

GEOGRAPHIC VARIATION IN SIZE AT MATURITY IN BRACHYURAN CRABS

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ABSTRACT

Geographic variation in size of sexually mature females was compared in five species of crabs at sites spanning about 10 degrees of latitude along the east and west coasts of North America. Populations were sampled along the west coast at six sites for *Pachygrapsus crassipes*, four sites for *Hemigrapsus nudus*, eight sites for *H. oregonensis*, and two sites for *Scyra acutifrons*, and along the east coast at eight sites for *Panopeus herbstii*. Four of the five species showed significant geographic variation in size at onset of maturity, mean size, and size frequency distribution. *P. herbstii* and *P. crassipes* exhibited latitudinal variations and marked changes in population structure of mature females at biogeographic boundaries; *P. herbstii* matured at larger sizes at latitudes below Cape Hatteras; while *P. crassipes* matured at smaller sizes below Point Conception. *H. nudus* showed variation in the size distribution of mature females, but little variation in size at onset of maturity. For *H. oregonensis* and *S. acutifrons*, size at maturity varied on a local scale among neighboring populations. For *S. acutifrons*, a difference of about seven molts before the terminal molt at puberty was deduced to produce the observed variation in maturity. Its molt increment percentage was constant across all sizes of crabs and did not differ between two populations with disparate size structures. For *H. oregonensis* variation in molt increment and in the number of molts appears to account for differences in size at maturity among populations. Variation in maturation within *H. oregonensis* populations occurs over one to two molts, and a difference of about two molts accounts for differences in size at onset of maturity among populations. Geographic variations in growth and size structure of mature females in these species are likely to have major consequences for population fecundity and demography.

Because size and age at maturity are critical determinants of brachyuran reproductive output (Hines, 1982) and the rate of population growth (Cole, 1954; Murphy, 1968; Stearns, 1976), it is important to consider patterns of variation in the size at maturity in brachyuran crabs. Intra-specific geographic variations in life histories are well-documented in many groups of crustaceans: mole crabs (Hippidae) (Efford, 1969; Wenner et al., 1987), stomatopods (Reaka, 1979), barnacles (Barnes and Barnes, 1965; 1968), copepods (McLaren et al., 1969; Lonsdale and Levinton, 1985), mysids (Lasenby and Langford, 1972), caridean shrimp (Alon and Stancyk, 1982), lobsters (Annala et al., 1980; Morizur et al., 1981), amphipods (Steele and Steele, 1975), and hermit crabs (Childress, 1972; Bach et al., 1976; Fotheringham, 1976; 1980; Bertness, 1981). Growth and size at maturity are important components in the dynamics of reproductive stocks and thus have significant indirect effects on population recruitment in many commercially fished crustaceans (Cobb and Phillips, 1980). Despite their economic and ecological importance, geographic variation in growth and size at maturity has been documented in only a few species of brachyuran crabs.

At least five species from four brachyuran families (Cancriidae, Grapsidae, Majidae, and Portunidae) exhibit geographic variation in size at maturity, although much of the documentation is derived incidentally from studies designed for other purposes. *Cancer magister* (Cancriidae) is an extensively studied species, but there does not appear to be significant differences in growth rates, size at maturity, number of molts to maturity, or maximum size among populations from central California to Washington along the west coast of North America (Mackay and

Weymouth, 1935; Mackay, 1942; Weymouth and Mackay, 1936; Cleaver, 1949; Butler, 1961; Poole, 1967; Collier, 1983; Hankin et al., 1985). In contrast, populations of *Cancer irroratus* in New England appear to differ significantly in size at maturity and perhaps growth rates (Krouse, 1972; 1976; Reilly and Sails, 1978). Similarly, populations of *Carcinus maenas* (Portunidae) on opposite sides of the Atlantic exhibit considerable differences in growth rate and size at maturity (Klein-Breteler, 1975; Berrill, 1982). The spider crabs *Chionoecetes bairdi* and *C. opilio* (Majidae) differ significantly in size of maturity and fecundity in regions of the Bering Sea and eastern Canada (Somerton, 1981; Elner and Robichaud, 1983; Davidson et al., 1985). In one of the few brachyuran studies which was designed to test for it, Jones and Simons (1983) measured significant geographic variation in size at maturity and other important life history variables among latitudinally separate populations of the intertidal grapsid species *Helice crassa* (Grapsidae) in New Zealand. Thus, with the exception of *C. magister*, the few brachyuran species with adequate data show geographic variation in size at maturity, but nothing is known about the causes or geographic correlates of the variability.

Here, I document significant variation in female size at maturity among populations of one xanthid species (*Panopeus herbstii*), three grapsid species (*Hemigrapsus nudus*, *H. oregonensis*, and *Pachygrapsus crassipes*), and one majid species (*Scyra acutifrons*). These five species were selected for study for four reasons. First, they represent families which have known differences in basic growth patterns. For example, majids have a terminal pubertal molt to maturity, while grapsids and xanthids continue to molt and grow after maturation (Hartnoll, 1982). Second, their geographic ranges provide interesting distributions spanning several biogeographic provinces along the east and west coasts of North America. *P. herbstii* is found from New York to Cape Canaveral, Florida (Williams, 1983). *H. oregonensis* and *H. nudus* are distributed from Alaska to Baja California, but *H. nudus* is never common south of Point Conception, California; *P. crassipes* is found from Oregon to the Gulf of California (Garth and Abbott, 1980). *S. acutifrons* also occurs from Alaska to Baja California (Garth and Abbott, 1980). Populations of three of the species were sampled north and south of known major biogeographic breaks at Point Conception in California and at Cape Hatteras in North Carolina. Third, several of the species occur abundantly in similar habitats, which allows interspecific comparison of geographic variation in population structure without introducing potentially confounding effects due to different habitats. Fourth, because these xanthid and grapsid species can be collected readily, a series of samples can be taken along the coasts on a single low tide series to minimize potential seasonal changes in population structure.

In addition to measuring geographic variation in size at maturity, this paper addresses the question of which component(s) of growth are responsible for the variability. Molt increment and the number of instars are the fundamental components of growth which could vary to produce a difference in size at maturity (Hartnoll, 1982). I attempt to distinguish whether one or both of these variables accounts for variation between populations of *Hemigrapsus oregonensis* and *Scyra acutifrons*.

METHODS

Size at maturity of females of five species of brachyuran crabs was determined at various sites along the east and west coasts of North America (Fig. 1). All west coast collections were made in June 1982 in a single two week period of low tides; all east coast collections were made in June 1983 in a single 2 week period of low tides. For four of the species (*Panopeus herbstii*, *Hemigrapsus nudus*, *H. oregonensis*, and *Pachygrapsus crassipes*), large numbers of juvenile and mature females (usually > 100,

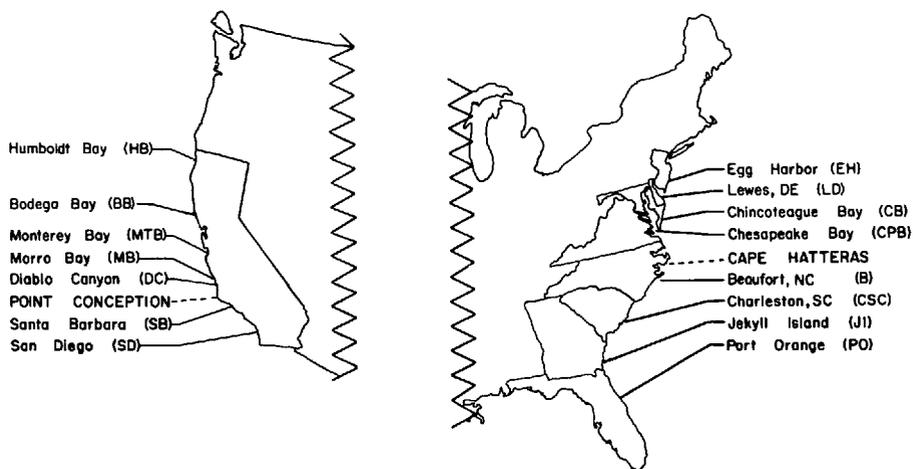


Figure 1. Sampling sites for populations of *Pachygrapsus crassipes*, *Hemigrapsus nudus*, *H. oregonensis*, and *Scyra acutifrons* along the west coast and of *Panopeus herbstii* along the east coast of North America. The biogeographic boundaries at Point Conception and Cape Hatteras are indicated. The abbreviations for each site are used in Figures 3, 4, and 5.

but occasionally only about 50) were collected haphazardly by hand at each site from similar habitats on muddy sand under rocks and cobble along breakwaters in high salinity, sheltered bays. Maximal carapace width was measured for all juvenile and mature females. Sexual maturation in females was distinguished by the allometric increase of abdominal width relative to carapace width for the three grapsid species (see Hartnoll, 1982). For female *P. herbstii* (and xanthids in general), abdominal width does not exhibit allometric growth at maturation; but maturity in females was distinguished by the allometric changes in the pleopods, which extend beyond the tip of the abdomen in mature individuals (personal observations). For each population of grapsid and xanthid species, the size at which 50% of the individuals were mature was determined from probability plots of size frequency distributions of juvenile and mature females using analogous methods to those of Wenner et al. (1974; 1985). The size at 50% maturity is also termed the size at onset of maturity for a population. In addition to the parameters from analysis of probability plots, the minimum, maximum, size below which 95% of mature females occurred, and arithmetic mean size of mature females was determined for each sample. Mature female *Scyra acutifrons* were collected haphazardly by hand using SCUBA in the shallow (10 m) subtidal zone from the algal-invertebrate turf of kelp forests. Size and sexual maturity of *S. acutifrons* were determined as explained above for the grapsids. Because majids have a terminal molt at puberty, size at 50% is not a very meaningful parameter. Instead, the size frequency distributions of populations of this species were simply compared statistically. For all species, sizes of mature crabs were compared statistically using ANOVA, Duncan's multiple range tests of means, and Kolmogorov-Smirnov tests for differences in size-frequency distributions.

To test whether differences in size at sexual maturity among populations of *Hemigrapsus oregonensis* and *Scyra acutifrons* were caused by differences in molt increments, samples from populations with disparate size at maturity were held under identical conditions in the laboratory. Haphazardly collected *H. oregonensis* from three locations (municipal harbor, Goleta Slough, and University of California lagoon) in the vicinity of Santa Barbara, California, were held in vented plastic compartment boxes placed in flowing ambient sea water ($14 \pm 1^\circ\text{C}$) and fed frozen *Artemia salina* every other day. *S. acutifrons* from two locations in central California were held similarly at $12 \pm 1^\circ\text{C}$ and fed brown algae (*Macrocystis pyrifera*) and snail (*Tegula funebris*) tissue. Data on change in maximal carapace width were taken only from crabs which molted within the first 2 weeks of captivity. I assumed that this procedure selected only crabs in premolt at the time of capture and that their molt increments reflected primarily the influence of their original habitat while minimizing any laboratory artifacts. Molt increments were compared among populations using ANCOVA with premolt carapace width as the covariate.

RESULTS

Populations were sampled along the west coast of North America at six sites for *Pachygrapsus crassipes*, four sites for *Hemigrapsus nudus*, eight sites for *H.*

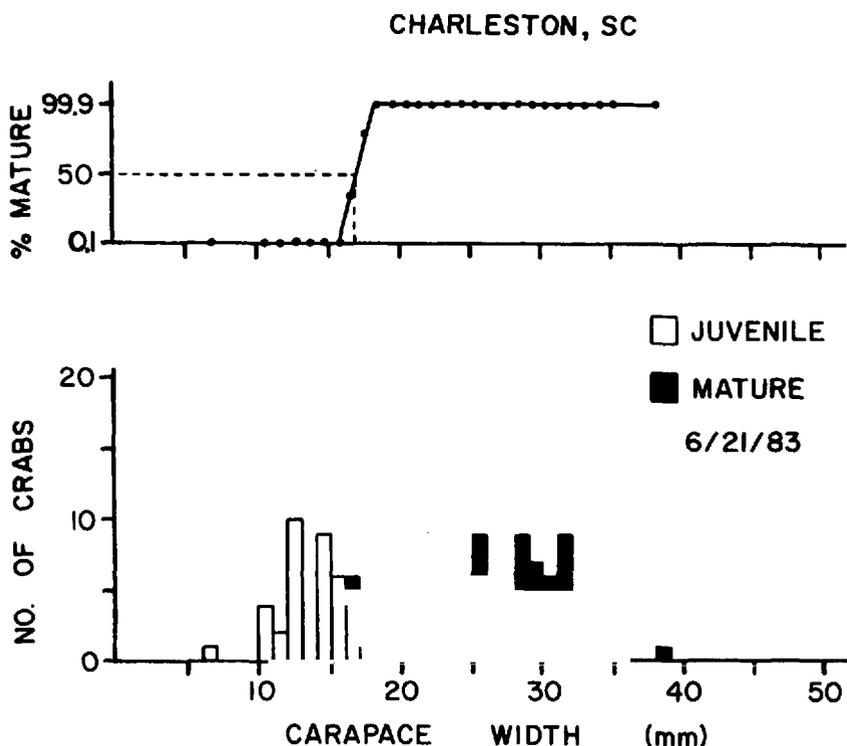


Figure 2. Size at sexual maturity of female *Panopeus herbstii* collected at Charleston, South Carolina, on 23 June 1983. Bottom: Size-frequency distribution of juvenile and mature females. Top: Percentages of mature females in each 1 mm size class on a probability scale and the size at 50% maturity (dashed line).

oregonensis, and two sites for *Scyra acutifrons*, and along the east coast at eight sites for *Panopeus herbstii* (Fig. 1). The range of sites spanned about 1,500 km and about the same 10 degrees of latitude along both coasts.

The xanthid and three grapsid species matured over a narrow size-range (3 mm carapace width) within each population, as illustrated by the size structure of *Panopeus herbstii* females from Charleston, South Carolina (Fig. 2). Among populations of each species, geographic variation in size at onset of maturity was reflected in other parameters of mature size for the xanthid and three grapsid species. For example, in populations of *Pachygrapsus crassipes* the minimum, mean, 95 percentile, and maximum size of mature females closely tracked the size at which 50% of a population matured (Fig. 3).

Size at onset of maturity differed among populations of the xanthid (Fig. 4) and three grapsid species (Fig. 5). On the east coast, populations of *Panopeus herbstii* south of Cape Hatteras matured at larger sizes than populations to the north (16.0 versus 12.5 mm, respectively) (Fig. 4; ANOVA, $P < 0.05$). Similarly, populations of *P. herbstii* south of Cape Hatteras had larger mean sizes of mature females (Duncan's multiple range test, $P < 0.05$) and size-frequency distributions with a significantly greater proportion of large adult females (Kolmogorov-Smirnov tests, $P < 0.01$) than did populations to the north.

In contrast, west coast populations of *Pachygrapsus crassipes* south of Point Conception matured about 5 mm smaller than populations to the north (Fig. 5). Mean size of mature female *P. crassipes* differed significantly among populations

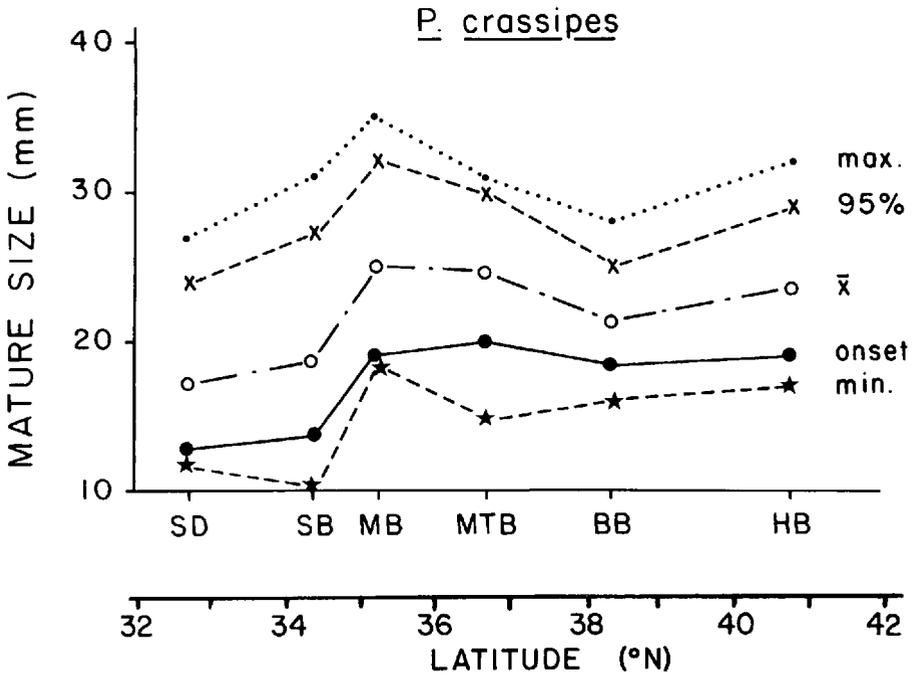


Figure 3. Covariation of size parameters of mature *Pachygrapsus crassipes* sampled along the California coast in June 1982. Minimum size (min), size at which 50% of size-class is mature (onset), mean size (\bar{x}), size at which cumulative 95% of the mature individuals occurs (95%), and maximum size (max) of mature females are plotted. Initials correspond to sampling sites indicated in Figure 1.

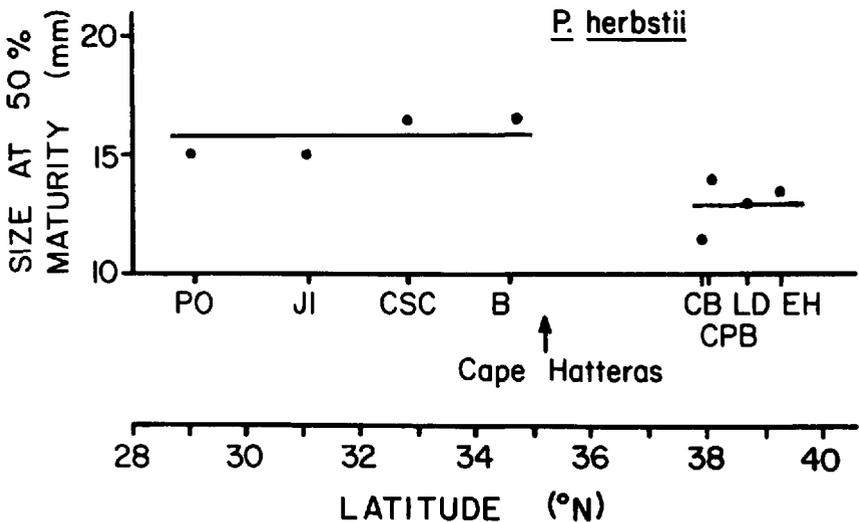


Figure 4. Size at 50% maturity for female *Panopeus herbstii* sampled from 8 sites from northern Florida to New Jersey in 1983. Lines indicate populations for which mean mature sizes are not significantly different (Duncan's multiple range test, $P > 0.05$). Initials correspond to sites indicated in Figure 1.

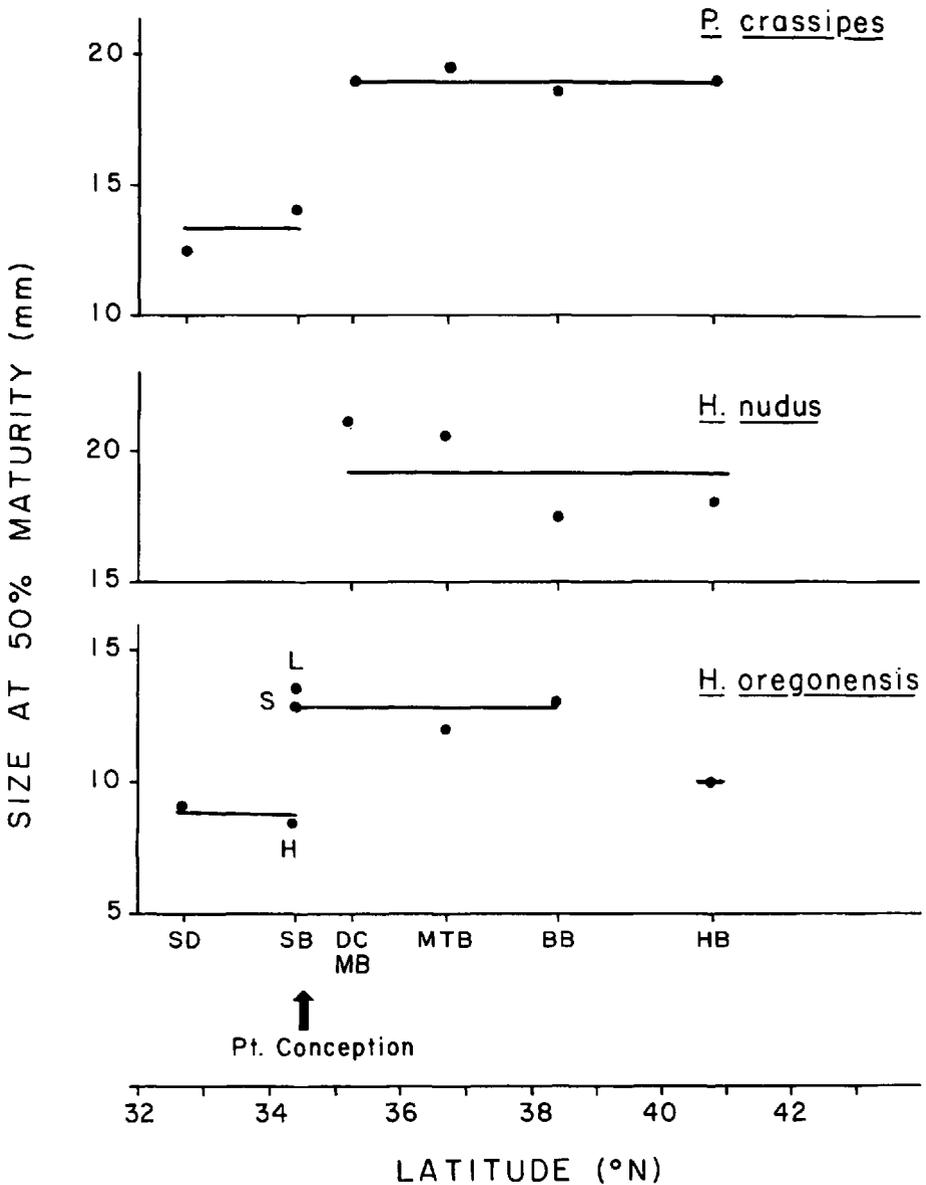


Figure 5. Size at 50% maturity for female *Pachygrapsus crassipes*, *Hemigrapsus nudus*, and *Hemigrapsus oregonensis* from southern to northern California in June 1982. Lines indicate populations for which mean mature sizes are not significantly different (Duncan's multiple range test, $P > 0.05$). Initials correspond to sampling sites indicated in Figure 1. For *H. oregonensis*, H, S and L correspond to harbor, slough and lagoon populations, respectively, sampled in the vicinity of Santa Barbara.

(ANOVA, $P < 0.05$), with the two southern California populations having smaller mean sizes than those north of Point Conception (13 versus 19 mm, respectively) (Duncan's multiple range test, $P < 0.05$). The southern California populations also had size frequency distributions with a significantly greater proportion of

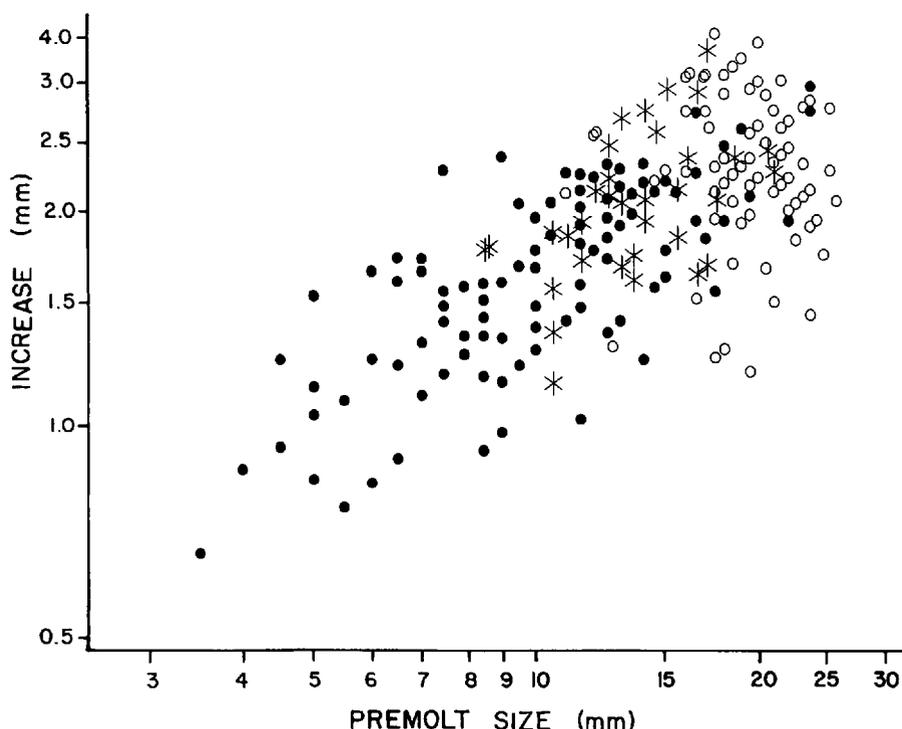


Figure 6. Increase in carapace width as a function of premolt size (carapace width) in three populations of *Hemigrapsus oregonensis* in the vicinity of Santa Barbara, California. Molt increments were measured for crabs held individually under identical conditions for less than 2 weeks in the laboratory. Closed circles = harbor population; open circles = lagoon population; stars = slough population.

small adult females than populations north of Point Conception (Kolmogorov-Smirnov tests, $P < 0.01$).

Onset of maturity varied slightly among populations of *Hemigrapsus nudus*, which were not sampled across any well-known biogeographic boundary (Fig. 5). Mean size of mature *H. nudus* females (19 mm) did not differ significantly among populations (ANOVA, $P > 0.05$), but their size frequency distributions were significantly different, with the two southern populations having a greater proportion of large females than the two northern populations (Kolmogorov-Smirnov tests, $P < 0.05$).

Onset of maturity, mean size, and size-frequency distributions of *Hemigrapsus oregonensis* populations showed perplexing variation, with smaller sizes (7 mm) in southern California and larger sizes (13 mm) north of Point Conception, but with a decrease in size (10.5 mm) in the northernmost population sampled (Fig. 5; ANOVA, $P < 0.01$; Duncan's multiple range test, $P < 0.05$; Kolmogorov-Smirnov tests, $P < 0.01$). Moreover, three populations of *H. oregonensis* within 10 km of each other in the vicinity of Santa Barbara, California, showed extreme variation in size at maturity (Fig. 5; ANOVA, $P < 0.01$; Kolmogorov-Smirnov tests, $P < 0.01$). The population at the Santa Barbara harbor matured at 7 mm, which was equivalent to the other southern California population (ANOVA, $P < 0.01$; Duncan's multiple range test, $P < 0.05$); whereas, nearby populations in the Goleta Slough and the lagoon on the campus of the University of California

Table 1. Regressions for increase in size at ecdysis for three populations of *Hemigrapsus oregonensis* sampled in the vicinity of Santa Barbara, California. Equations for log increase in carapace width (log INC) versus log premolt carapace width (log PRECW) are shown with R^2 values for the data plotted in Figure 6

Site	Regression equation	R^2
Harbor	$\log \text{INC} = 0.556(\log \text{PRECW}) - 0.349$	0.53
Slough	$\log \text{INC} = 0.538(\log \text{PRECW}) - 0.296$	0.26
Lagoon	$\log \text{INC} = 0.508(\log \text{PRECW}) - 0.204$	0.23

at Santa Barbara matured at 13.5–14 mm, which did not differ significantly from the maturation size of northern populations (ANOVA, $P > 0.1$; Duncan's multiple range test, $P > 0.05$).

Increase in carapace width at ecdysis was quite variable within populations of *Hemigrapsus oregonensis*, but the amount of growth increased with premolt size (Fig. 6; ANOVA, $P < 0.001$). After log-transformation of the increase in carapace width and premolt carapace width, the variances and slopes of the regressions did not differ among the populations from Santa Barbara harbor, slough and lagoon (F_{\max} -test, ANCOVA, $P < 0.2$; Sokal and Rohlf, 1981). Regression equations for the three populations are given in Table 1. Increase in carapace width differed slightly, but highly significantly among the three populations when adjusted statistically for differences in premolt size among the populations (ANCOVA on log increase with log premolt carapace width as covariate, $P < 0.01$). The least squares means (at the grand mean premolt carapace width of 13.3 mm) for the populations were: harbor = 1.9 mm; slough = 2.0 mm; and lagoon = 2.3 mm. When calculated as a percentage increase in carapace width, the molt increment decreased with increasing body size from about 24% for 5 mm crabs to about 11% for 25 mm individuals. At the grand mean premolt carapace width of 13.3 mm, the molt increments were 14.2%, 15.3%, and 17.5% for the harbor, slough, and lagoon populations, respectively.

Size distributions of mature female *Scyra acutifrons* in populations at Diablo Canyon and Monterey Bay (Hopkins Marine Life Refuge) were not normally distributed and thus could not be tested for significant differences in mean size by ANOVA (Fig. 7). However, the size frequency distribution at Diablo Canyon with a pronounced mode at 25 mm carapace width was significantly larger than that at Monterey Bay with a peak at 8 mm (Kolmogorov-Smirnov test, $P < 0.01$). Molt increments did not differ significantly between the two populations (ANCOVA on log increase in carapace width with log premolt carapace width as covariate, $P > 0.4$), and molt increments remained constant at 18.9% across all sizes of juveniles (Fig. 7).

DISCUSSION

Four of the five species studied showed significant geographic variation in size at onset of maturity, as well as in mean size and the size frequency distribution of mature females. *Panopeus herbstii* and *Pachygrapsus crassipes* exhibited latitudinal variations with marked changes in population structure of mature females at the biogeographic boundaries of Cape Hatteras and Point Conception, respectively. Both *Hemigrapsus oregonensis* and *Scyra acutifrons* differed markedly in size at maturity between populations not separated by the faunal boundary at Point Conception, and the complete range in population size variation occurred

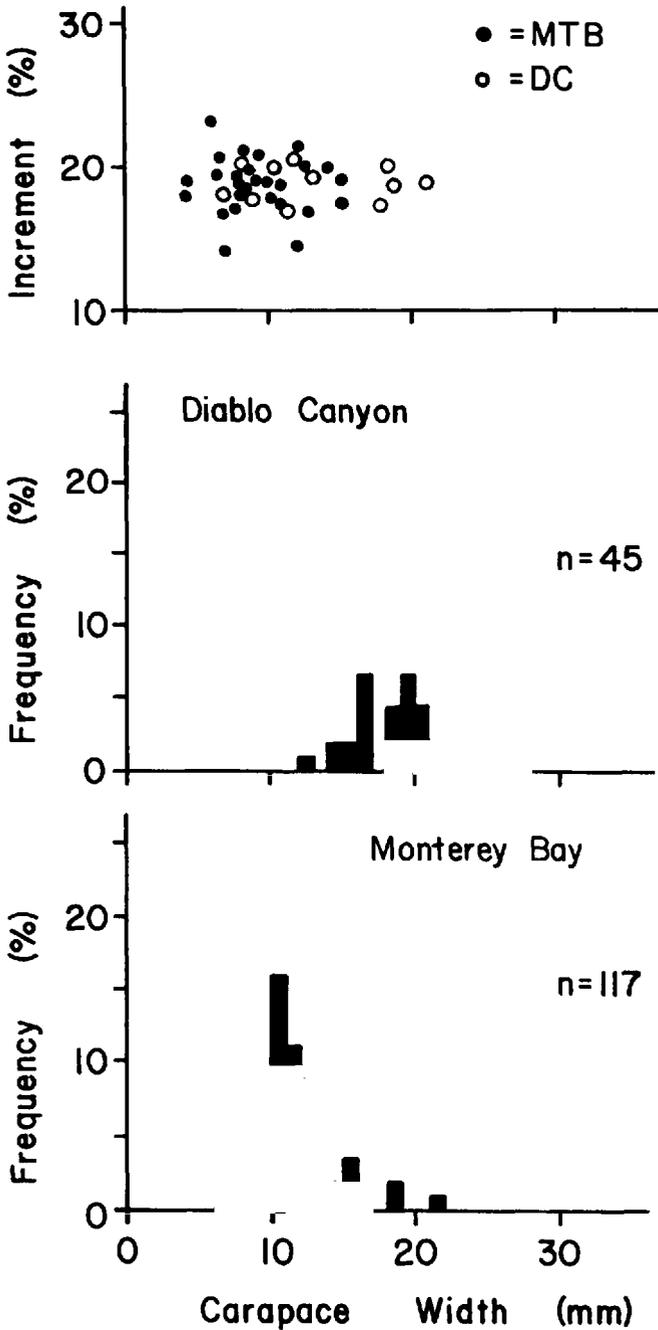


Figure 7. Size frequency distributions of mature females and molt increments of *Scyra acutifrons* sampled at Diablo Canyon and Hopkins Marine Life Refuge in Monterey Bay, California. Molt increments were measured for crabs held individually under identical conditions for less than 2 weeks in the laboratory.

on a local scale in the former species. The sampled populations of *H. nudus* were all north of Point Conception and did not differ greatly in size at maturity.

What are the causes of these patterns of geographic variation? Temperature and temperature-photoperiod interactions have long been proposed as variables which can produce latitudinal clines in metabolic rates, growth, and size, resulting in slower growth to larger, older individuals and delayed maturity at higher latitudes (Giese, 1959; Kinne, 1970; Annala et al., 1980; Jones and Simons, 1983; Lonsdale and Levinton, 1985). However, delays in maturation have marked demographic consequences which affect population dynamics (Murphy, 1968; Stearns, 1976), and which cannot be considered without knowledge of survivorship schedules. Latitudinal clines of increased predation pressure at low latitudes can also select for smaller size at maturity and reduced maximum size compared to populations encountering reduced predation and increased survivorship at high latitudes (Wallerstein and Brusca, 1982).

Cape Hatteras and Point Conception function as biogeographic boundaries for many North American species, apparently because major discontinuities in currents affect thermal regimes and larval dispersal at those locations (Bolin and Abbott, 1962; Abbott and North, 1972). Although *Pachygrapsus crassipes* conformed with the aforementioned general prediction of larger size at higher latitudes and the colder side of the biogeographic boundary, *Panopeus herbstii* showed the opposite pattern. This discrepancy could be explained by the difference in seasonal extremes between the two coasts. The seasonal fluctuation of about 4°C in sea temperature along the California coast is not nearly as great as the more than 20°C seasonal change in sea temperature north of Cape Hatteras on the east coast. Although molting and growth are reduced in cooler months on the west coast (e.g., in *Hemigrapsus oregonensis*; Kuris, 1971), near freezing shore temperatures halt growth in *P. herbstii* during winter on the north east coast while growth apparently continues at a slow rate in the south of its range (McDonald, 1977; personal observations). Without data on variation in survivorship among *P. herbstii* populations, it is not possible to speculate on consequences of delayed maturity for population dynamics. Evidently, however, growth in northern populations of *P. herbstii* to a size equivalent to southern populations would result in an intractably long delay to maturity as a result of the winter period of arrested growth in the north.

For *Hemigrapsus oregonensis*, and probably for *Scyra acutifrons*, variation in size at maturity fluctuates on a local scale. This pattern of variation indicates that small-scale factors such as food availability, population density or subtle changes in substrate, rather than latitudinal factors are important in regulating size at maturity. However, for *Helice crassa*, a grapsid species in New Zealand with a very similar niche to *H. oregonensis*, Jones and Simons (1983) found that population density but not crab size was related to food availability as indicated by sediment organic content; although size at maturity in *H. crassa* did increase at higher latitudes. Extreme variation in size on the local scale observed for *H. oregonensis*, where larvae from the sampled populations are presumably mixing in the same planktonic pool, is probably not based on genotype differences in the populations.

Clearly, variations in the molt increment or in the number of molts to maturity, or in both affect the pattern in size regulation in crab growth. For *Scyra acutifrons*, the molt increment percentage was constant across all sizes of crabs and did not differ between the two populations with disparate size structures (Fig. 7). Maturation results in a terminal molt and no further growth for the Majidae in general

and for *S. acutifrons* in particular (Hartnoll, 1982; Hines, unpubl.). Therefore, the mechanism acts upon the number of molts to maturity to produce differences in size at maturity. At the observed mean molt increment of 18.9%, about 7 additional molts would be required to attain the increased size from the Monterey population mode of 8 mm to the Diablo Canyon mode of 25 mm. In another majid species, *Pugettia producta*, O'Brien (1984) showed that parasitism by rhizocephalan cirripedes similarly reduced size at maturity by reducing the number of instars to puberty.

For *Hemigrapsus oregonensis*, it is not as clear which growth variable is affected. Molt increments for the three Santa Barbara populations differed significantly, with the populations attaining the largest size having the largest increment. However, the change in increment was not large enough to account for the size difference in the populations. Assuming a first crab size of 1.0 mm carapace width (Kuris, 1971) and using the regressions for size-specific molt increments (Table 1), 9 instars would be required to attain the 7 mm size at onset of maturity in the Santa Barbara harbor population, whereas 10 instars are required to attain the 12.5 mm size at onset of maturity in the lagoon population. The slightly increased molt increment in the lagoon population results in about 2 less instars to reach the 12.5 mm size than the harbor population would require to attain the same size. However, unlike *S. acutifrons*, molting in *H. oregonensis* does continue after puberty and the molt increment percentage decreases rapidly at large sizes. The small change in molt increment for the lagoon population reduces the number of instars at larger sizes. For example, the harbor population would require 18 instars to attain 25 mm, while the lagoon population would require only 15 instars to grow to 25 mm. Thus, for *H. oregonensis* a combination of variation in molt increment and in the number of molts is likely to account for the differences in size at maturity among populations. It is clear from the molt increment data and the narrow size-range of the onset of maturity that variation in maturation within *H. oregonensis* populations occurs only over one to two molts, while comparing variation in size at maturity of the Santa Barbara harbor and lagoon populations indicates that about two molts are required to account for the differences in size at onset of maturity among populations.

Geographic variation in size at maturity will have important fecundity and demographic consequences regardless of the growth mechanisms producing population differences on a local or latitudinal scale (Jones and Simons, 1983). Egg production in all five of the study species is markedly size-dependent (Hines, 1982), and changes in growth rates may produce large age-dependent effects on egg production as well as size-dependent differences (Wenner et al., 1987). The present paper demonstrates that size at maturity and growth are important sources of geographic variation in the life history and population dynamics of brachyuran crabs.

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