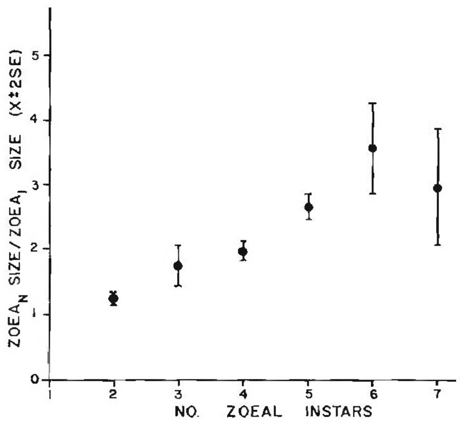


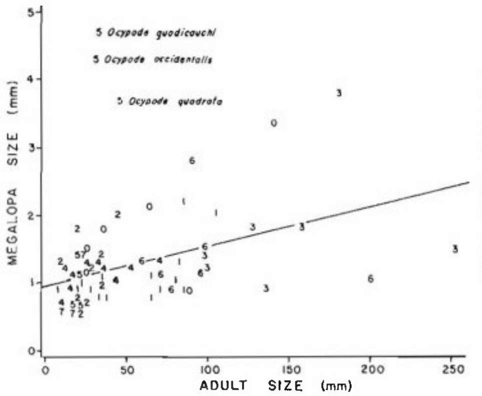
Figure 1. (Left) Egg diameter versus adult size (maximum female carapace width). Each number plotted represents a species coded by family. 1 = Majidae; 2 = Grapsidae; 3 = Cancridae; 4 = Xanthidae; 5 = Ocypodidae; 6 = Portunidae; 7 = Pinnotheridae; 0 = other families. Regression line for majid species only is shown: egg diam = 0.0028(adult size) + 0.397.

Figure 2. (Right) Zoeal growth increment versus number of zoeal instars.

increment from the first to the last zoeal instar increased significantly with adult body size (ANOVA, $P < 0.05$), adult body size accounted for very little of the variation in growth increment ($r = 0.08$). On the other hand, the zoeal growth increment was highly positively correlated with the total number of zoeal instars in larval development (Fig. 2). Megalopal size as function of adult size was extremely variable, particularly as a result of the very large megalopas of *Ocypode* spp. (Fig. 3). When these unusual species were removed from the analysis, megalopal size also increased significantly with adult size (ANOVA, $P < 0.0001$), but megalopal size was quite variable ($r = 0.48$). Similarly, with the exception of the unusual, direct-developing potamid species, size of the first crab increased significantly with adult size (ANOVA, $P < 0.002$), albeit with considerable variation ($r = 0.51$) (Fig. 4).

There was no significant effect of egg size or adult size on incubation time of the brood, and egg size and larval period were not correlated (ANOVA, $P > 0.2$). However, species which produced only a single brood per year had significantly longer brood incubation and total larval periods, and larger sizes of last zoea, first crabs, and adult size (ANOVA, $P < 0.05$; Fig. 5), but egg size and zoeal period were not significantly different among single and multiple brood species. Some of these differences may be complicated by the cancrid species, which produce only one brood per year and are restricted to cold waters (Nations, 1975). In addition, ocypodids and portunids are multiple brooders which are mainly restricted to warm waters. Because cold-water species exhibited significant differences from warm-water species for most of these variables (see below under Habitat), it is difficult to separate the effect of brood number from water temperature.

Family Patterns.—Representative species of a few unusual families are included in the data set. Potamids are freshwater crabs which have direct development lacking larval stages entirely, and dromiids have very abbreviated development



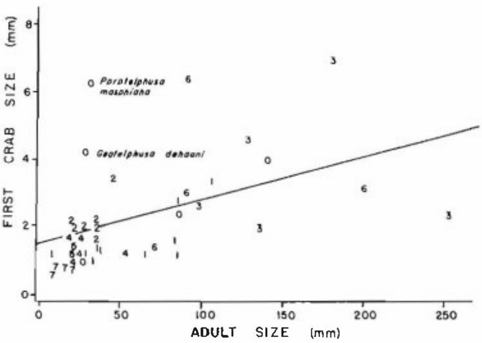


Figure 3. (Left) Megalopal size (carapace width) versus adult size (maximum female carapace width). Symbols as in Figure 1. Regression excludes *Ocypode* spp.: meg. size = 0.0056(adult size) + 0.925.

Figure 4. (Right) First crab size (carapace width) versus adult size (maximum female carapace width). Regression excludes potamid species with direct development: (C1 size) = 0.014(adult size) + 1.33.

with larvae which may be brooded by the female through metamorphosis. Although quantitative data are available for very few species in these families, they appear to be characterized by very large eggs (Fig. 1), and potamids had very large first crabs (ANOVA, $P > 0.0001$; Fig. 4). Other families with unusual habits (e.g., commensalism in Hapalocarcinidae and Pinnotheridae) did not exhibit developmental stages out of the range of normal variation in more typical families.

Among the seven families with data for the most species (Cancridae, Grapsidae, Majidae, Ocypodidae, Portunidae, Pinnotheridae, and Xanthidae), there were several significant patterns (Table 2). Although the species in the data set were selected for information on larval development and are not representative of the extant data on body size, there were highly significant differences in adult body size among families. The frequency of species producing only a single brood per year was significantly different among families (χ^2, $P < 0.001$). The brood incubation period was different among families (ANOVA, $P < 0.01$) with cancrids having a significantly longer period (Sheffé's test, $P < 0.05$). Egg size was significantly different among families, with spider crabs (Majidae) having larger eggs (Sheffé's tests, $P < 0.05$). Although there was no significant effect of adult body size on egg size among all species, majid species did show a significant increase in egg size with body size (ANOVA, $P < 0.05$; Fig. 1), whereas other families did not (ANOVA, $P > 0.1$). Similarly, size of the first zoea was significantly different among families (ANOVA, $P < 0.001$; Table 2), with majids having larger larvae than other species (Sheffé's tests, $P < 0.05$). However, size of the last zoea (adjusted for adult size) was not different among families (ANCOVA, $P > 0.1$). Number of zoeal instars was significantly different among families (χ^2, $P < 0.01$). The effect of zoeal growth increment (Fig. 2) in combination with the family differences in number of zoeal instars eliminated the initial family differences in first zoeal size due to egg size. Size of the megalopa adjusted for adult size showed significant differences among families (ANCOVA, $P < 0.01$), but this was entirely due to the very large megalopae of *Ocypode* spp. in the Ocypodidae. There were no significant differences among other families and ocypodids not in the genus *Ocypode* (ANCOVA, $P > 0.1$). Size of the first crab was different among families

Table 2. Developmental and larval patterns for seven families of crabs. Means (±SE) are shown. Significant differences among families are indicated (χ^2 for variables 2 and 7; ANOVA for variables 1, 3, 4, 5, 6, 10, and 11; ANCOVA with adult size for variables 8 and 9). a = when *Ocypode* spp. are excluded, there are no significant differences in megalopa size among families

		Cancridae	Grapsidae	Majidae	Ocypodidae	Pinnotheridae	Portunidae	Xanthidae	*P*
1	Adult size (CW in mm)	139 (21)	27 (4)	51 (7)	27 (3)	16 (3)	85 (14)	34 (7)	0.0001
2	% spp. with/1 brood/yr	100	8	31	0	0	33	15	0.001
3	Incub. time (days)	118 (27)	51 (7)	64 (21)	20 (6)	61 (15)	19 (7)	27 (11)	0.01
4	Egg diam (mm)	0.40 (0.03)	0.45 (0.08)	0.55 (0.02)	0.43 (0.14)	0.34 (0.05)	0.31 (0.01)	0.36 (0.02)	0.05
5	Zoea 1 size (CL in mm)	0.55 (0.05)	0.54 (0.05)	0.90 (0.03)	0.52 (0.09)	0.53 (0.08)	0.47 (0.02)	0.55 (0.04)	0.001
6	Zoea N size (CL in mm)	1.52 (0.19)	1.25 (0.14)	1.08 (0.04)	1.11 (0.23)	0.75 (0.05)	1.25 (0.10)	1.17 (0.13)	NS
7	No. zoeal stages	5.0 (0)	4.5 (0.1)	2 (0)	5 (0)	3.5 (0.5)	5.4 (0.3)	4.2 (0.1)	0.01
8	Megalopa size (CW in mm)	1.67 (0.32)	1.22 (0.12)	1.06 (0.06)	2.05 (0.50)[a]	0.79 (0.14)	1.35 (0.11)	1.07 (0.07)	0.001[a]
9	1st crab size (CW in mm)	3.68 (0.91)	1.73 (0.17)	1.50 (0.17)	1.33 (0.10)	0.81 (0.12)	2.89 (0.64)	1.28 (0.08)	0.01
10	Zoeal period (days)	44 (10)	31 (7)	18 (3)	17 (10)	22 (1)	27 (4)	19 (2)	0.05
11	Larval period (days)	65 (11)	39 (8)	30 (4)	29 (16)	40 (6)	45 (7)	31 (3)	0.01

(ANCOVA, $P < 0.01$), as were zoeal period and total larval period (ANCOVA, $P < 0.05$).

There were significant differences among families for latitudinal zone and some habitat categories. For example, cancrid species occurred only in cold zones (polar and cold temperature zones) and grapsid species occurred primarily at intertidal "depths" (χ^2 tests, $P < 0.05$). However, while these differences may be real (Nations, 1975 and Rathbun, 1918), the present data set was not designed to test these questions and does not reflect the extant data on crab habitat and distribution in the literature.

Adult Habitat and Climatic Zone.—Adult habitat and climatic zone correlate with water temperature. Cold-water species (polar, cold-temperate, and deep water) had significantly longer brood incubation times, longer zoeal and total larval periods, and larger adult size than warm-water species (tropical, subtropical, and warm-temperate species dwelling shallower than 100 m) (ANCOVA, $P < 0.05$; Fig. 5). However, the remaining parameters (i.e., egg size, zoeal sizes, megalopal size, first crab size) did not differ significantly among warm- and cold-water species. Species with life cycles entirely restricted to freshwater/terrestrial habitats (i.e., potamids, *Metopaulias depressus, Uca subcylindrica*) had significantly larger eggs than species with larval development in marine habitats, which includes terrestrial gecarcinids (ANCOVA, $P > 0.05$; Fig. 1). Some species inhabiting sandy wave-swept beaches (i.e., *Ocypode* spp.) had significantly larger megalopae adjusted for adult size than species from other habitats (ANCOVA, $P < 0.01$; Fig. 3). Based on data for a small number of species, only freshwater, direct-developing species (i.e., potamids) had significantly larger first crabs adjusted for adult size (ANCOVA, $P < 0.05$; Fig. 4); data on first crab size was not available for *Ocypode* spp. Intertidal species had significantly smaller eggs and adult size than subtidal species to depths of 100 m (ANCOVA, $P < 0.05$; Fig. 5). However, other comparisons of species by habitat (e.g., estuaries, coral reefs) and substrate (e.g., hard versus soft bottoms) showed no significant differences in any of the variables (ANCOVA, $P > 0.1$).

Species Range and Length of Larval Life.—The linear dimension of a species range was a valid indicator of range size; it had significant positive linear correlations with range in both degrees latitude and degrees longitude ($P < 0.05$; $r = 0.75$ and $r = 0.89$, respectively). Species with greatly reduced larval periods or no free-living larvae in freshwater terrestrial habitats (e.g., potamids, *Metopaulius depressus, Uca subcylindrica*) had very small ranges. However, among marine species there was no significant relationship between extent of the range and duration of the zoeal period or duration of the total larval period (ANOVA, $P > 0.1$; Fig. 6). Although there was an indication that species with larger ranges may have slightly longer larval periods, four species (*Pachygrapsus crassipes, Cancer productus, Cancer magister,* and *Troglocarcinus corallicola*) without extensive ranges had very long larval periods (Fig. 6). Although *T. corallicola* has a much larger range than indicated in the literature (Raymond Manning, National Museum of Natural History, Washington, D.C., pers. comm.), the data for the other three species appear to be accurate.

Discussion

In many invertebrate groups (e.g., echinoderms, molluscs, polychaetes), increased egg size is generally correlated with a longer prefeeding period, shorter planktonic period, and shorter total development time to metamorphosis (Thor-

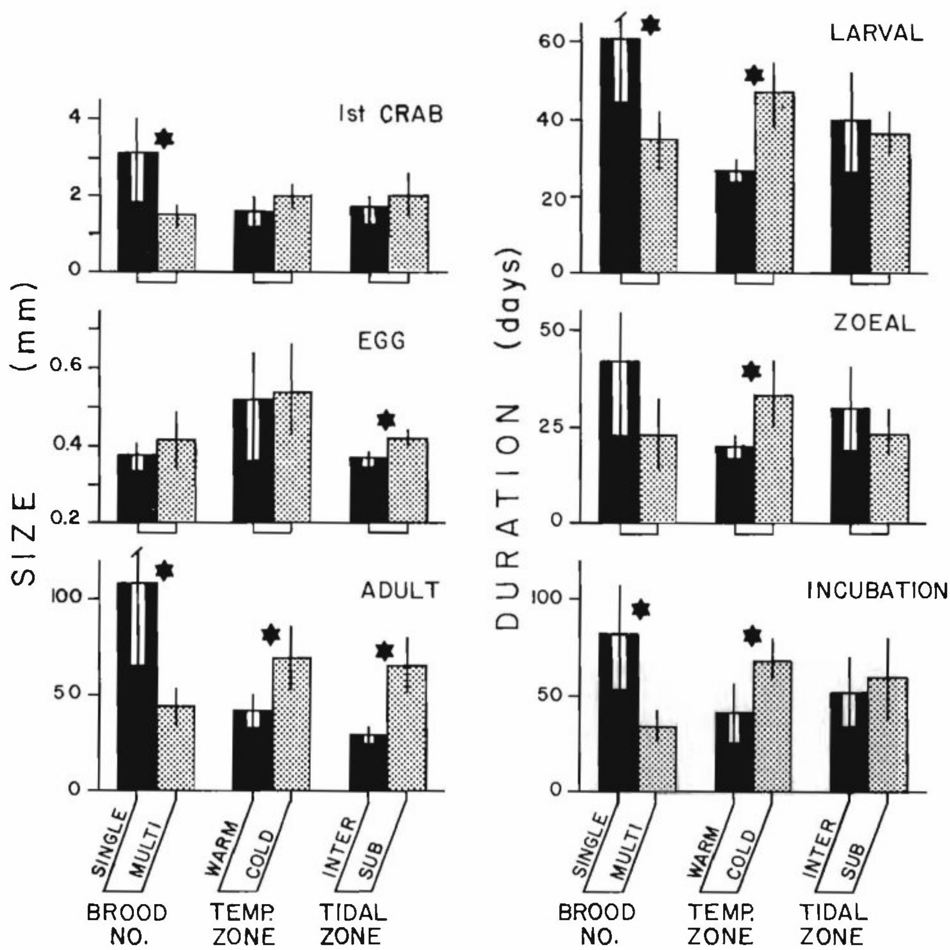


Figure 5. Developmental and larval comparisons of species categorized by: brood number (single versus multiple broods per season); temperate zone (polar, cold-temperate, and deep water versus tropical, subtropical, and warm-temperate species shallower than 100 m); and tidal zone (intertidal versus subtidal to 200 m depth). Means ± 2 SE are shown for sizes of adult, egg, and first crab (left set of histograms) and durations of incubation, zoeal and total larval periods (right set of histograms). Stars indicate significant differences (ANOVA, $P < 0.05$).

son, 1950; Mileikovsky, 1971). Direct or unusually abbreviated development also is correlated with large egg size and large settlement size in brachyuran crabs, though these are unusual species. Even spider crabs (Majidae), which have only two zoeal stages, have significantly larger eggs than other families (Kurata and Matsuda, 1980; Hines, 1982). However, the interrelationship between egg size, larval growth, size at settlement, and adult size is not simple in most brachyurans. Contrary to the pattern of increased egg size with adult size in an earlier study (Hines, 1982), larger crabs with the exception of the Majidae generally do not have larger eggs. Increased egg size correlates with longer development time in many crustacean groups (Steele and Steele, 1975a), 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

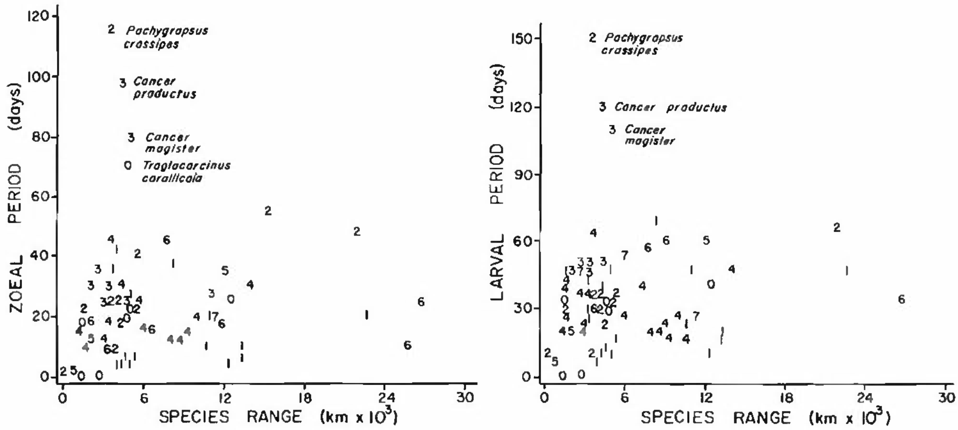


Figure 6. Length of zoeal and total larval periods versus size of species range. Symbols as in Figure 1.

in Steele and Steele, 1975a). On the other hand, Strathmann (1977) showed that prefeeding and pelagic feeding intervals in larvae of some barnacles and hermit crabs are not correlated with egg size; rather, larger eggs result in increased larval and settlement size. Reaka (1979; 1980) showed in stomatopods that durations of the brood incubation period and larval periods are not correlated with egg size, but larger egg size results in larger size at settlement. Egg size in fairy shrimps is also correlated with increased larval and settlement size (Belk, 1977). In the brachyurans of the present study, egg size was not significantly correlated with brood incubation period or larval period. While larger zoeae did hatch from larger eggs, larval growth was primarily a function of the number of zoeal instars. This larval growth obscured initial differences in larval size resulting from egg size, so that species with larger eggs and first zoeae but few larval instars (e.g., majids) did not have larger megalopae or first crabs than species with small eggs and first zoeae but many larval instars (e.g., portunids). When unusual species (e.g., potamids, *Ocypode* spp.) were excluded, large crabs did have slightly, but significantly larger megalopas and first crabs. The high variance in these latter size relationships and the case of the very large *Ocypode* megalopas indicate that selective pressures associated with the settlement habitat may be as, or more important than, growth patterns per se. However, Hines (in press) showed that even small increases in size at settlement can appreciably reduce the number of molts and time to reach maturity in crabs.

Evolutionary constraints by lineage on life history traits have been demonstrated for reproductive patterns in families of amphipods (Nelson, 1980), stomatopods (Reaka, 1979; 1980; Reaka and Manning, in press), and lobsters (Phillips and Sastry, 1980). Among the euphausiids and decapod crustaceans, Knowlton (1974) proposed that there is an 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 in the following ranking: Euphausiacea, Penaeidea, Caridea, Anomura, Macrura, and Brachyura. Rice (1980) showed consistent family differences in larval developmental patterns and considered larval development with more zoeal instars and greater variability in number of zoeal instars to be primitive. Apparently, most of the differences among the seven major families in the present study were related to the consequences of these familial differences in number of zoeal instars. Reduced larval growth as a function of fewer zoeal instars in the Majidae was compensated by having larger eggs, which produced larger first zoeae. Thus, megalopal size and last zoeal size did not vary significantly among families.

Although differences among brachyuran families were demonstrated (Table 2), the concept of evolutionary constraints by lineage should be viewed cautiously in brachyurans for two reasons. First, although the present study represents the extant knowledge of brachyuran larval development, it may not be representative of the extant species because there are good data for only a small proportion of all species. Second, there are obvious exceptions to familial patterns. For example, the Jamaican freshwater *Metopaulias depressus* (and probably a few other sesarmin grapsids) with large eggs and only two zoeal stages developing in rainwater trapped in bromeliads is very different from the grapsid pattern (Hartnoll, 1964). Similarly, direct development of *Pilumnus lumpinus, P. novaezealandiae,* and *P. vestitus* in marine habitats is very different from other xanthids, and the abbreviated development of *Uca subcylindrica* in desert puddles of Texas differs from other ocypodids (Rabalais and Cameron, 1983). Indeed, the large megalopas of *Ocypode* spp. provide an important difference from *Uca* spp. in the Ocypodidae and brachyurans in general. These exceptions indicate that apparent "constraints" by lineage may be more flexible than described in the family patterns of brachyurans.

Consistent differences in reproductive strategies among habitats have been documented for several groups of crustaceans. Amphipods have significant differences among epifaunal versus infaunal species and among estuarine versus freshwater and marine species (Nelson, 1980; Van Dolah and Bird, 1980). Corey (1981) showed significant differences among arctic, temperate, littoral, and deep water cumaceans. Epipelagic mysids also have different reproductive tactics than meso- and bathypelagic species (Mauchline, 1973). In brachyurans, evolution of large eggs and direct development in freshwater habitats is consistent with the pattern in macruran and caridean decapods. The pattern of longer brood incubation time, longer larval periods, and larger adult size in cold-water species is consistent with many invertebrate groups in general (Thorson, 1950; Mileikovsky, 1971), and with several crustacean groups in particular (Reaka, 1979; Barnes and Barnes, 1965; 1968; McLaren et al., 1969; Steele and Steele, 1975b). However, unlike many of these invertebrates and crustacean groups, brachyuran crabs in cold-water habitats apparently do not have larger eggs than warm-water species, perhaps because of their allometric constraints on brood size and trade-offs between fecundity and egg size (Hines, 1982), or perhaps because the relationship between egg size and zoeal size makes changes in egg size disadvantageous developmentally or ecologically. I am unaware of other crustacean groups which show differences in life history traits between intertidal and subtidal species, as is apparently the case for brachyurans. However, it may be difficult to separate potential family constraints from adaptations to a particular habitat or latitudinal zone: intertidal species are primarily grapsids and ocypodids; ocypodids and portunids are primarily warm-water, tropical species; and cancrids are restricted to cold waters.

The lack of correlation between length of larval period and geographic range in brachyurans appears to be different from mollusks (Scheltema, 1978; 1979; 1981; Jablonski, 1982; Jablonski and Lutz, 1983) and stomatopods (Reaka, 1980; Reaka and Manning, in press). However, crabs may not rely on simply increasing larval duration to disperse passively by currents. A sizeable and growing body of literature indicates that crabs have sophisticated hatching rhythms and larval behavior to take advantage of current patterns and to control larval dispersal (Forward and Costlow, 1974; Cronin and Forward, 1983; Sulkin, 1984; Christy, 1982; and many others). Moreover, these mechanisms may result in crab larvae having significantly different dispersal patterns than larvae of other groups (Christy and Stancyk, 1982; however, see Shanks, 1983).

The larval patterns in brachyuran life histories described here should be accepted only with considerable caution. As discussed above, data are available for only a small fraction of species in any family, habitat, latitudinal zone, or the Brachyura as a whole. There may be considerable artifacts in the data due to sampling biases. For example, the majority of species with described larvae are concentrated in a few geographic locations as a result of a few prolific researchers and their colleagues (J. D. Costlow, C. G. Bookhout, and R. H. Gore in the southeast coast of North America; M. V. Lebour, R. W. Ingle, and A. L. Rice in Great Britain; H. Kurata and K. Baba in Japan; and R. G. Wear in New Zealand). Most descriptions are for small, easily collected (e.g., intertidal) species or a few large, commercially important species. Even so, larvae have not been described for the majority of species from several areas which are otherwise well-studied (e.g., the southwestern coast of North America). In addition, the question of intra-specific variation is ignored in the present analysis, but is known to be important in crustaceans.

I hope the present paper will stimulate additional work for species in the following categories. First, species should be studied in families with relatively few species (e.g., Cancridae, Geryonidae) so that the effect of small sample size on family patterns can be evaluated. Second, more endemic marine species should be studied, as should more (non-introduced) species with very large ranges. Little is known about the life histories of species at either end of the zoogeographic spectrum. Similarly, more species should be studied from several zoogeographically important centers of speciation (e.g., the Indo-Pacific and tropical eastern Pacific). More congeneric species should be studied to test for patterns of covariation in closely related species. Even in genera with data for several species (e.g., *Cancer, Cyclograpsus, Hemigrapsus, Sesarma, Libinia, Mithrax, Pugettia, Ocypode, Uca, Portunus, Thalamita, Pinnotheres*), data for most key variables are incomplete. More large species in all families should be studied so that the effect of body size and allometry can be determined more precisely. The majority of data are for small to medium sized species, but data for large species markedly influence regression slopes in the statistical analyses. More unusual species such as *Metopaulias depressus* and *Uca subcylindrica* should be studied as possible exceptions to "test the rules." Larval development rates in the laboratory should be compared to those in the field for many more species. Finally, the existing data would be much more useful if authors had simply published more complete data on developmental parameters: provide scale lines in drawings; provide complete descriptions of larval rearing conditions, including comparisons of lab temperatures with typical field temperatures; provide developmental times for each larval stage, not just morphological descriptions; measure the adults and eggs as well as the larvae; include descriptions of the first crab in descriptions of larvae reared through first crab; and report estimates of the number of broods produced per year.

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Appendix I. Brachyuran species with sources of data used in analysis of larval patterns

ATELECYCLIDAE: *Erimacrus isenbechii*—Kurata, 1963a; *Telmessus acutidens*—Kurata, 1963a; *Telmessus cheiragonus*—Kurata, 1963a.

CALAPIDAE: *Hepatus epheliticus*—Costlow and Bookhout, 1962a.

CANCRIDAE: *Cancer antennarius*—Mir, 1961; Roesijadi, 1976; Carroll, 1982; *Cancer anthonyii*—Anderson, 1978; Anderson and Ford, 1976; *Cancer borealis*—Sastry, 1970; Sastry, 1977b; *Cancer gracilis*—Ally, 1975; *Cancer irroratus*—Sastry, 1970; Krouse, 1976; Sastry, 1977a; Reilly and Saila, 1978; *Cancer magister*—Poole, 1966; Butler, 1961; Wild, 1983; *Cancer pagurus*—Lebour, 1928; Hancock and Edwards, 1967; Ingle, 1981; *Cancer productus*—Trask, 1970.

CORYSTIDAE: *Corystes cassivelaunus*—Ingle and Rice, 1971; Hartnoll, 1972.

DROMIIDAE: *Cryptodromia octodentata*—Hale, 1982; *Cryptodromia hilgendorfi*—McLay, 1982; *Dromia erythropus*—Laughlin et al., 1982.

DORIPPIDAE: *Dorippe granulata*—Kurata, 1964.

GECARCINIDAE: *Cardisoma carnifex*—Kannupandi et al., 1980; *Cardisoma quanhumi*—Costlow and Bookhout, 1968a; Henning, 1975; *Gecarcinus lateralis*—Klaasen, 1975; Willems, 1982.

GERYONIDAE: *Geryon quinquidens*—Perkins, 1973; Haefner, 1977; VanHeukelem et al., 1984.

GONEPLACIDAE: *Eucate crenata*—Kurata and Matsuda, 1980a; *Tritodynamia atlantica*—Bocquet, 1965.

GRAPSIDAE: *Acmaeopleura parvula*—Kurata, 1968a; *Aratus pisoni*—Warner, 1967; 1968; *Carcinoplax longimanus*—Kurata, 1968c; *Chasmagnathus convexus*—Baba and Fukuda, 1972; *Chasmagnathus granulata*—Boschi et al., 1967; *Cyclograpsus cinereus*—Costlow and Fagetti, 1967; *Cyclograpsus insularum*—Wear, 1970; *Cyclograpsus integer*—Gore and Scotto, 1982; *Cyclograpsus lavauxi*—Wear, 1970; *Cyclograpsus punctatus*—Broekhuysen, 1941; Fagetti and Campodonico, 1971b; *Euchirograpsus americanus*—Wilson, 1980; *Helice crassa*—Wear, 1970; *Helice tridens*—Baba and Moriyama, 1972; *Hemigrapsus crenulatus*—Wear, 1970; *Hemigrapsus edwardsi*—Wear, 1970; *Hemigrapsus nudus*—Hart, 1935; Hines, 1982; *Hemigrapsus oregonensis*—Hart, 1935; Kuris, 1971; *Hemigrapsus sanguineus*—Kurata, 1962; 1968b; *Leptograpsus variegatus*—Wear, 1970; *Metapograpsus messor*—Rajabai, 1961; *Metasesarma rousseauxii*—Rajabai, 1961; *Metasesarma rubripes*—Diaz and Ewald, 1968; *Metopaulias depressus*—Hartnoll, 1964b; *Pachygrapsus crassipes*—Schlotterbeck, 1976; Hiatt, 1948; *Plagusia chabrus*—Wear, 1970; *Plagusia depressa*—Wilson and Gore, 1980; Rajabai, 1961; *Planes marinus*—Wear, 1970; *Sesarma bidentatum*—Hartnoll, 1964b; *Sesarma cinereum*—Costlow and Bookhout, 1960; Costlow et al., 1960; *Sesarma dehaani*—Baba and Miyata, 1971; *Sesarma erythrodactylum*—Baba and Fukuda, 1975; *Sesarma intermedium*—Baba and Fukuda, 1975; *Sesarma plicatum*—Baba and Fukuda, 1975; *Sesarma reticulatum*—Costlow and Bookhout, 1962b; *Sesarma ricordi*—Diaz and Ewald, 1968; *Sesarma tetragonum*—Rajabai, 1961.

HAPLOCARCINIDAE: *Haplocarcinus marsupialis*—Gore et al., 1983; *Troglocarcinus corallicola*—Scotto and Gore, 1981.

HYMENOSOMIDAE: *Hymenosoma orbiculare*—Broekhuysen, 1955.

MAJIDAE: *Acanthophrys longispinosus*—Kurata, 1969; *Achaeus cranchii*—Kurata, 1969; Bocquet, 1954; *Achaeus tuberculatus*—Kurata, 1969; *Chionoecetes bairdi*—Haynes, 1973; Jewett and Haight, 1977; Haynes, 1981; Donaldson et al., 1981; *Chionoecetes japonica*—Motoh, 1976; *Chionoecetes opilio*—Kurata, 1963b; Motoh, 1973; Kon, 1970; Davidson et al., 1985; *Epialtus dilatatus*—Yang, 1968; *Eurypodius latreillei*—Campodonico and Guzman, 1972; *Huenia proteus*—Kurata, 1969; *Hyas araneus*—Christiansen, 1973; *Hyas coarctacus*—Christiansen, 1973; *Hyas pyratus*—Hart, 1960; *Hyastenus diacanthus*—Kurata, 1969; *Inachus dorsettensis*—Lebour, 1927; Ingle, 1977; *Leptomithrax bifidus*—Kurata, 1969; *Leptomithrax edwardsii*—Kurata, 1969; *Libidoclaea granaria*—Fagetti, 1969a; *Libinia dubia*—Sandifer and Van Engle, 1971; *Libinia emarginata*—Johns and Lang, 1977; Hines, 1982; *Libinia erinacea*—Yang, 1967; *Libinia spinosa*—Boschi and Scelzo, 1968; *Loxorhynchus crispatus*—Hines, in press; *Macrocheira kaempferi*—Kurata, 1969; *Microphrys bicornutus*—Hartnoll, 1964a; *Macropodia longirostris*—Lebour, 1927; *Maia squinado*—Lebour, 1927; Tessier, 1935; *Micippa thalia*—Kurata, 1969; *Mimulus foliatus*—Hines, in press; *Mithrax coryphe*—Scotto and Gore, 1980; *Mithrax forceps*—Wilson et al., 1979; *Mithrax pleuracanthus*—Goy et al., 1981; *Mithrax spinosissimus*—Provenzano and Brownwell, 1972; *Naxioides histrix*—Kurata, 1969; *Oregonia gracilis*—Hart, 1960; *Pisa armata*—Ingle and Clark, 1980; *Pisoides edwardsi*—Fagetti, 1969b; *Pisoides ortmanni*—Kurata, 1969; *Pleistacantha sanctijohannis*—Kurata, 1969; *Pugettia incisa*—Kurata, 1969; *Pugettia producta*—Hines, in press; *Pugettia quadridens*—Kurata, 1969; *Pugettia richii*—Hines, in press; *Rochinia carpenteri*—Ingle, 1979; *Schizophrys aspersa*—Kurata, 1969; *Scyra acutifrons*—Hines, in press; *Stenorhynchus seticornis*—Yang, 1976; *Taliepus dentatus*—Fagetti and Campodonico, 1971a; *Tiarinia cornigera*—Kurata, 1969.

MICTYRIDAE: *Mictyris longicarpus*—Cameron, 1965; Fielder et al., 1984.

OCYPODIDAE: *Ilyoplax gangetica*—Feest, 1969; *Macrophthalmus dilatus*—Terada, 1979; *Macrophthalmus japonicus*—Terada, 1979; *Ocypode albicans*—Crane, 1940; *Ocypode gaudicauchi*—Crane, 1940; *Ocypode occidentalis*—Crane, 1940; *Ocypode quadrata*—Diaz and Costlow, 1972; *Ocypode stimpsoni*—Terada, 1979; *Paracleistostoma cristatum*—Terada, 1979; *Uca annulipes*—Feest, 1969; *Uca lactea*—Muraoka, 1976; Terada, 1979; *Uca minax*—Hyman, 1920; *Uca panacea*—Novak and Salmon, 1974; *Uca pugilator*—Hyman, 1920; *Uca pugnax*—Hyman, 1920; O'Connor and Epifanio, 1985; Rabalais and Cameron, 1983; *Uca subcylindrica*—Rabalais and Cameron, 1983; *Uca tangeri*—Novak and Salmon, 1974; *Uca triangularis*—Feest, 1969.

PARTHENOPIDAE: *Parthenope validus*—Kurata and Matsuda, 1980b.

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