RELATIVE GROWTH AND SEXUAL MATURATION IN THE ESTUARINE GHOST SHRIMP CALLIANASSA LOUISIANENSIS SCHMITT, 1935

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ABSTRACT

In *Callianassa louisianensis,* ovarian development becomes evident in December and continues through the spring. Ovigerous females occur primarily from early June through August, less frequently into September. Recruitment occurs throughout the summer and early fall, and juveniles reach large enough size to be detected in our samples by early spring. First-year females enter the breeding population the following summer; the smallest ovigerous among these have attained a carapace length (CL) of almost 11 mm. Analysis of relative growth suggests that females enter a maturation growth phase at about 11 mm CL, while males enter a maturation phase at near 15.5 mm CL. In males, this transition is marked by a strong increase in the relative growth of the major chela, together with a change in shape of the chela. In females, there is a decrease in the relative growth of the major chela after maturation. Carapace lengths in females do not attain the size of those in the largest males. In the maturation phase, female growth appears directed toward lengthening of the abdomen and development of ovaries, while in males it is directed toward development of the major chela, a secondary sexual structure that may be utilized in aggressive encounters.

The ghost shrimp *Callianassa louisianensis* (treated formerly as *Callianassa jamaicense* var. *louisianensis* Schmitt, 1935) is a widespread and abundant component of the estuarine macroinvertebrate assemblage in the northern Gulf of Mexico (Willis, 1942; Hedgpeth, 1950; Wass, 1955; Phillips, 1971; Felder, 1973). Concentrated in intertidal and shallow subtidal substrates ranging from sandy mud to organic silty sand, this fossorial species is adapted to oligohaline habitats of coastal marshes, tidal channels, and estuarine embayments. Its range extends from western Florida through the Gulf states and southward at least to the Rio Carrizal estuary in Tamaulipas, Mexico. Osmoregulatory adaptations of adults and larvae have been documented (Felder, 1978; Felder *et al.,* 1986), as have adaptations of the adults to periodic anoxia in their burrows (Felder, 1979). However, given the difficulty of monitoring natural populations in their fossorial habitats, little is known of growth, maturation, and reproduction in the species.

The dominance of this species among the estuarine infauna, its role in marine food chains, its impact on plant and animal communities, and its contribution to sediment and nutrient turnover likewise have received little attention, though some of these qualities have been evaluated in populations of other western Atlantic thalassinoids

(Pohl, 1946; Weimer and Hoyt, 1964; Frankenberg *et al.,* 1967; Howard and Dorjes, 1972; Pryor, 1975; Hill and Hunter, 1976; Howard *et al.,* 1977; Suchanek, 1983, 1985). *Callianassa kraussi* Stebbing, an ecological equivalent of *C. louisianensis* in South African estuaries, is known to play a dominant role in sediment turnover and to influence macrobiotic and microbiotic community structure (McLachlan and Grindley, 1974; Branch and Pringle, 1987). A major ecological role for the eastern Pacific species *C. californiensis* Dana in sediment turnover and community structure has also been documented (see reviews by Posey, 1986, 1987; Griffis and Chavez, 1988). Ott *et al.* (1976) have particularly shown the potential impact of burrowing thalassinoids on redox potential and nutrient cycling.

The wide distribution of *C. louisianensis* on salt flats and bay bottoms of Aransas Refuge, Texas, and its probable inclusion there in the diet of the whooping crane was noted by Hedgpeth (1950), who first commented on the absence of information on breeding for this common ghost shrimp. Reproductive cycles and growth are poorly documented for thalassinoid crustaceans in general. However, larval life histories (see Heegaard, 1963; Forbes, 1973; Sandifer, 1973; Sankolli and Shenoy, 1975; Rodrigues, 1976, 1979, 1984; Vaugelas *et al.,*

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1986, and works they review) and growth to maturation (works reviewed by Dworschak, 1988) have been described for a few members of the Callianassidae. The present paper addresses the reproductive cycle in *Callianassa louisianensis* and applies techniques described in a companion paper (Lovett and Felder, 1989) in order to analyze relative growth and to estimate size at maturation.

MATERIALS AND METHODS

Collections were restricted to a single population inhabiting the shallow perimeter of a weakly flushed tidal pond on Grand Terre Island, Louisiana. During routine sampling from December 1973 through November 1974, midday to afternoon surface water temperatures at the pond's edge ranged from a winter low of 12°C in December 1973 to a summer high of 39°C in July 1974, and exceeded 30°C on all sampling days from May through September 1974. Collections were made by flushing specimens from substrate with a pump-driven hydraulic jet; animals collected were maintained in individual vials (see Felder, 1978). To ensure that an unbiased sample of the population was obtained on each collecting date, areas previously jetted were avoided on subsequent trips. Observations were also made during collecting trips in summer to fall of 1972 and 1973, and late spring through summer of 1975, 1983, 1984, and 1988. Over 1,200 animals were collected in the course of the study.

Upon return to the laboratory, morphometric measurements and wet weights were determined on live animals immobilized by brief exposure to chilled sea water. Individuals with carapace deformities, missing chelae, or incompletely regenerated chelae were omitted from the sample measured, yielding a total measured sample of 537 for the December 1973 through November 1974 period. Animals were blotted with tissue paper prior to determination of wet weight (WW) on a top-loading balance. Morphometric measurements were made with dial calipers to the nearest 0.1 mm in chela features and to at least the nearest 0.5 mm in both carapace and total length. Carapace length (CL) was measured from the tip of the rostrum to the posterior margin of the cardiac region. Total length (TL) was measured from the tip of the rostrum to the posterior margin of the telson. Chela measurements included chela height (ChH, maximum height of the propodus, ventral margin to dorsal margin) and chela width (ChW, maximum width of propodus from bulbous area on flexor surface to extensor surface). Sex was determined by examination of the anterior pleopods, unless evident by conspicuous presence of ovaries. For females, ovarian width (OW, width of right ovary visible dorsally through the third abdominal segment) was also measured. To provide an index of ovarian development, OW was corrected for carapace length to yield the ratio mm OW/mm CL; as these ratios were normally distributed, means and confidence limits were plotted for untransformed data. Color and general shape of the ovarian mass was also noted.

Regression techniques were as described in a companion paper (Lovett and Felder, 1989). Carapace length was selected as the indicator of body size because it was less dependent on gonadal development than were total length and wet weight and because it was subject to minimal error in measurement. Allometric coefficients (Huxley, 1932) were determined from least squares estimate regression of log-transformed data which were subdivided at the transition point. Transition points at which data sets are subdivided represent optima (to the nearest 0.5 mm) that maximize randomness of combined residuals along regression lines (by reduced major axis with untransformed data) above and below the point (see Lovett and Felder, 1989). The carapace length at sexual maturity in females was also estimated independently for the August 1974 sample by the probit method of Wenner et al. (1974).

RESULTS

While ovaries were narrow and undeveloped in early fall (mean = 0.069 OW/CL for 40 females in September), their width began to increase in December (mean = 0.122 OW/CL for 25 females), increased more conspicuously in January and February, and then continued to increase moderately until egg deposition occurred in the summer (Fig. 1). During summer, well-developed orange ovaries (0.241–0.321 OW/CL) were evident in females just before egg deposition; narrow ovaries (<0.06 OW/CL) typified most ovigerous females just after egg deposition, though several with mature eggs on their pleopods showed evidence (0.071–0.123 OW/CL) that the ovaries were again developing for production of a second clutch. While substantial numbers of ovigerous females occurred in the August sample, additional development of ovaries was not evident, and the abundance of spent females with pale narrow ovaries accounted for the annual minimum in size of ovaries (<0.059 OW/CL).

Ovaries of small immature females (<10.0 mm CL) were less than 0.5 mm OW and pale yellow green in color when first evident through the integument. However, even when first evident as minute yellow strands, they appeared to extend almost the length of the abdomen. In the process of maturation, evident in widening of the ovarian mass, the ovaries became opaque yellow (sometimes yellow brown), then yellow orange, and finally reddish orange just prior to egg deposition. As the ovarian mass increased in size and developed a more intense yellow color, it became more lobate and individual ova became readily identifiable. In most females (>12.0 mm CL) each
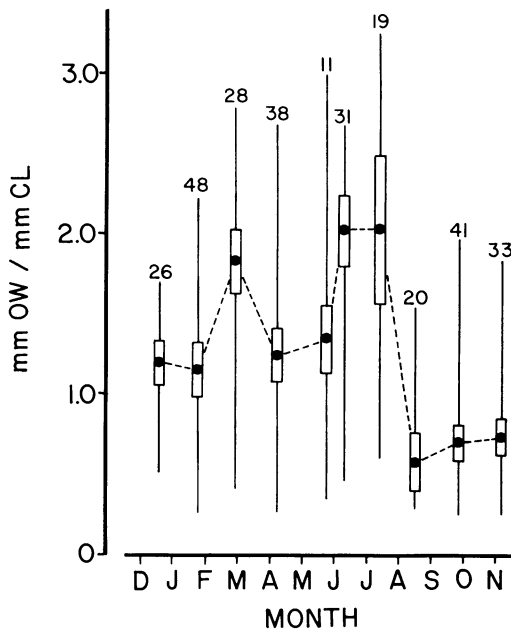
Fig. 1. Relative ovarian development in females of *Callianassa louisianensis* collected from December 1973 through November 1974. OW = width of right ovary in third abdominal segment; CL = carapace length including rostrum; solid dots indicate means; vertical bars define 95% confidence limits and vertical lines define ranges; numbers indicate sample size.
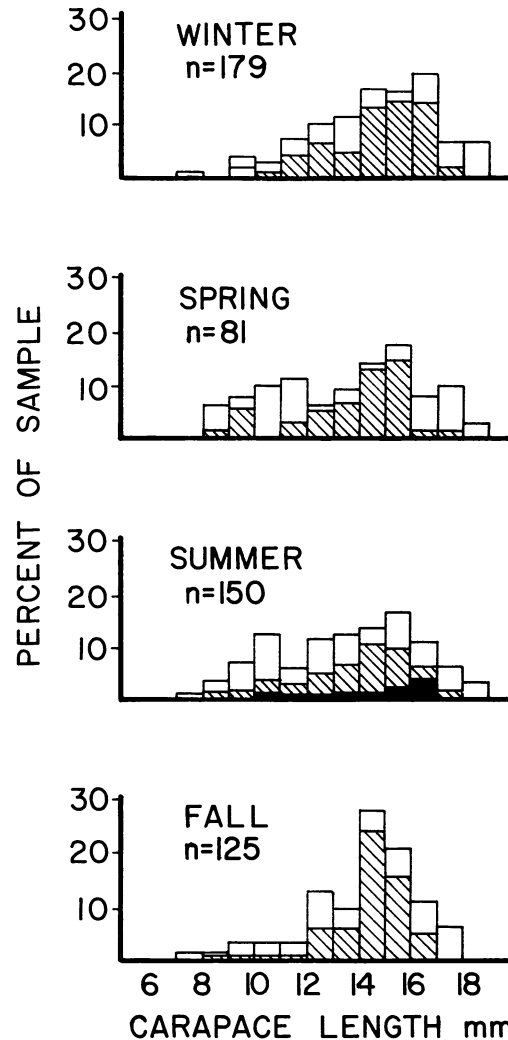

Fig. 2. Seasonal size-class (carapace length) frequency distributions for males (open bars), nonovigerous females (hatched bars), and ovigerous females (solid bars) of *Callianassa louisianensis*. Seasonal samples were taken over the following time periods: winter = 18 December 1973–28 February 1974; spring = 5 April–26 May 1974; summer = 11 June–15 August 1974; fall = 24 September–5 November 1974.

ovary had grown to 4–5 mm OW in the third abdominal segment and become bright orange in color just prior to egg deposition; this condition was observed commonly among females during May, June, and July.

Ovigerous females occurred primarily from early June through late August (Fig. 2), although a few appeared in our samples as early as mid-May (in 1975 and 1984) and a few persisted into late September (in 1973 and 1974). The smallest ovigerous female collected had a carapace length (CL) of 10.7 mm; by comparison, probit analysis of female size in the August 1974 sample indicated that mean minimum size at sexual maturity was 11.2 mm CL. All but one of the ovigerous females exceeded this size in 1974 samples, with the largest being 16.8 mm CL. The highest percentage of ovigerous females for any one size class occurred in the range of 16–16.9 mm CL, wherein about 70% were ovigerous in the summer samples. Neither ovigerous nor nonovigerous females reached carapace lengths equal

to those of the largest males at any point during the annual cycle.

Following egg deposition, the ovarian mass was usually narrow, translucent, and yellow green to yellow brown in color; alternatively, as noted above, there was sometimes evidence of a developing second clutch. During June and July, it was not uncommon to find ovigerous females with intense yellow to bright orange ovaries ex-
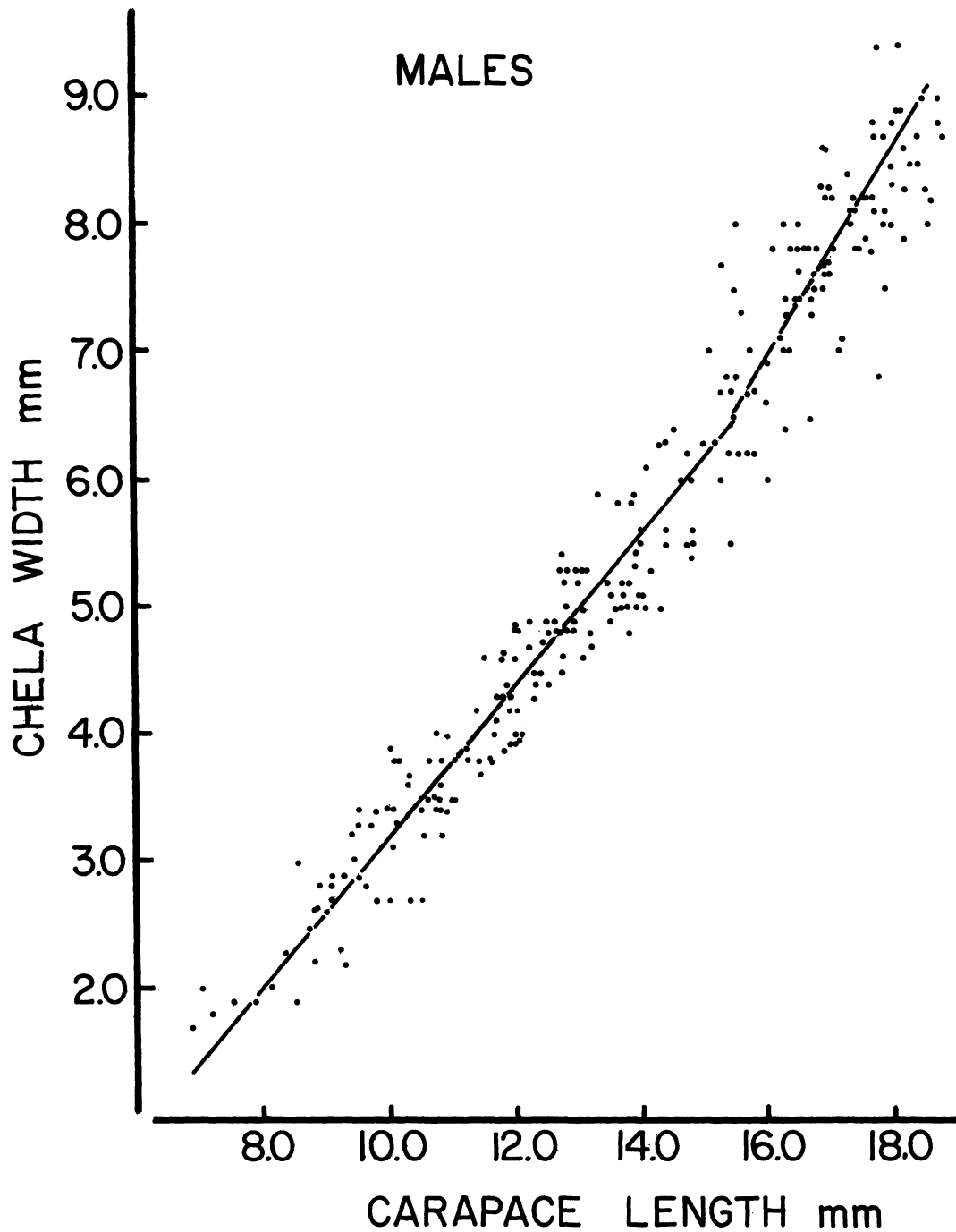
Fig. 3. Regression (by reduced major axis with untransformed data) of chela width on carapace length for males of *Callianassa louisianensis*. Location of transition point at which data set is subdivided was selected to maximize randomness of combined residuals for lines above and below point.

ceeding 3.0 mm OW; these likely accounted for deposition of a subsequent summer egg clutch. However, by late August and September ovigerous females rarely showed evidence of further ovarian development, and almost all had ovaries that were pale yellow brown to yellow green and less than 1.8 mm OW. This condition persisted until

Table 1. Formulae and statistics for linear regressions (by reduced major axis, with untransformed data) of chela width on carapace length (ChW:CL), chela height on carapace length (ChH:CL), and chela width on chela height (ChW:ChH) for males and females of *Callianassa louisianensis*. Regressions were calculated for entire data set (all) and for data set subdivided at transition point (yielding separate regressions for data points < X and data points ≥ X, where X = estimated size at onset of sexual maturity). N = sample size; R^2 = coefficient of determination; 95% CI = confidence interval of slope.

| | | | ChW:CL | | ChH:CL | |
	N	R^2	Formula	95% CI	N	R^2
Males:						
All	251	0.95	ChW = (0.655 × CL) − 3.433	±0.018	251	0.97
< X	161	0.91	ChW = (0.593 × CL) − 2.734	±0.027	161	0.93
≥ X	90	0.54	ChW = (0.826 × CL) − 6.300	±0.120	90	0.65
Females:						
All	286	0.71	ChW = (0.332 × CL) − 0.180	±0.021	286	0.82
< X	21	0.85	ChW = (0.588 × CL) − 2.796	±0.110	21	0.89
≥ X	265	0.46	ChW = (0.288 × CL) − 0.048	±0.026	265	0.65

December when ovaries once again began to become more massive and take on a deeper yellow coloration.

The largest mean size of individuals in the population occurred in the fall and winter months (Fig. 2). However, those samples excluded the most recently recruited cohort, since small postlarval stages were not reliably captured by the methods we employed. With growth of juveniles and apparent mor-
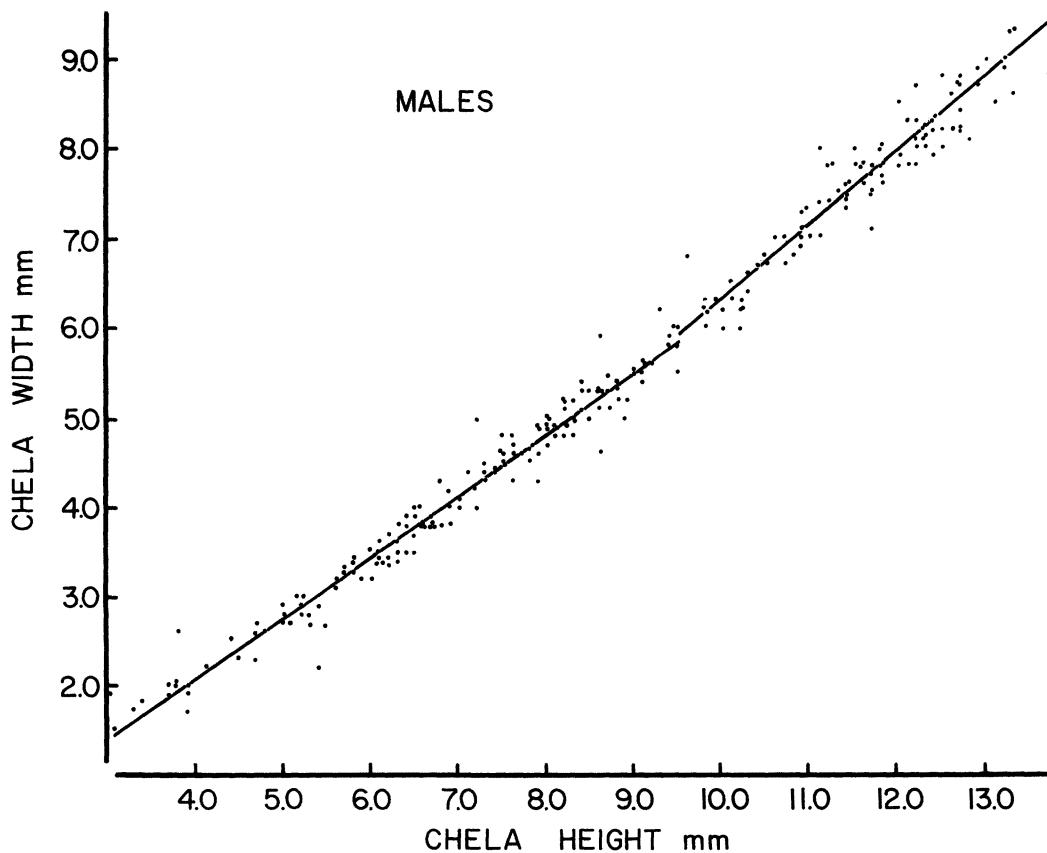

Fig. 4. Regression (by reduced major axis with untransformed data) of chela width on chela height for males of *Callianassa louisianensis*. Location of transition point at which data set is subdivided was selected to maximize randomness of combined residuals for lines above and below point.

Table 1. Continued.

ChH:CL				ChW:ChH	
Formula	95% CI	N	R²	Formula	95% CI
ChH = (0.867 × CL) − 3.036	±0.020	251	0.98	ChW = (0.755 × ChH) − 1.140	±0.012
ChH = (0.824 × CL) − 2.550	±0.033	145	0.96	ChW = (0.697 × ChH) − 0.754	±0.022
ChH = (0.991 × CL) − 5.103	±0.125	106	0.89	ChW = (0.821 × ChH) − 1.872	±0.052
ChH = (0.579 × CL) + 0.101	±0.028	286	0.88	ChW = (0.574 × ChH) − 0.238	±0.023
ChH = (0.844 × CL) − 2.737	±0.136	21	0.96	ChW = (0.697 × ChH) − 0.890	±0.065
ChH = (0.506 × CL) + 1.190	±0.036	265	0.72	ChW = (0.569 × ChH) − 0.200	±0.037

tality in the larger size classes, the population sample became bimodal in the spring, clearly depicting young-of-the-year in the population. By spring, most young-of-the-year reached sizes near 10 mm CL, with males being slightly larger than females. Bimodality was particularly pronounced among males in the spring samples, with the larger mode exceeding a size of 15 mm CL. Most young-of-the-year females in spring samples had developing ovaries (0.092–0.129 OW/CL) and later accounted for the smallest carapace length size classes of ovigerous females in summer population samples. The progressive growth of size classes for both sexes suggests a life cycle in which hatching and recruitment to the burrowed population occur during summer and early fall, maturation is reached in the following spring (perhaps later for males), and reproduction occurs during breeding seasons of up to two following summers; the typical life span thus appears to be from 2–2.5 years.

Maturation was also evident in relative growth of secondary sexual characters such as the major chela. Asymmetry of the chelae was marked in both sexes but was particularly strong in males. Neither sex showed consistent tendency toward right or left handedness in occurrence of the major chela. In males, relative growth rate of the major chela changed abruptly at sizes ≥15.5 mm CL, the approximate optimal transition point (to nearest 0.5 mm) identified by reduced major axis (Fig. 3); beyond this size, increase in both chela height (ChH) and chela width (ChW) occurred more rapidly than did increase in CL (Table 1), yielding strong positive allometric growth (Table 2). Shape of the male chela also changed slightly but significantly over the course of development

(Fig. 4, Tables 1, 2), as growth in ChW became more positively allometric with respect to ChH at chela sizes ≥9.5 mm ChH. From regression of male ChH on male CL, we found this transition point equivalent to 15.3 mm CL, or very near the male growth transition size of 15.5 mm CL estimated above.

The relative growth of the major chela (and the respective allometric growth coefficient) in females did not differ significantly from that of males up to the point of maturation, there being strong positive allometric growth in the chelae of both sexes (Tables 1, 2). However, above an approximate transition point of 11 mm CL (to nearest 0.5 mm) there was pronounced decrease in the relative growth rate of the chela in females (Fig. 5, Table 1), as growth in the chela became negatively allometric when compared to growth in CL (Table 2). The shape of the major chela also changed with maturation in females (Fig. 6, Tables 1, 2), as the growth in ChW became negatively allometric with respect to growth in ChH at chela sizes ≥6.5 mm ChH. From regression of female ChH on female CL, we found this transition point equivalent to 10.7 mm CL; this value is very near the female transition carapace length of 11.0 mm estimated above and is equal to the smallest carapace length at which an ovigerous female was collected in the study.

Where data points for male and female growth are treated as single sets (instead of being subdivided at a transition point), it is not evident that relative growth is very similar between the sexes prior to maturation (Tables 1, 2). Furthermore, where the male and female samples are each characterized by a single regression across all sizes, comparison leads to the erroneous impression

Table 2. Allometric coefficients measured as slopes for linear regressions (by least squares estimate, with log-transformed data) of chela width on carapace length (ChW:CL), chela height on carapace length (ChH:CL), and chela width on chela height (ChW:ChH) for males and females of *Callianassa louisianensis*. Coefficients were determined for entire data set (all) and for data set subdivided at transition point (yielding separate regressions for data points < X and data points ≥ X, where X = estimated size at onset of sexual maturity). Allom. coef. = allometric coefficient, 95% CI = confidence interval of coefficient.

	ChW:CL		ChH:CL		ChW:ChH	
	Allom. coef.	95% CI	Allom. coef.	95% CI	Allom. coef.	95% CI
Males:						
All	1.659**[a]	±0.043	1.362**[d]	±0.031	1.214**[g]	±0.019
< X	1.638**[b]	±0.072	1.356**[e]	±0.054	1.185**	±0.037
≥ X	1.353**[a,b,c]	±0.267	1.165[d,e]	±0.183	1.190**[h]	±0.079
Females:						
All	0.976[a,c]	±0.065	0.958[d,f]	±0.048	1.032[g,h]	±0.038
< X	1.900**[c]	±0.371	1.456**[f]	±0.246	1.309**[i]	±0.109
≥ X	0.612**[a,c]	±0.079	0.701**[e,f]	±0.061	0.882**[g,h,i]	±0.067

** = allometric coefficient significantly ($P < 0.05$) different from 1.0.
a–i = allometric coefficients with same superscript are significantly ($P < 0.05$) different from each other (only selected cases indicated).

that differentiation in the chelae of males and females begins long before maturity. However, when data points are treated as separate sets above and below the hypothesized transition point, there is a significant difference in slopes above and below transition points for all regressions examined. This is true both in analyses of relative chela size (ChH and ChW versus CL) and in analyses of chela shape (ChW versus ChH). Thus, development of sexually dimorphic chelae begins near the putative maturation point in growth, and results in acquisition of a larger and more massive major chela in the mature males than in the mature females.

In addition to having smaller major chelae, mature females also do not attain carapace lengths equal to those in the larger size classes of the male population (Figs. 3, 5). The largest carapace length class (Fig. 2) consisted solely of males and the second largest was dominated by males, even though overall sex ratios of the population were skewed toward females and females strongly dominated size classes from 12–16 mm CL. However, total lengths (TL) of larger mature females with developed ovaries closely approached maximum TL in mature males, especially at peak female gonadal development when the abdomen appeared to be slightly distended by the ovary. This observation suggested that growth in abdominal length, as well as in the major chela, is sexually dimorphic and further justified selection of CL rather than TL as the least variable measure of animal size. Beyond maturation size in females, relative increase in both TL and wet weight (WW) exceeded

that in the prematuration phase of growth (Table 3). However, rate of increase in WW of females at no time reached that of post-maturation males, in which wet weight increased precipitously with growth in the major chela.

DISCUSSION

In many thalassinoids, as well as in penaeoids (see Levi and Vacchi, 1988), the translucent cuticle facilitates macroscopic examination of the ovaries in vivo. Such examinations have been used previously in *Callianassa australiensis* Dana by Hailstone and Stephenson (1961) and in *Callianassa kraussi* by Forbes (1977) to evaluate degree of ovarian development. Developmental changes are evident as changes in color and shape of the ovarian mass. With maturation of ova, the ovaries become more massive and more opaque, while taking on color changes attributable to synthesis of carotinoid pigments (Levi and Vacchi, 1988). These features can be used to document the chronology of ovarian development in *C. louisianensis* and other thalassinoids, regardless of how they may vary between species.

In collections of the callianassids *Callichirus islagrande* (Schmitt) and *C. major* (Say) from Louisiana beach habitats, we observed developmental changes in ovarian shape and color that were somewhat different from those in *Callianassa louisianensis*. The ovarian mass in these species was orange to red (as reported for *Callichirus major* by Pohl, 1946) in color year-round, be-
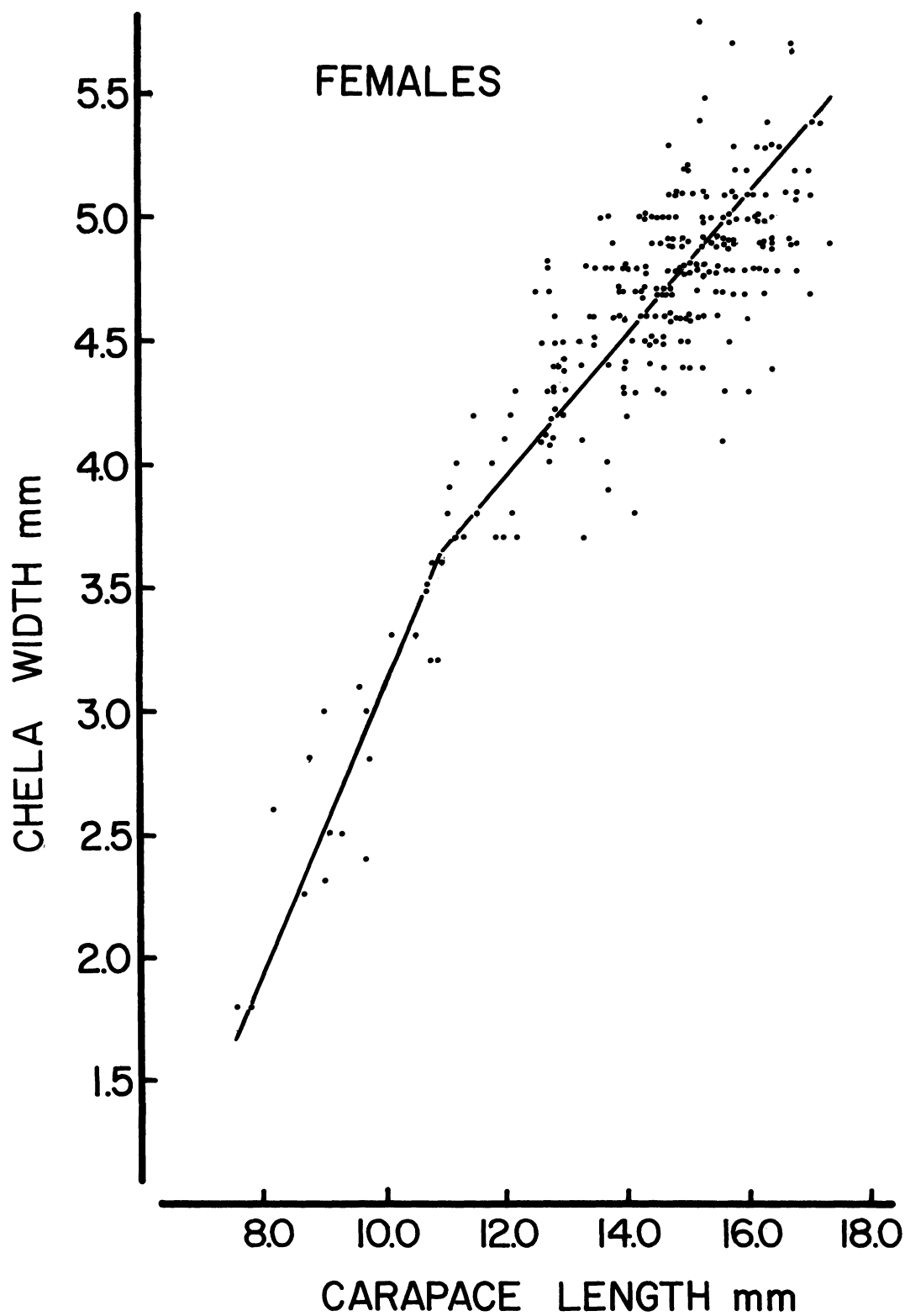
Fig. 5. Regression (by reduced major axis with untransformed data) of chela width on carapace length for females of *Callianassa louisianensis*. Location of transition point at which data set is subdivided was selected to maximize randomness of combined residuals for lines above and below point.
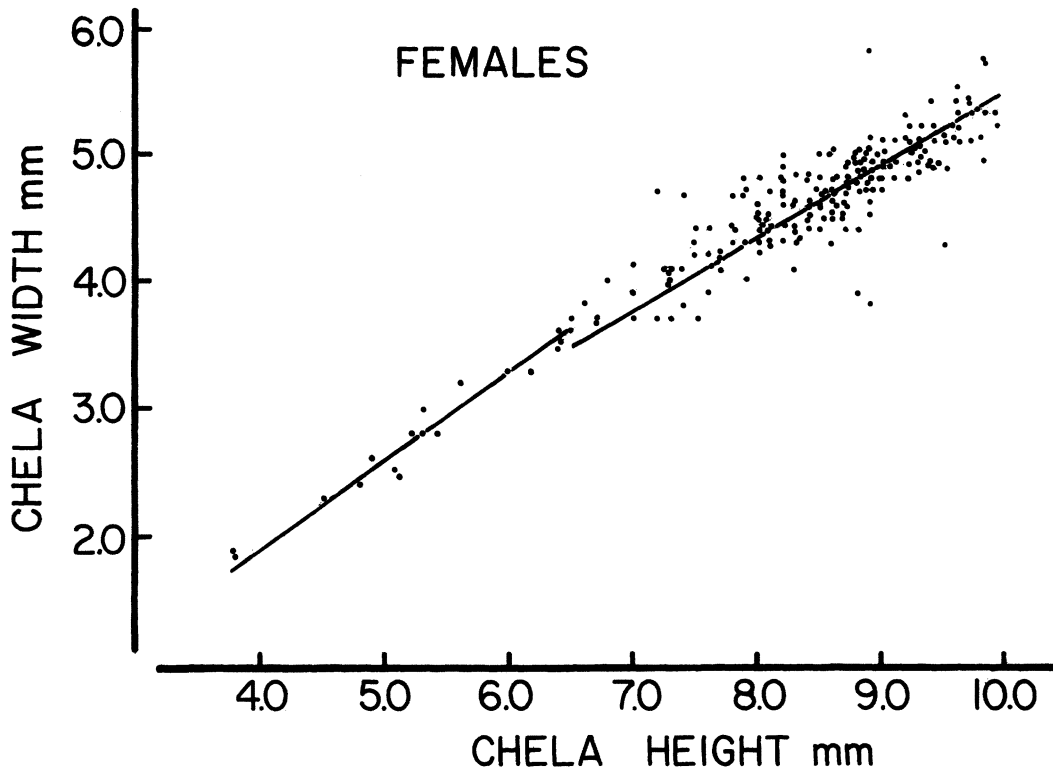
Fig. 6. Regression (by reduced major axis with untransformed data) of chela width on chela height for females of *Callianassa louisianensis*. Location of transition point at which data set is subdivided was selected to maximize randomness of combined residuals for lines above and below point.

coming intense scarlet in the matured ovary just prior to egg deposition in late spring and early summer. The matured ovaries in *Callichirus* were also particularly swollen in the anterior two to three abdominal segments in *Callichirus*, and much less massive in the posterior segments, in most cases barely reaching into the sixth abdominal segment. The anterior two abdominal segments also tended to become particularly elongated and distended by the developing ovarian mass in these species. In *Callianassa louisianensis*, as well as in *Corallianassa longiventris* (A. Milne Edwards) and *Calliax quadracuta* (Biffar) that we have observed in tropical western Atlantic habitats, the ovaries are instead less intensely colored at most if not all stages of their development and are more uniform in width throughout their length, extending well into the sixth abdominal segment.

For females of *Callianassa louisianensis* that mature early in the summer, there is ample time within the breeding season for

more than one clutch, given that eggs appear to be carried by the female for no longer than 25–30 days before hatching (observed during culture experiments in our laboratory; temperature varying from 20–24°C). This is somewhat shorter than the incubation times reported for *C. australiensis* (6 weeks; Hailstone and Stephenson, 1961) and *Callianassa filholi* A. Milne Edwards (5.5 weeks; Devine, 1966), but appears to be near that reported for *C. kraussi* (30 days; Forbes, 1973). Like *C. kraussi*, *C. louisianensis* has large eggs and highly abbreviated larval development (two briefly planktonic zoeal stages; Shipp,1977; Felder *et al.*, 1986). *Glypturus armatus* (A. Milne Edwards) appears to have a minimum incubation period of 18–21 days at 26°C, but the complete larval history remains unknown for that species (Vaugelas *et al.*, 1986).

From winter through spring, ovarian development in *C. louisianensis* progressed steadily in most of the female population. This group included some individuals that

Table 3. Formulae and statistics for linear regressions (by reduced major axis, with untransformed data) of total length on carapace length (TL:CL) and wet weight on carapace length (WW:CL) for males and females of *Callianassa louisianensis*. Regressions were calculated for entire data set (all) and for data set subdivided at transition point (yielding separate regressions for data points < X and data points ≥ X, where X = estimated size at onset of sexual maturity, or 15.5 mm for males, 11.0 mm for females). N = sample size; R^2 = coefficient of determination; 95% CI = confidence interval of slope.

			TL:CL				WW:CL	
	N	R^2	Formula	95% CI	N	R^2	Formula	95% CI
Males:								
All	248	0.96	TL = (4.061 × CL) + 0.082	±0.110	248	0.93	WW = (0.758 × CL) − 6.799	±0.028
< X	160	0.93	TL = (4.220 × CL) − 1.664	±0.199	160	0.91	WW = (0.555 × CL) − 4.499	±0.030
≥ X	88	0.65	TL = (4.031 × CL) + 0.349	±0.589	88	0.76	WW = (1.141 × CL) − 13.134	±0.138
Females:								
All	285	0.93	TL = (4.502 × CL) − 3.799	±0.162	285	0.92	WW = (0.606 × CL) − 5.233	±0.023
< X	21	0.88	TL = (3.973 × CL) + 1.486	±0.772	21	0.91	WW = (0.310 × CL) − 2.053	±0.052
≥ X	264	0.87	TL = (4.550 × CL) − 4.513	±0.231	264	0.89	WW = (0.670 × CL) − 6.194	±0.031

were slightly less than the 10.7–11.0 mm CL thought to represent size at maturity. Thus, while either the smallest observed size at first egg deposition or the size at the transition point in growth of secondary sex characters may be identified as the "maturation" size, internal development of the first egg mass and perhaps even mating may slightly precede the putative minimum size of female "maturation." The puberty molt in decapods need not coincide with maturation of the gonads (Hartnoll, 1982); in males of some species "precocious sexual maturity" in males may even include mating prior to the puberty molt (Charniaux-Cotton, 1965). In the present case, females with "maturing" ovaries were never less than 10.2 mm CL, and were probably within one molt of "mature size" as defined by morphometry. It also appeared that both young-of-the year and second-year females deposited eggs during a single prolonged summer breeding period. There was no evidence of widely separated major and minor breeding peaks as described for *C. australiensis* by Hailstone and Stephenson (1961) or *C. kraussi* by Forbes (1977).

While Chaud (1984) has observed mating in *Upogebia,* the location, timing, and frequency of mating remain unknown for *C. louisianensis* and all other callianassid species. Because these animals are rarely observed outside the burrows, where they appear to be vulnerable to predation, we and others (Pohl, 1946; Rodrigues, 1976) suggest that mating occurs in intersecting burrows, as in *Upogebia.* However, evidence of the requisite shared burrow system in natural populations is lacking, except in populations of *C. filholi* observed by Devine (1966). To date we have observed neither pairing nor mating between burrowed animals in laboratory fossaria. Rather, we have observed aggressive interactions, as reported for other thalassinoids (MacGinitie, 1934; Pearse, 1945; Rodrigues, 1976; Buchanan, 1963; Tunberg, 1986), whenever animals of the same or opposite sex encounter one another in intersected burrows. Such interactions involve combative use of the major cheliped, and could play a role in both territorial defense and mating behavior. They may also result in regulation of population densities, as has been proposed to occur in populations of *Upogebia* (Tunberg, 1986).

Displacement of immature recruits or other factors could induce migrations such as those postulated for populations of *Callianassa australiensis* by Hailstone and Stephenson (1961); migration by specific size classes or predominantly females in this species was suggested to account for observed differences in population structure and sex ratios between sampling areas. For the present study of *C. louisianensis*, structured sampling was (by design) restricted to characterization of a single, well-established intertidal population without attempt to compare population structures between adjacent sampling areas. The sex ratio was skewed in this population with females dominating the overall sample, but especially dominating size classes >12 mm CL and <16 mm CL. However, we suggest that neither the observed sex ratio nor the observed population structure represent conditions in all adjacent populations. Variations in population structure, as reported for populations of *Callianassa* and *Upogebia* in South Africa (Hanekom and Erasmus, 1988), should be expected between alternative physical settings and are apparent in our errant collecting from assorted sites along the Louisiana coast. In an extreme example, adults in several sites west of our study area were largely eliminated by major sand displacements during a late-summer hurricane, and those sites were thereafter populated almost exclusively by small juveniles during the fall. As size and age structure in our established study area suggests a life-span of about 2–2.5 years, at least that amount of time would be required for a newly established or perturbated population to attain a mature structure of size classes and sex ratios.

Large numbers of small (apparently juvenile) *C. louisianensis* of both sexes have been observed recently in midwater plankton samples during late spring equatorial slack tides in lower Mobile Bay, Alabama (personal communication, T. Matthews, Dauphin Island Sea Lab, Alabama). While this phenomenon could result from physical erosion of burrows by tides or predators, or could represent active swarming for precocious breeding, we suggest that it instead represents some redistribution of juveniles as is thought to take place in *C. australiensis* and other species. Forbes (1978) has reported such a phenomenon in populations of *C. kraussi,* a species in which larval life history is very abbreviated (nonplanktonic) and dispersal is deferred to the later postlarvae. In both *C. kraussi* and *C. louisianensis,* tolerance of low salinity improves with development (Forbes, 1978; Felder, 1978; Felder et al., 1986) and stages following the brief larval period are better equipped to tolerate salinity fluctuations experienced in estuarine migrations. Migration is also well documented for *C. turnerana* White, which periodically moves up rivers in west Africa (Monod, 1927).

The sexual dimorphism observed in the major chela of mature *C. louisianensis* (a more massive chela in mature males than in mature females) may reflect sexual specificity for combative behavior (perhaps including competition for females). In dense subterranean aggregations of this and other species, heavy chelipeds and aggressive behavior of males could maximize access to burrows of adjacent females, prevent encroachment by burrowing of other males, and contribute to "neighbourhood stability" (see Buchanan, 1963; Tunberg, 1986). Where combative interactions result in mortalities or displacements of vanquished males, they could contribute to the skewed sex ratios observed in populations of *C. louisianensis* and other species. While we have made no direct observations to support these hypotheses, we did note that damaged chelae on males were particularly common in samples taken from January through April. It remains to be seen whether these injuries result from combative interactions during a winter-spring mating period, competition related to growth and increased density of burrows from first-year recruits, or other factors.

The sexual dimorphism in chelae of mature thalassinoids has led investigators to evaluate relative growth in this feature as an indicator of maturation in *Callianassa* (see Hailstone and Stephenson, 1961; Devine, 1966), *Callichirus* (see Rodrigues, 1985), and *Upogebia* (see Tucker, 1930; Dworschak, 1988). Presentation and analysis of data sets in these studies has varied, with some investigators characterizing overall growth with single regression lines for each sex and others subdividing growth for each sex into two or three developmental

phases. However, it is usually evident that relative growth of the major chela in both sexes is very similar up to a distinct transition point identified as a minimum carapace length or total length. Beyond this transition point, growth of the male major chela is usually positively allometric and growth of the female major chela is near isometric or negatively allometric. Where growth of the minor chela has been examined (Rodrigues, 1985), there is no evidence of sexual dimorphism or transition in its relative growth.

Largely from studies of the Brachyura, it appears that relative growth tends to be isometric in an early undifferentiated phase. Subsequent growth of sexually dimorphic features in males often becomes more positively allometric following a prepuberty molt, with male chela growth increasing abruptly after a puberty molt. Relative growth in females tends to remain more nearly isometric in all phases (Hartnoll, 1982). In the present study, we did not effectively sample small, undifferentiated postlarval stages. In our collections, differences in the anteriormost pleopods (subtle in the smallest individuals) allowed us to sex all individuals of our sample. In the primary dimorphism that we examined (major chelae), we did not distinguish an undifferentiated phase from a prepuberty (juvenile) phase. However, rates of relative growth were very similar between males and females at sizes <10.0 mm CL. Although growth in that phase was not isometric, it was nearer isometry than it was at larger sizes. We also did not recognize a precise size as the "puberty molt." Rather, growth transition points were positioned to the nearest 0.5 mm CL so as to minimize total error about independent regression lines for the sample above and below these points. The transition sizes of 15.5 mm CL in males and 11.0 mm CL in females thus represent rounded estimates of the mean size for each sex at maturity. However, in most regressions the remaining variability is highest adjacent to the optimized transition points. This suggests that the "puberty molt" actually takes place over a short range of sizes.

In females of *Callianassa australiensis*, pronounced increase in length of the body occurred without an increase in the chela depth. This suggested a critical molt in the life cycle (Hailstone and Stephenson, 1961). However, in the present study and other instances, increase in TL may result without molting as growth of the ovarian egg mass distends the female abdomen. While molting occurs periodically in at least early phases of the ovary's maturation (see Hailstone and Stephenson, 1961; Forbes, 1977), most growth of the ovarian mass is an intermolt phenomenon. Given the elasticity of the poorly calcified abdomen, some change in shape or weight of the abdomen might well occur without molting. Regardless of the relationship to molting, it is clearly evident that growth in the maturing female is not vested in the major chela, as it is in males. Rather, substantial growth is vested in egg production. This may be measured as increases in total length, abdominal length or wet weight, without a significant change in carapace length. This appears to reflect a general pattern of development in thalassinoids examined to date, and has been concluded in various terms by other investigators (Tucker, 1930; Hailstone and Stephenson, 1961; Dworschak, 1988).

In males, by contrast, growth of the major chela is enhanced with maturity, though it is not simply an increase in size as some passive result of less demand for gonadal development. As males of *C. louisianensis* and other thalassinoids (Rodrigues, 1985; Dworschak, 1988) reach maturation, changes commence in both relative size and shape of the chela, often yielding a striking sexually dimorphic feature of probable advantage in competitive interactions. Increase in the chela mass of postmaturation males largely accounts for weight increases that exceed even those of maturing, ovary-laden females. The degree to which the male chela has become developed as a sexual dimorphism likely correlates to the degree of sexual specialization in behavior patterns, as has been noted among other decapods (Hartnoll, 1982).

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