

STUDIES ON DECAPOD CRUSTACEA FROM THE INDIAN RIVER
REGION OF FLORIDA. XXV. CARAPACIAL AND ABDOMINAL
ALLOMETRY IN FIVE SPECIES OF SUBTROPICAL
PARTHENOPID CRABS (BRACHYURA, PARTHENOPIDAE)

BY

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INTRODUCTION

Relative growth in crustaceans has been studied in a variety of ways over a long period of time (see Teissier, 1960, for review). Among the decapod crustaceans, numerous recent investigations have attempted to predict various growth phenomena, including onset of anatomical or functional sexual maturity (Crane, 1941; Haley, 1969, 1973; Hartnoll, 1974; Wenner et al., 1974), occurrence of protogyny or protandry (Butler, 1964; Wenner, 1972), neoteny (Efford, 1967), sex ratios (Gray & Powell, 1966; Wenner, 1972), sex prediction (Allen, 1962), rate of growth (Hiatt, 1948; Newcombe et al., 1949; Gifford, 1962; Tagatz, 1968), determination of relative age or stage of individuals in a given population (cf. Hartnoll, 1972, 1974; Mauchline, 1976), and in taxonomy (Chace, 1951; Stephenson, 1967; Griffin, 1970; Williams et al., 1980).

Basic to the concept of maturation is the observation that an attribute such as the abdominal somites in females, or gonopods in males, expands or lengthens dramatically compared to previous sizes at earlier stages, thereby facilitating egg deposition and carriage in the females, or copulatory behavior in males (Teissier, 1960). The ecdysis or series of molts from the nonmature juvenile, or anatomically maturing subadult precopulatory stage, to the functionally mature adult stage has been commonly termed the pubertal molt (after Perez, 1928, and subsequent authors), and can often be graphed as a discontinuity in a regression line derived from a comparison of carapace and abdominal dimensions.

Studies on the pubertal molt have often used carapace length and width measurements as the sole reference dimensions (Weymouth & McKay, 1936; Newcombe, 1948; Newcombe et al., 1949; Allen, 1962; Gifford, 1962; Hartnoll, 1965b; Herreid, 1967; Griffin, 1970). However, in many brachyurans the relative growth of these two parameters by itself probably provides fewer overt indications of the onset of maturity than do other allometric dimensions. More

often, carapace measurements are utilized as one reference dimension in comparison with skeletal or abdominal features, such as cheliped length and height, walking leg measurements, female abdominal length and width, and male gonopod length (e.g. Williams et al., 1980, and previous citations). When bivariate ratios of appendage or abdominal characters to carapace dimensions are calculated it can often be shown that the ratio of the former to the latter remains more or less constant over a series of molts or growth stages, and then changes abruptly before returning to a new but relatively stable value (Tagatz, 1968; Hartnoll, 1972; among others).

The mathematical treatment of relative growth generally consists of linear regression line analysis derived from statistical comparison of the meristic data for each species. The traditional allometric growth equation is: $y = bx^a$, graphing a power curve which can be linearized by logarithmic transformation to $\log y = a \log x + \log b$. The log power function (a) is easy to interpret because a standard of 1 indicates that growth is isometric between the selected variables, whereas values greater or less than 1 indicate either positive or negative allometry, respectively. In other instances straight line equations ($y = ax + b$; e.g., Donaldson et al., 1981) have been employed. Wenner et al. (1974) suggested the use of probability paper, and Mauchline (1976) recommended the use of a hyperbolic plot, especially in attempting to predict pre- or postmolt sizes (but see Somerton, 1980, for objections).

It is, of course, desirable that measurements be made on complete specimens. Unfortunately, collections of deep-sea decapod crustaceans do not always yield perfect specimens, and in such cases analyses on chelipeds, walking legs, or even abdomens cannot be made owing to damage inflicted during collecting, or by autotomy or autotomy by the crustaceans themselves. Comparative meristic data are then usually restricted to carapace measurements because this part of the animal often undergoes relatively less extensive damage than do the associated appendages.

This situation is seen in the brachyuran crab family Parthenopidae, the members of which are small, semi-cryptic forms that usually lie buried in the rocky, pebbly, or shell-hash substrata of the nearshore continental shelf in temperate and tropical regions of the world. Although much is known about the systematics of this family, there are few data available on aspects of their relative growth or reproductive biology. No data exist, for example, on carapacial or abdominal allometry associated with growth, the onset and duration of the pubertal molt, or whether such a molt is terminal.

In a recent survey of the coastal waters of central eastern and western Florida nearly 1100 specimens of parthenopid crabs were collected (Gore & Scotto, 1979). Allometric comparisons using pereopodal measurements were immediately ruled out because nearly 80% of this material exhibited partial or complete autotomy of appendages during trawling or dredging, or in subsequent preservation. However, in five species sufficient specimens were

obtained which suffered relatively little carapacial damage, and measurements were possible on carapace and abdominal parameters. In this paper we provide these data and consider their applicability in extrapolating the size range over which the pubertal molt may occur, and whether this molt is terminal or not.

MATERIALS AND METHODS

The 5 species used: *Parthenope agona* (Stimpson, 1871), *P. fraterculus* (Stimpson, 1871), *Cryptopodia concava* (Stimpson, 1871), *Heterocrypta granulata* (Gibbes, 1850), and *Solenolambrus tenellus* (Stimpson, 1871) (fig. 1) were dredged from continental shelf waters no deeper than 200 m, from off the central eastern or western Florida coasts (lat. 26-30°N) during 1965-1967, and 1973-1974. Adults and subadult (sexable) and juvenile (non-sexable) individuals were measured with dial calipers, or a stage micrometer calibrated with an ocular reticle in a binocular dissecting microscope, to the nearest 0.1 mm, as follows: CW (carapace width) or SCW (spinal carapace width), across the widest part of the carapace; RCL (rostral carapace length), dorsally along the midline from the tip of the rostrum to the posterior carapace margin; MGL (male gonopod length), with the abdomen fully opened, along the entire gonopod as it was held against the sternites, from its junction at the expanded base to the spiny, curved tip, distally; FAW (female abdominal width), across the widest part of somite 5, with the abdomen closely appressed against the sternal region of the carapace. Abdominal somites 6 and 7 in females were similar in form to male somites, expanding more slowly with age than somites closer to the cephalothorax, hence our selection of somite 5. Preliminary calculations using regression analyses of RCL or SCW against female abdominal length showed the latter measurement to be of little use in determining the possible occurrence of the pubertal molt, so it was not considered further.

Incipient (subadult) or well-formed (adult) gonopores distinguished females, and developing (subadult) or fully elongated (adult) first gonopods separated males, from juvenile specimens which lacked these characters entirely.

Carapace allometry. — No actual consecutive molting series was obtained. Instead, a large number of individuals encompassing a wide size range was present in the 2 species of *Parthenope*, and to a lesser extent in the 3 other species. However, the measurements obtained from all 5 species appeared generally similar to that which might be obtained from a consecutive molting progression. Each species-series consisted of numbers of individuals which could be ranked in more or less regularly increasing size increments. Cross-sectional data such as these can be useful in extrapolating parameters of growth (see Marchand-Hellegouarch, 1973; Mauchline, 1977; Kaufmann, 1981).

Males, females-ovigerous females, and juveniles were separated into series within each species, and scatter diagrams of CW or SCW were plotted against

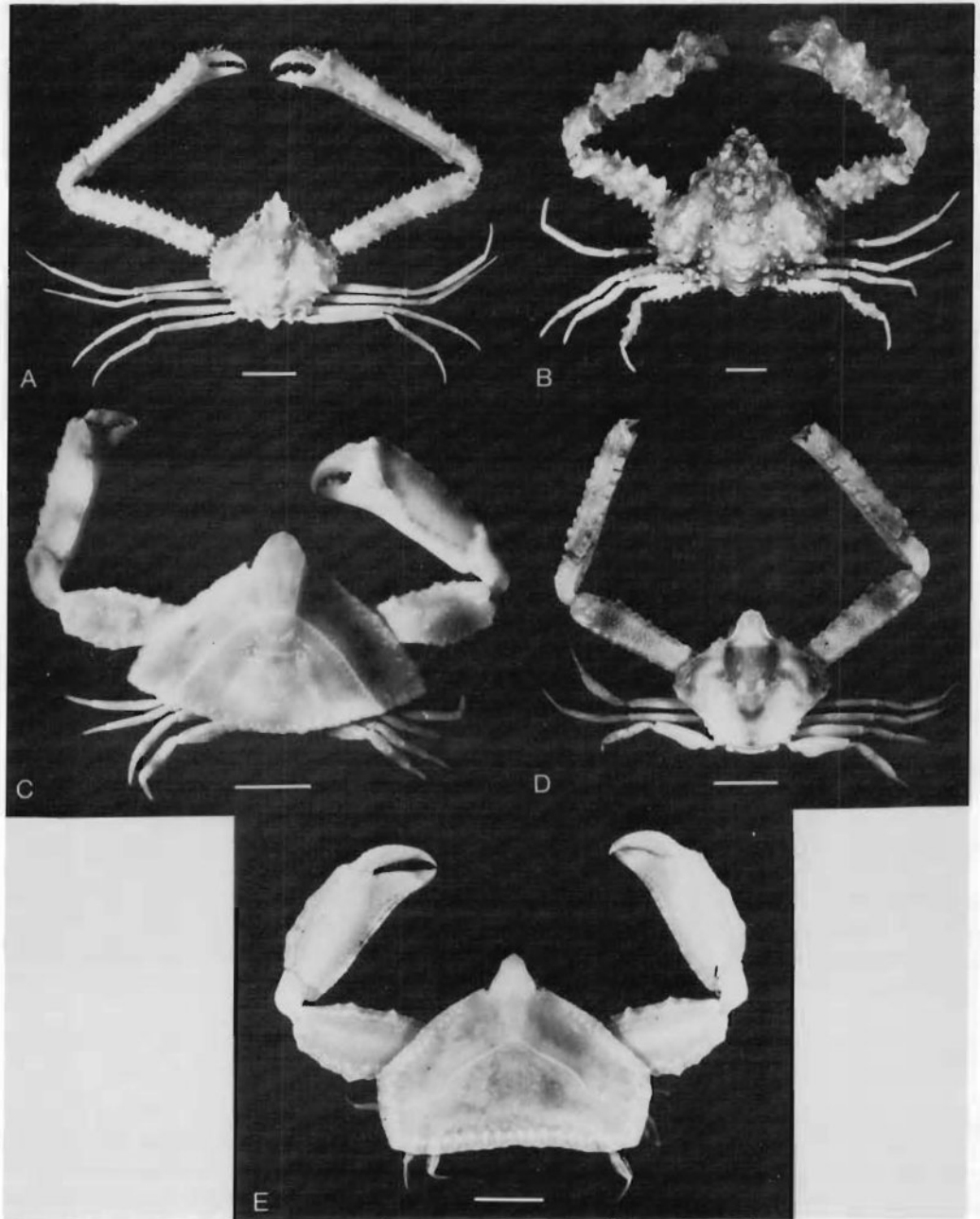


Fig. 1. The five species of parthenopid crabs discussed in this report A, *Parthenope agona* (Stimpson); B, *Parthenope fraterculus* (Stimpson); C, *Heterocrypta granulata* (Gibbes); D, *Solenolambrus tenellus* (Stimpson); E, *Cryptopodia concava* (Stimpson). Scale lines equal 3 mm.

TABLE I

Relative growth of carapacial and abdominal characters in five species of parthenopid crabs

Species	Sex	N	Size range (SCW-CW mm)	\bar{X}	Median	Mode	Carapacial growth		Bivariate ratio ranges	
							SCW-CW:RCL	r ²	MGL/SCW-CW	FAW/SCW-CW
<i>Parthenope agona</i>	Males	82	3.5-18.1	11.1	10.0	13.5	$y = 0.93X^{1.08}$	0.99	0.11-0.30	
	Females	91	4.2-18.5	10.8	10.2	6.4	$y = 1.02X^{1.03}$	0.99	0.23-0.47	
	Ov. females	24	7.4-18.3	14.4	15.3	14.3	$y = 1.04X^{1.03}$	0.98	0.39-0.46	
	Juveniles	20	2.3- 8.9	4.5	4.6	4.6	$y = 0.82X^{1.17}$	0.98	---	
<i>Parthenope fraterculus</i>	Males	30	3.6-17.6	9.9	7.6	14.1	$y = 0.95X^{1.03}$	0.99	0.12-0.28	
	Females	30	5.0-14.0	7.8	7.3	5.5, 7.3	$y = 0.95X^{1.05}$	0.99	0.22-0.36	
	Ov. female	1	11.4	—	—	—	—	—	0.32	
	Juveniles	37	2.1- 6.4	3.6	3.8	3.8	$y = 0.77X^{1.18}$	0.95	---	
<i>Heterocrypta granulata</i>	Males	17	5.4-11.8	9.1	9.4	8.1, 9.4	$y = 1.11X^{1.12}$	0.98	0.19-0.24	
	Females	10	5.8-11.9	8.6	8.8	10.0	$y = 1.14X^{1.12}$	0.98	0.15-0.25	
	Ov. females	3	8.1-12.4	—	—	—	—	—	0.20-0.25	
	Juveniles	2	3.1- 6.9	—	—	—	—	—	---	
<i>Solenolanbrus tenellus</i>	Males	25	2.9- 7.3	4.8	4.6	4.4	$y = 0.97X^{1.07}$	0.99	0.24-0.34	
	Females	20	1.8- 5.4	3.9	4.0	4.0	$y = 0.94X^{1.10}$	0.99	0.28-0.48	
	Ov. females	12	4.8- 7.3	5.5	5.3	5.3	$y = 1.10X$	0.87	0.45-0.48	
	Juveniles	8	1.8- 3.1	2.6	2.4	2.4	$y = 0.96X^{1.09}$	0.99	---	
<i>Cryptopodia concaua</i>	Males	16	3.8- 8.4	6.3	6.6	7.5	$y = 0.98X^{1.12}$	0.97	0.09-0.21	
	Females	20	2.6- 9.5	7.6	8.1	8.1	$y = 0.94X^{1.18}$	0.98	0.19-0.21	
	Ov. females	1	8.0	—	—	—	—	—	0.19	
	Juveniles	3	2.5- 3.0	—	—	—	—	—	---	

TABLE I (continued)

	Abdominal growth Adult males		Subadult males		Adult females		Subadult females	
	$y =$	r^2	$y =$	r^2	$y =$	r^2	$y =$	r^2
<i>Parthenope agona</i>	$y = 0.21X^{1.09}$	0.89	$y = 0.07X^{1.49}$	0.95	$y = 0.25X^{1.21}$	0.97	$y = 0.25X^{1.11}$	0.90
MGL or FAW/SCW ratios	0.25-0.30		0.11-0.19		0.37-0.47		0.23-0.33	
Extrapolated pubertal molt range (SCW)	ca. 7 mm				5-7 mm			
<i>Parthenope fraterculus</i>	$y = 0.19X^{1.05}$	0.74	$y = 0.07X^{1.61}$	0.86	$y = 0.32X$	0.91	$y = 0.20X^{1.10}$	0.98
MGL or FAW/SCW ratios	0.18-0.28?		0.16-0.22?		0.30-0.36		0.22-0.29	
Extrapolated pubertal molt range (CW)	5-9 mm if widescale variation is the norm				7-10 mm with apparent widescale variation			
<i>Heterocrypta granulata</i>	$y = 0.31X^{0.84}$	0.79	Unavailable	—	$y = 0.21X^{0.99}$	0.68	Unavailable	—
MGL of FAW/CW ratios	$\approx 0.20?$				0.20-0.25 (see text)		0.17-0.19?	
Extrapolated pubertal molt range (CW)	5-6 mm				<7 mm based on bivariate ratios of ovigerous females			
<i>Solenolambus tenellus</i>	$y = 0.22X^{1.21}$	0.94	Unavailable	—	$y = 0.03X^{2.57}$	0.92	Unavailable	—
MGL or FAW/CW ratios	$\approx 0.24-0.34?$				0.28-0.30 or higher			
Extrapolated pubertal molt range (CW)	3-4 mm				3.6-4.5 mm			
<i>Cryptopodia concava</i>	$y = 0.03X^{1.89}$	0.96	Unavailable	—	$y = 0.14X^{1.16}$	0.89	Unavailable	—
MGL or FAW/CW ratios	0.17-0.24?		0.09-0.13?		0.19 or less			
Extrapolated pubertal molt range (CW)	3-4 mm				> 5 < 8 mm			

RCL on log-log paper, and regression lines using power curve equations were calculated. These data are illustrated in figs. 2A-E, and equations given in table I.

Gonopodal and abdominal allometry. — For this part of the investigation we arbitrarily selected CW or SCW, depending on the particular carapace morphology of the species, as the independent variable. A bivariate ratio derived from the relative increase in width of abdominal somite 5 in females (FAW/CW or SCW), or the relative increase of the major gonopod in males (MGL/CW) was calculated. Noticeable discontinuities in this type of ratio can demonstrate changes in the rate of growth of either FAW or MGL when compared against the consecutively listed CW or SCW in a given series, thus indicating the size range over which a pubertal molt or molting series has occurred. These data can then be compared with those obtained from simple carapace or abdominal measurements described earlier, and with the presence or absence of ovigerous females or obviously mature males, in an attempt to determine the smallest size at which a pubertal molt may occur in the material at hand. These data are provided in figures 3 and 4, and table I.

We are aware that data from a sized-series of non-molting, field-collected individuals may not be an accurate reflection of a natural growth series. On the other hand, all of the individuals within a species presumably are subjected to similar environmental conditions, and probably respond in a similar manner of growth. The methodology we are using thus allows at least a first approximation of growth and subsequent maturity for these little known crabs. Obtaining actual molting series from nature or in the laboratory will provide further data confirming or denying our supposition.

RESULTS

Parthenope agona (Stimpson, 1871)

A total of 217 specimens were examined. The 20 juveniles in this species were equal in carapace length and width at very small stages (ca. 3 mm), becoming slightly longer than wide owing to the increasing length of the rostrum (4-5 mm), or wider than long as lateral spines and branchial regions became more developed (4-6 mm). Although broken lateral or rostral spines could conceivably result in the illusion of negative allometric growth in the very young stages, juveniles in this species generally exhibited positive allometry (table I, fig. 2A).

As seen SCW was positively allometric to RCL; growth in both sexes can be considered identical (fig. 2A). Males exhibited greater allometry than females, although carapace dimensions between the two sexes were generally similar. Males of *P. agona* are sexually dimorphic, however, in having more inflated branchial regions and better developed lateral carapace spines than females (fig. 1A), thus appearing wider.

Developing females cannot be separated from non-sexable juveniles until about 4 mm SCW, when incipient gonopores first become evident; gonopod development in males is first seen at about 3.5 mm SCW. Both FAW and MGL increased within the ranked series of either sex, from smallest to largest specimens. However, notable changes in the bivariate ratios of FAW/SCW in females occurred at 5 to 7 mm SCW, the ratios ranging from 0.23 to 0.33 below 5 mm, to 0.37-0.47 above 7 mm. We classified those females with FAW/SCW ratios of 0.33 or less as probably prepubertal/subadult stages, whereas those with ratios of 0.37 or higher were considered to be adults. Anatomically maturing females may not mature functionally until about 7 mm SCW, the size when ovigerous females were first noted. The smallest ovigerous female in our material (represented by an asterisk, fig. 2A) measured 7.4 mm SCW and the FAW/SCW ratio was 0.39 (see also fig. 3A and table I).

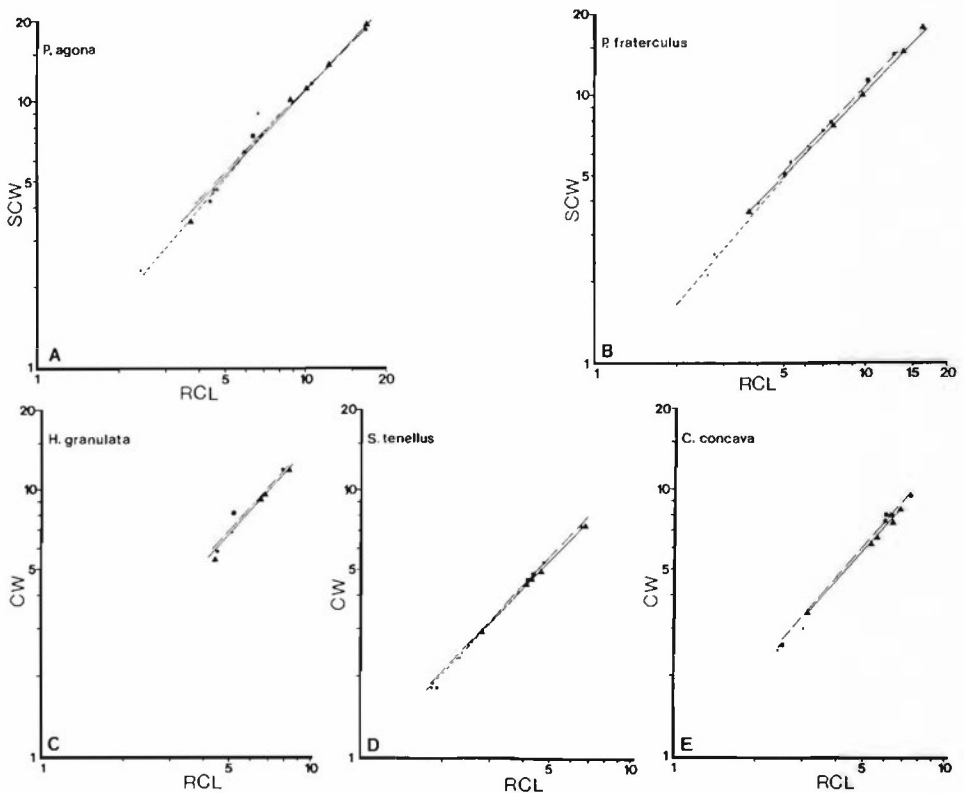


Fig. 2. Relative growth of the carapace in five species of parthenopid crabs. Solid lines, males; long dashed lines, females; short dashed lines, juveniles. For clarity of regression lines only data points representing minimum, mean, median, modal and maximum sizes plotted for males (triangles), females (large dots), smallest ovigerous female (asterisk), and juveniles (small dots).

See text and table I for further information.

In males the ratio of MGL/SCW increased from 0.11-0.19 between 3.5 and 7.4 mm SCW, to 0.25-0.30 at 7.6 mm and larger SCW. Some overlap in the upper ranges of these values was observed, but males are probably anatomically and functionally immature to about 7 mm SCW, although maturing rapidly thereafter. Variation in capture size with maturity was reflected in 2 specimens having MGL/SCW ratio of 0.25 at 6.3 and 7.3 mm SCW, respectively. We considered these individuals to be "precociously" mature males within a nor-

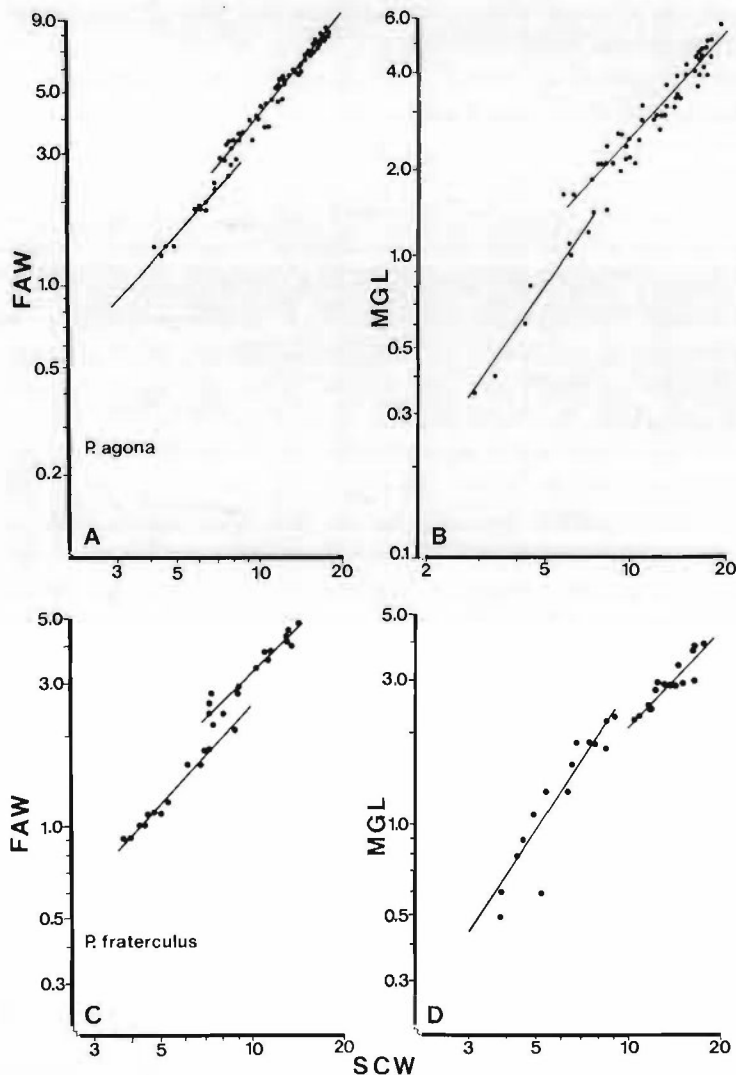


Fig. 3. \log_{10} allometric growth of female abdominal somite 5 (FAW) and male gonopod length (MGL) in relation to spinal carapace width (SCW) in *Parthenope agona* (A, B) and *P. fraterculus* (C, D). Data points represent only measurable specimens from total number available (see text).

mally subadult size range of the series. On the other hand, 2 male specimens of 8.1 and 9.0 mm SCW, with MGL/SCW ratios of 0.17 and 0.21, respectively, seemed to be anomalously immature, although sexable, specimens lagging far behind their siblings in gonopod development. Although such variation is not unexpected, the rather restricted size range over which the bivariate ratios changed so noticeably in other material implies that these 4 specimens were outside the norm. A similar variation was noted in 2 females of 8.0 and 8.4 mm SCW, both exhibiting anomalous FAW/SCW ratios of 0.35 and 0.23, respectively, again implying that they were "delayed" subadult stages within an ordinarily mature size class.

Allometric growth of abdominal features differs between adults and subadults (fig. 3A, B). Overall abdominal somite width is positively allometric in females, becoming more strongly allometric to carapace width in the adult than in the subadult stages. In males, overall gonopod development is also positively allometric, but approaches isometry with the expanding carapace in maturing males.

The relatively large size ranges recorded for obviously mature males and females suggest that molting continues beyond the pubertal ecdysis. Data from several specimens, and 1 molted dorsum, also confirm that the pubertal molt in *P. agona* is not a terminal molt in either sex. For example, 1 male specimen was a complete molted carapace (11.3 mm SCW), another (10 mm SCW) bore pereopod buds on right W 2-3, and both had well-developed gonopods having MGL/SCW ratios of 0.28 and 0.33, respectively. Both specimens were smaller than the largest recorded male, 17.9 mm SCW. Several ovigerous females were also substantially larger (e.g. 13.9, 16.1 mm SCW) than the smallest ovigerous specimen (7.5 mm SCW). The single dorsum cast, lacking sternum and abdomen and consequently un-sexable, measured 17.5 mm SCW, distinctly larger than the aforementioned ovigerous females, and close to the size of a large (17.4 mm SCW) non-ovigerous female. Rathbun's (1925) largest specimen was a male at 18.6 mm SCW.

Remarks. — The nearly isometric growth of gonopods in males suggests that maximum reproductive potential (*sensu* Hartnoll, 1974) may not be developed in *P. agona*. Large males (e.g. 16 mm SCW) probably are unable to copulate with the smallest ovigerous females (e.g. 8 mm SCW), and breeding may therefore be limited to those crabs of approximately equal size. Copulation would presumably be discouraged on both behavioral and morphological grounds in functionally immature females, if they lack the necessary behavioral responses until the proper physiological changes occurred. Unfortunately, data on mating behavior in this species are non-existent.

Maturational variation (i.e. "precocious" adults, or "delayed" subadults) has been observed in other brachyurans. Morgan (1923) for example, noted variations in size of newly matured grapsoid crabs, as did Weymouth & McKay (1936) in cancrids, and Swartz (unpubl.) in a xanthid crab.

***Parthenope fraterculus* (Stimpson, 1871)**

The size range for the 98 specimens examined in this species was smaller than that of *P. agona*, and the size increments were more widely spread with the ranked series.

In nearly all the juveniles, and in some of the subadult males (below 7 mm SCW) RCL was always greater than SCW. In most other males, and in all of the female specimens SCW exceeded RCL. In general, carapace growth within each ranked series differed by sex until maturity was attained, at which time growth in both males and females approached but did not attain isometry, a situation similar to that in *P. agona* (fig. 2B).

Abdominal allometry in *Parthenope fraterculus* was difficult to interpret. In both subadult and adult females FAW seemed to increase in a regular manner with increasing SCW (fig. 3C). The FAW/SCW ratios in subadults ranged from 0.22 to 0.29 up to about 8 mm. At larger sizes, classified as adults, the ranges increased from 0.30 to 0.35. Overlap in these ratios was recorded between about 7 and 8 mm SCW, suggesting that anatomically maturing crabs were becoming functionally mature. However, if the rather low ratio values of 0.24-0.29 seen in 2 females at 8.9 and 9.9 mm SCW are indicative of "delayed" subadult stages, then the range of the pubertal molt might extend from about 7 to 10 mm SCW. Regrettably, little other evidence is available and the only ovigerous female in our material (noted by the asterisk, fig. 2B) measured 10.1 × 11.4 mm RCL × SCW. No measurements for other ovigerous females, larger or smaller, exist in the literature.

Males of *P. fraterculus* were just as difficult to assess (fig. 3D). There seemed to be substantial variation in MGL relative to SCW, and progressively larger stages did not always have proportionately larger appendages. The MGL/SCW ratios in subadults showed wide variation, from 0.16 to 0.22 at about 5 mm SCW, fluctuating in value thereafter (0.12-0.28) up to a size of about 9 mm SCW, before dropping to values of 0.18 to 0.24 at adult sizes larger than 9 mm SCW. One explanation is that MGL increases rather irregularly at the smaller stages up to about 5 mm SCW. Near this size a prepubertal molting series may occur, as suggested by the resultant large scale increase in MGL/SCW ratios. At the presumed termination of this phase about 9 mm SCW (the pubertal molt?), and larger sizes thereafter, the carapace expands more rapidly in relation to gonopod length than in the subadult stages. In the larger crabs the lateral spines of the carapace become quite prominent, thus accounting for the decreased MGL/SCW ratios. An alternative explanation, however, is that widescale variation in gonopod length and carapace spine formation occurs over the entire size range from 5 to 9 mm SCW, and these morphological changes continue throughout an extended period of pre- or postpubertal molting. Specimens of 5.2 and 8.5 mm SCW,

with MGL/SCW of 0.12, 0.21, respectively could exemplify "delayed" subadult stages, if the latter explanation is true.

Some unsexable juveniles were recorded up to 6.4 mm SCW. In general, however, both male gonopod development and the appearance of female gonopores (thus indicating anatomically maturing individuals) could be distinguished in specimens as small as about 4.5 mm SCW. In the males, MGL is strongly and positively allometric to SCW during subadult stages, becoming weakly but still positively allometric (almost isometric) during adulthood. The pubertal molt phase may occur over a size range of 5 to 9 mm.

In females, the overall growth of the fifth abdominal somite is also positively allometric to SCW, especially in subadults and during what seems to be the pubertal molt phase from 7 to 9 mm SCW. Thereafter, FAW becomes isometric to SCW. The maturational size range is thus more conservative in the females than in males.

No molted carapaces, nor specimens with limb-buds were recorded in our material. The large SCW values recorded for some specimens (up to 17.6 mm in males, 14.0 mm in females) certainly suggests that further molting occurs after maturity is attained. From our data maturity in males seems to occur no later than about 9 mm SCW and in females at about 10 mm; the only ovigerous female measured 11 mm, as noted earlier. Rathbun (1925) listed a female at 18.3 mm SCW.

Remarks. — The relative isometry between abdominal and carapacial growth in males is enigmatic. The limited data suggest that either individual *P. fraterculus* males reach maturity over a wide size range, or that a series of prepubertal molts (instead of a single definitive molt) takes place in each crab. Although we suspect individual variation in attainment of maturity to be more likely, extended pubertal molting series, as has been noted in other brachyurans, cannot be dismissed. Hartnoll (1964), for example, working with the freshwater grapsid crab *Metopaulias depressus* Rathbun, found no marked change at any particular molt which would indicate the onset of maturity; instead he observed several changes in pleopod setation over a series of molts, and correlated these changes with histological examinations to show that maturity was ultimately reached at about 12 mm CW. Haley (1969) noted an analogous situation in the ghost crab, *Ocypode quadrata* (Fabricius), which had a varying rate of growth in MGL until a carapace width of 25 mm, when MGL became isometric with CW. Either situation could obtain in *P. fraterculus*.

Growing males may be increasingly restricted from breeding with smaller, newly maturing females because of isometric growth of the gonopods, although this may be a relatively minor disadvantage provided the population of larger females is sufficient. There are no data as to whether such males would be reticent to copulate with females larger than themselves, as seen for example, in males of the xanthid crab *Neopanope sayi* (Smith) (cf. Swartz, unpubl., 1976).

Heterocrypta granulata (Gibbes, 1850)

Only a small series of 32 specimens was available. Anatomically (if not functionally) maturing males and females were recorded at 5.4 and 5.8 mm CM, respectively. The smallest ovigerous female measured 8.1 mm CW, the largest (and the largest specimen of all the series) was 12.4 mm CW. The 2 juveniles were 3.1 and 6.9 mm CW (table I).

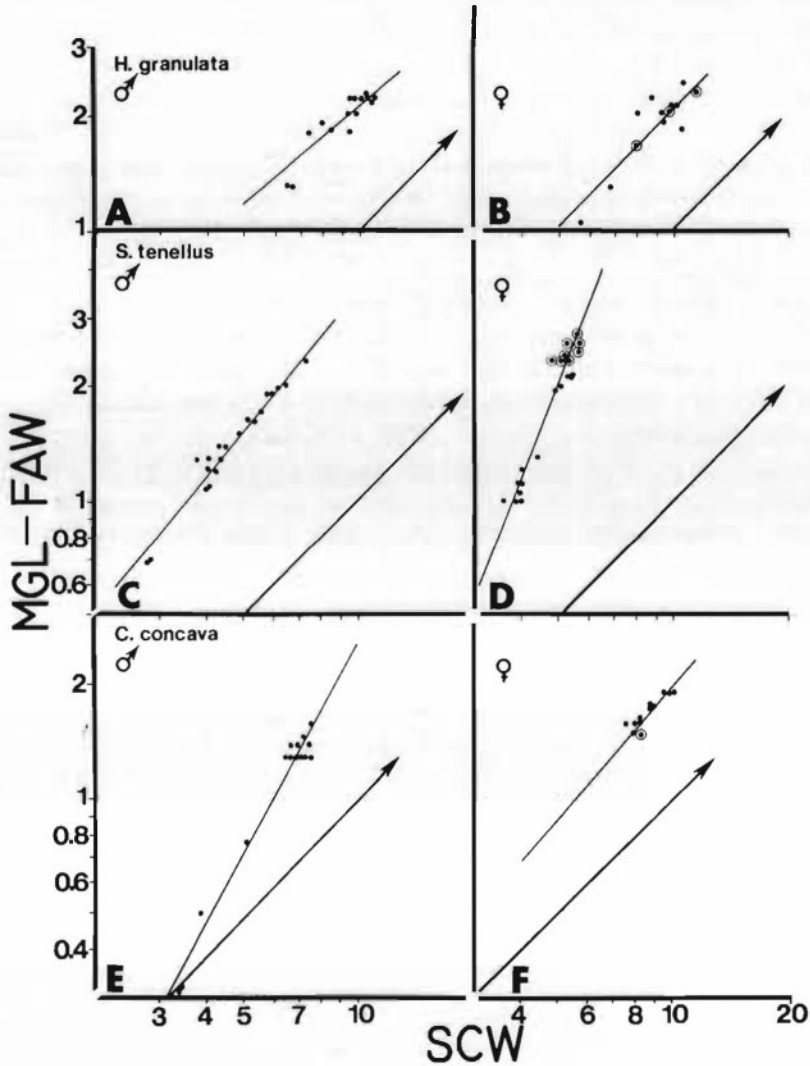


Fig. 4. Log₁₀ allometric growth of male major gonopod length (MGL) and female abdominal somite 5 width (FAW) in relation to carapace width (CW) in three species of Parthenopidae. Data points represent only measurable specimens from total number available (see text). Circled dots indicate ovigerous females; arrows denote line of isometry on 1:1 ratio.

Carapace width in males and females was positively allometric to RCL in both sexes, and although females were usually wider than their male counterparts at a given RCL (fig. 2C), relative growth was about equal (table I). Because cephalothorax shape in adults of both sexes is distinctly triangular-pentagonal (fig. 1C), the pubertal molt is probably indeterminable by outward change in carapace dimensions alone.

Only 2 juveniles were available. Gonopodal growth in relation to carapace width in anatomically adult males was generally negatively allometric (fig. 4A). Whether a distinct pubertal molt is present in these males is uncertain. It may have occurred between 5 and 6 mm CW, and perhaps even smaller sizes (i.e. MGL/CW ratios of 0.20 or less), but no smaller specimens were available to confirm this supposition. In the females of this species (fig. 4B) abdominal somite growth was nearly isometric to carapace width. The adult stage is entered by about 8 or 9 mm CW (0.20), the smallest available ovigerous females. We may infer that a pubertal molting phase probably takes place before 7 mm CW is attained, based on FAW/CW ratios of 0.17 to 0.19 obtained from two small females measuring 5.8 and 6.9 mm CW.

There is little to base conclusions on whether the pubertal molt is a terminal molt. If our suppositions on size of maturity in males (5-6 mm CW) and females (8-9 mm CW) are correct then molting may continue thereafter. The largest specimens of the sexes were recorded at 11.8 mm CW (σ), 11.9 (\varnothing) and 12.4 (ovigerous \varnothing); Rathbun (1925) records a specimen of 21 mm CW.

Remarks. — The series of *H. granulata* consisted primarily of well-developed adults. The carapace in this species, much expanded in juveniles, becomes even more widely triangular with maturity. The continually increasing carapace width compared to male gonopod length results in calculations of negative allometry because apparently this appendage does not really "grow" much more once it reaches a terminal size of about 2.2 mm total length. The gonopods of 5 males (9.4-11.8 mm CW), including the largest available in our series, did not exceed 2.3 mm in length; males smaller than about 9.5 mm CW had gonopods measuring 2.0 mm or less. Hartnoll (1965a, 1972) considered negative allometry of male gonopods as a type of standardization in a study made on grapsid crabs. He suggested that a standard size of gonopod would allow greater sexual compatibility between the 2 sexes regardless of the size of the male carapace. Although an intriguing concept it may not be applicable to *H. granulata*. All members of the genus *Heterocrypta* are characterized by a remarkably expanded, shelflike lateral carapace margin. If mating females are to be carried by males (as commonly observed in other brachyurans) it is easy to visualize some difficulty being encountered if the female is the same size as the male. A standardized gonopod might be of lesser benefit in such a case, and may even limit the size of the female to be mated.

***Solenolambrus tenellus* (Stimpson, 1871)**

Anatomically maturing males were recognized at 2.9 mm CW, and females with incipient gonopores were noted at 1.8 to 3.0 mm CW (table I). Quite a fragile species, the smallest female with an undamaged measurable abdomen measured 3.6 mm CW, the smallest ovigerous female 4.8 mm, and every female larger than this was ovigerous. Thus, functional maturity is attained in females of this species at about 5 mm CW. However, non-sexable juveniles ranged in size from 1.8 to 3.1 mm CW, so there is variability in anatomical maturation within females, at least.

Little relative change in carapace dimensions takes place either within a sex, or with the attainment of maturity (fig. 2D). Males, females and juveniles all exhibited roughly similar allometry, although females remained slightly wider than males over most size increments. The growth of the carapace in ovigerous females was isometric.

In *Solenolambrus tenellus*, but MGL and FAW is positively allometric to CW (fig. 4C, D; table I). In males, the gonopod increases in length relative to CW, and the relative increase of MGL/CW ratios were greatest between 3 and 4 mm CW, suggesting that a pubertal molting phase may begin near these values. However, a wide range of values for MGL/CW ratios (0.24-0.34) between about 4 and 7 mm CW suggests that the pubertal molting phase may encompass a large growth range, with subsequent adult molts occurring thereafter. Similarly, in the females, the initiation of a pubertal molting phase may take place anywhere within a size range of 3.6 to 4.5 mm CW. The pubertal molt probably occurs when FAW/CW ratios are greater than 0.30, i. e. with CW greater than about 4.5 mm. The molt also does not appear to be terminal, with ovigerous females recorded from 4.8 to 5.6 mm CW. Rathbun's largest specimen, a male, measured 6.3 mm CW.

Remarks. — No noticeable spines, tubercles or other protrusions are present on the lateral carapace margins in this species (fig. 1D), thus accounting in part for the nearly identical allometric growth coefficients in the male, female, and juvenile series (table I). The very high regression coefficients obtained for the relative growth of FAW and MGL suggest that maturity may be rapidly attained in this species, over a restricted series of molts, or perhaps even a single molt.

***Cryptopodia concava* (Stimpson, 1871)**

Anatomically maturing males were noted at 3.4 mm, females at 2.6 mm, and the sole ovigerous female in the material measured 8.0 mm, and non-sexable juveniles occurred from 2.5 to 3.0 mm CW (table I). The females were always slightly wider than the males in this species. Both sexes exhibited strong positive allometry in relative growth of the carapace, not surprisingly because the overall shape of these crabs approximates an expanded pentagon (fig. 1E). Data were insufficient to determine whether allometry existed in juveniles or ovigerous females.

Relative growth in the abdominal parameters MGL/FAW in both sexes was also positively allometric (fig. 4E, F), in males very strongly so. Based on the most noticeable changes in MGL/CW ratios (0.19-0.13), a pubertal molting phase may begin between 3 and 4 mm CW; the next size increment, 5.3 mm (0.24) had matured gonopods. Females with incipient gonopores were noted between 2.6 and 5.1 mm CW, but all of these specimens were too badly damaged to allow accurate abdominal measurements. The next size measurement was 7.7 mm, and this specimen had well-formed gonopores. Consequently, the data on FAW/CW ratios are all based on adult females, so the size range of any pubertal molt remains unclear. It probably occurs after 5.0 mm and perhaps at or before 8 mm CW, the size of the sole ovigerous female in our material.

The wide range of values between pre- and postmaturational increments reflects continued growth after the pubertal molt. But with only a single ovigerous female available the data must remain speculative. We think it unlikely, however, that a wide range of terminal maturational values occurs within this species. Otherwise this would presume that some individuals do not undergo a final pubertal molt until approaching maximum size for the species, noted by Rathbun (1925) as 12 mm CW.

Remarks. — In *Cryptopodia concava* strong positive allometry in male abdominal features is seen, and standardization of gonopod length seems to be a feature attained in this species, similar to that seen in *Heterocrypta granulata*. That is, once a length of about 1.3 to 1.4 mm is reached, the now presumably mature organ does not grow further, although the carapace, which has a pentagonal shape similar in general morphology to that seen in *H. granulata*, continues to expand. The relatively high allometry values for carapace growth in this species (the highest of any of the species in this report excluding the juveniles series of both species of *Parthenope*), are a result of the remarkably expanded shelf-like lateral margins of the carapace. But the same argument advanced for a limiting size in mated females of *H. granulata* may also apply to *C. concava*; viz., a standardized gonopod may be of lesser importance than the general carapace size of a female, if the latter is carried during the mating act in a manner similar to other brachyurans. There may be "standardization" sensu Hartnoll of FAW in females, too. We noted three specimens with nearly identical FAW occurring over a size range of 6 to 7 mm CW. The implication from our data is that both MGL and FAW are limited to a certain maximum size at maturity, but that carapace expansion may continue to take place. Just why this is so is an interesting but as yet unanswered question.

DISCUSSION

With the exception of ovigerous female *Solenolambrus tenellus*, none of the parthenopid crabs in this report exhibited isometric carapace growth, although

females were usually larger than the males at any given length. Bivariate ratios of abdominal features to carapace widths in both sexes increased noticeably over a concomitant but generally limited increase of carapace widths, providing evidence that males undergo a relatively rapid carapace expansion, corresponding to a noticeable maturational growth of the gonopods, although the relative growth of the carapace is not on the same scale as that seen in females. There is, however, size-differentiated sexual dimorphism in these crabs. By extrapolation of both a beginning and end point using these ratios, and in some instances recording ovigerous females within the range of such points, we defined the range of maturational ecdysis. The species investigated, however, showed variability in this phase, some having a rather restricted range extending over 2 to 3 mm CW, others such as *Parthenope fraterculus* encompassing 5 mm CW.

We must be careful, however, to distinguish morphological or anatomical sexual maturity, indicated at least by gonopod or gonopore presence and development, from functional sexual maturity. In females, functional maturity is overtly indicated by fertilized eggs carried on the abdominal somites, whereas in males the evidence is more circumstantial and relies on the presence of fully developed gonopods. Functional maturity is best confirmed by histological examination in both sexes (e.g. Hiatt, 1948; Haley, 1969) but is time consuming and involves damage to the specimens, neither of which was feasible at the time of our study. As a consequence, we have assumed that the smallest ovigerous females in our material are at least representative of the general size at which females in the 5 species first become ovigerous. However, we cannot completely rule out the possibility of seasonal or geographical variability in the size of smallest ovigerous parthenopids in other parts of their range. We are especially cognizant of this objection in regard to *Parthenope fraterculus*, in which the smallest (and only) ovigerous female in our material plotted well beyond the point of divergence in male and female RCL/SCW regressions. Both Cox & Dudley (1968) and Wenner et al. (1974) noted similar variability in the smallest ovigerous females of the anomuran mole crab *Emerita*. The same considerations may be applicable to our males (see also e.g. Somerton, 1981), but we believe the sizes recorded to be at least provisionally indicative of what transpires in nature.

We noted an apparent difference in the rate of maturity between male and female parthenopids, so that it was often possible to detect females at a smaller stage (based on incipient gonopore formation) than males (with almost unnoticeable major gonopod development). Yet if our consideration of abdominal ratios is correct, males appeared to enter pubertal molt stages at a smaller size than females. Thus, while females may begin to anatomically mature sooner than males, the latter may become functionally mature at an earlier stage.

The occurrence of variant stages termed "precocious" adults, or "delayed" subadults, especially in the genus *Parthenope*, is another indication of this type

of maturational variation. For example, several "precocious" female individuals in *P. agona* were certainly anatomically mature, and although overtly non-ovigerous, might still be functionally mature as virgin females, sensu Hartnoll (1965a, b). That author, investigating some grapsid and majid crabs, distinguished between virgin (non-copulatory) and non-virgin (copulatory) females; the latter exhibited spermatophore plugs but nevertheless retained immature ovaries. Females such as these represent another example of what we referred to as anatomically, but not functionally, mature individuals. Hartnoll also pointed out that the molt of puberty may be a misnomer in some majid males, because they can be potentially functionally mature (i.e. having ripe sperm, well-developed gonopods) although not yet having undergone a pubertal molt. The "precocious" males we noted may belong to this category, especially if maturation occurs over a period of ecdyses, as seems to be the case in *Parthenope fraterculus*.

Yet another aspect that relates directly to maturational variability has been recently investigated by Hartnoll & Dalley (1981). They found that size variation in postlarval *Palaemon elegans* Rathke increased through several instars and then decreased noticeably, before again increasing, followed in turn by a second period of reduced variation. These authors postulated the operation of an undefined "negative feedback" mechanism which imposes a limit on instar size variation at certain ontogenetic phases, so that individuals of a species would all be relatively similar in ("optimal") size at crucial periods in their life cycle, such as at the onset of puberty. This concept, if of widespread occurrence in other crustaceans, would remove a serious restriction on the use of cross-sectional data such as used in our report. It would now be possible, for example, to define the relative age of a species at which the pubertal molt takes place, as well as the size-range over which it occurred. If the Parthenopidae required a more-or-less fixed number of instars before a pubertal molt could occur (and there is no evidence for or against this idea at present), then individuals undergoing the pubertal molt would all presumably be of approximately equal sizes, provided they had utilized the "negative feedback" postulated by Hartnoll & Dalley. An important drawback to the consideration of this concept, however, is that in the cited study the authors cultured the shrimp under constant and closely controlled conditions of temperature, a situation not usually seen in nature. And because fluctuating temperature, and seasonality (perhaps as a correlated derivative) are known to influence both molting and growth (e.g. Somerton, 1981; and *Parthenope fraterculus*?, this study), the hypothesis may not be universally applicable. It remains an extremely interesting possibility.

We are unable to determine if a terminal anecdysis occurred in the five species of this report. The recorded size increments continued to increase well beyond the preliminary size range of functional sexual maturity, suggesting that growth was continuing. However, Hartnoll (1965b) has also demonstrated

that a large size range can be found in some majid crabs extending beyond that of the pubertal molt. Moreover, as far as is known, the Majidae are the only Brachyura in which the pubertal molt is also usually the terminal molt (Hartnoll, 1965b; but see Somerton, 1981 for exception). Chaix et al. (1976), following Carlisle (1957), have shown that the Y-organ in majids degenerates very soon after the pubertal molt, thus arresting the entire ecdysial cycle. Physiological studies are clearly needed to see if the same situation applies to the Parthenopidae.

The data provided in this study agree with observations made on other brachyurans. For example, changes in carapace allometry and the subsequent initiation of the pubertal molt has been documented in *Pachygrapsus crassipes* Randall (Grapsidae; Hiatt, 1948), and *Cardisoma guanhumi* Latreille, a gecarcinid crab studied by Herreid (1967). The latter author was able to distinguish differentiation of major and minor cheliped sizes in *Cardisoma* at a CW of 45 to 60 mm. Although he did not expressly note this particular size range as that of the pubertal molt, Herreid did state that profound morphological and physiological changes occurred at this size. Earlier, Gifford (1962) stated that the beginning of sexual dimorphism becomes evident in this species at a carapace weight of about 40 gms (= 45 mm CW, Herreid, 1967), and this correlated with an abrupt increase in carapace width compared to orbital width. Females of *C. guanhumi* could attain sexual maturity and spawn at any weight over 40 gms (i.e., 45 mm CW and larger) but the weight of first sexually mature males in this species was not known.

Relative size discrepancy with age between the sexes has also been noted in other decapods, e.g., *Spirontocaris*, a caridean shrimp (Allen, 1962) and portunid crabs (Tagatz, 1968). An analogous situation was described in protandric pandalid shrimp by Butler (1964) who found that transitional and secondary females were longer than males of the same species. In some cases either a trend toward paedogenesis was suggested, as in the precocious functional maturity of larger, pre-pubertal males of some species of majid crabs (Hartnoll, 1965b), or has apparently been realized, as noted in the anomuran mole crab *Emerita* (Efford, 1967). Without histological examination, however, the situation in parthenopids remains undefined.

Finally, 3 pubertal molt categories were suggested by Hartnoll (1965b), viz., 1) the molt of puberty is fixed over a relatively small size range, with subsequent molting thereafter; 2) the molt of puberty occurs over a wider size range with subsequent molting afterwards; and 3) the pubertal molt is manifested over a wider range of carapace sizes, but in effect becomes the terminal molt of the crab. The parthenopids we examined could be assignable to at least the first 2 of these categories, with *Parthenope agona* and perhaps *Solenolambrus tenellus* fitting the first, *P. fraterculus* and the other three species the second. The available evidence seems to preclude any of the 5 species fitting the third category.

Our conclusions, of course, are based on the assumption that the meristic

data obtained from the 5 species of parthenopid crabs reflect the average rate of change for different sized individuals, these in turn presumably being affected by similar average environmental conditions along the Floridan continental shelf. As pointed out by Kaufmann (1981) cross-sectional data of this kind have the advantage of being easy to obtain. Longitudinal data (i.e., consecutive molting series as obtained either from nature or in the laboratory) are certainly more accurate. But such data are also subject to limitations and may be variable, owing to changes in environmental conditions in the field to which the crabs respond during growth periods, or more importantly, because the growth series obtained under more or less constant laboratory conditions may actually be less realistic than that taking place in a typically fluctuating natural environment.

ACKNOWLEDGEMENTS

We thank Drs. Lawrence G. Abele, Florida State University, Tallahassee, and Richard G. Hartnoll, University of Liverpool, England, for critically reading earlier drafts of the manuscript. The comments of Mr. Wright C. Finney, Florida State University, and those of two anonymous reviewers are also greatly appreciated.

RÉSUMÉ

La croissance relative de caractères céphalothoraciques et abdominaux choisis a été examinée chez cinq espèces de crabes parthénopides recueillis sur le plateau continental, à l'est et à l'ouest de la Floride. En général la largeur de la carapace présentait une allométrie positive par rapport à sa longueur dans des séries de mâles, de femelles, de femelles ovigères et de juvéniles, rangés par taille, avec une expansion de la carapace plus prononcée chez les femelles, ovigères ou non. En vue d'essayer de déterminer la taille à la mue de puberté, les rapports bivariés de la longueur du gonopode mâle ou de la largeur du cinquième somite abdominal des femelles à la largeur de la carapace ont été calculés et schématisés sous la forme de régressions log-log. La divergence dans les lignes de régression a permis l'extrapolation d'une phase de mue pubérale, laquelle chez la plupart des espèces se produit entre des limites restreintes, de 3 mm environ.

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