Abstract.–Growth and sexual maturation were studied in the ghost shrimp *Lepidophthalmus sinuensis*, a pest species infesting oligohaline penaeid shrimp culture ponds on the Caribbean coast of Colombia. Sex ratio was significantly female-biased over four years of sampling. Development of ovaries, indexed as relative width, peaked prior to peak occurrence of ovigerous females and either coincided with or immediately followed the quarter of lowest ambient salinity. Ovigerous females occurred in all months, but the greatest mean percentage occurred in the first or second quarter of each year. Size and coloration of ovaries varied by maturational stage, and monthly counts of eggs per female peaked in February–April. Detection of recruits <8–10 mm carapace length (CL) was sporadic, and tracking of growth in recruitment cohorts was not possible. Mean CL of the population increased slowly over the first two years of sampling, as the percentage of males in the population increased. Sexual maturity in both males and females was evident in relative growth changes of the major chela. Analysis of growth in chela width, scaled to carapace length, suggested that males mature at about 11.0–11.3 mm CL, whereas females mature near 10.8–11.2 mm CL. Prematuration positive allometric growth did not differ between sexes, whereas postmaturation negative allometric growth in females differed significantly from strongly positive allometric growth in postmaturation males. Relative growth in wet weight of postmaturation males significantly exceeded that of postmaturation females. Expected female weight accumulations from episodic ovarian development were perhaps offset by simultaneous negative postmaturation growth of the female major chela. An understanding of growth, maturation, and the reproductive cycle of this shrimp species will help develop management strategies to control infestations by this callianassid pest species.

Growth and maturation of the ghost shrimp *Lepidophthalmus sinuensis* Lemaitre and Rodrigues, 1991 (Crustacea, Decapoda, Callianassidae), a burrowing pest in penaeid shrimp culture ponds*

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In northern South America, the ghost shrimp *Lepidophthalmus sinuensis* Lemaitre and Rodrigues has been found restricted to oligohaline estuaries on the Caribbean coast of Colombia (Lemaitre and Rodrigues, 1991). From previous study of a congeneric species, osmoregulatory capacity and tolerance of hypoxia in this genus (Felder, 1978, 1979; Felder et al., 1986) appear to exceed abilities reported in most other callianassid genera (Thompson and Pritchard, 1969; Forbes, 1974, 1978; Mukai and Koike, 1984; Posey, 1987). Such adaptation has allowed members of the genus to exploit extensively low salinity habitats, especially richly organic silty bars and banks of lower river mouths or intertidal mudflats (Felder and Manning, 1997). In *L. sinuensis* and some eastern Pacific congeners (Nates and Felder, 1998), this adaptation also includes sediments of tropical, estuarine ponds in which penaeid shrimp are cultured.

Dense accumulations of ghost shrimp in these penaeid culture ponds are favored by their abbreviated larval development (Nates et al., 1997). At high levels of infestation by these burrowers, metabolic impacts and bioturbation appear to decrease penaeid shrimp production by reducing survival rates of post-larvae and slowing growth to marketable size (Nates and Felder, 1998). A thorough understanding of maturation and reproductive cycles in *L. sinuensis* is essential to devising effective long-term control measures for such infestations, especially to limit or replace the pesticide treatments that have been used to date (Nates and Felder, 1998). Thus far, timing and frequency of pesticide applications in shrimp mariculture have been devised by trial and error effects on penaeid production, without specific attempts to target treatments to peaks in reproductive activity of ghost shrimp or to achieve control by modifications in water management.

Although some species of the Callianassidae burrow to depths of 2 m or more (Pohl, 1946; Poore and Suchanek, 1988; Manning and Felder, 1991; Felder and Griffis, 1994), the difficulty of monitoring many natural populations has been overcome by collecting them with yabby pumps (see Manning, 1975). Several aspects of population biology for varied genera are now well documented (Pohl, 1946; Hailstone and Stephenson, 1961; Phillips,

1971; Poore and Suchanek, 1988; Witbaard and Duineveld, 1989; Tamaki and Ingole, 1993; Rowden and Jones, 1994, 1995; Dumbauld et al., 1996), and the importance of callianassids in sediment turnover and nutrient cycling has been noted (Rowden and Jones, 1993; Ziebis et al., 1996). Ecological impacts of *Lepidophthalmus* spp. can dominate those of other estuarine infauna, as noted in recent studies of the warm-temperate species *L. louisianensis* in the northern Gulf of Mexico (Felder and Lovett, 1989; Felder and Griffis, 1994) and the tropical species *L. sinuensis* on the Caribbean coast of Colombia (Nates and Felder, 1998). Larval life histories for both *L. louisianensis* and *L. sinuensis* have been described (Nates et al., 1997), but later life stages and maturation remain little known for the tropical species *L. sinuensis.* Objectives of the present study were to analyze the periodicity and frequency of reproductive activity, to determine rates of growth in morphological features, and to define allometric indicators of maturation for populations of *L. sinuensis.* Resulting implications for management of penaeid shrimp ponds are discussed.

Materials and methods

All animals were obtained at the Agrosoledad S.A. shrimp farm on the upper Cispata estuary of the Río Sinú, Departamento de Cordoba, Colombia, near 9°17'N, 75°50'W. In order to avoid overt effects of pond harvesting, feeding, and other management activity, collections were restricted to bottom sediments of earthen drainage canals that extend for several kilometers through the farm. Specimens were individually extracted from burrows with yabby pumps (Manning, 1975), and samples included all animals retained when extracted sediments were washed on coarse (5-mm) sieves. All population samples were taken within 500 m of the upper end (origin) of the drainage canal system where colonized bottom muds ranged from about 3 to 6 m in width and population density ranged from 15 to 40 animals per m^2.

Monthly sampling of populations extended over four years from December 1991 through December 1995. Each monthly sample consisted of animals obtained from burrow openings encountered at random during walks along transects that crossed exposed mudflats at the sampling site during a period of reduced pond discharge. The sample consisted of at least 60 animals, and over 3200 animals were collected in the course of the study. Following collection, animals were transported in individual perforated vials (Felder, 1978) to the farm laboratory for morphological analysis. Specimens lacking chelipeds,

having incompletely regenerated chelae, or with other obvious appendage deformities were excluded from the analyses that involved measures of those appendages but included in analyses of population size-class structure. In the laboratory, each individual was sexed on the basis of anterior pleopod morphological features and evidence of ovaries visible through the integument. Wet weight (WW) was determined to ±0.1 g on a top-loading balance after animals were blotted with tissue paper. Dry weight was estimated by drying the animals at 60°C for 48 h, and ash content was estimated from weight after ignition at 500°C for 6 h. When present, eggs on pleopods were included in weights of ovigerous females.

Morphometric measurements (Felder and Lovett, 1989) were made with dial calipers to ±0.05 mm. Because carapace length (CL) is usually less dependent on gonadal development than are most other size measurements (Hartnoll, 1982; Felder and Lovett, 1989), it was selected to represent body size and 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 extended telson. Major chela height (ChH) was measured as the maximum height of the propodus, inferior margin to superior margin. Major chela width (ChW) was measured as the maximum width of the propodus from the most convex area on the internal surface to the opposite convex area on the external surface. Major chela length (ChL) was measured as the maximum length from the superior proximal articulation of the propodus with the carpus to the superior distal articulation with the dactylus. Between November 1992 and December 1995, ovarian width (OW) of females (the width of the right ovary visible dorsally through the integument of the third abdominal segment) was determined. An index of relative ovarian development was estimated from the ratio OW/CL. Color and number of eggs, color of the ovaries, evidence of parasites, and occurrence of damaged or missing chelae were also recorded. Egg size was measured under a light microscope and ocular micrometer. Volume of the eggs was calculated from the mean of the long and short axes used as the single diameter measurement for a sphere (McEdward and Chia, 1991).

Temperature and salinity were measured twice daily (dawn and dusk) at the surface and bottom of filled ponds. Temperature was measured ±1 °C with the probe of a YSI® model 57 temperature-compensated oxygen meter. Salinity ±1 ppt was measured with a temperature-compensated refractometer.

All means were reported along with the 95% CI (confidence interval). Monthly population samples were pooled to compare quarterly variations in the

distribution of size cohorts and the occurrence of ovigerous females in the population. Temporal trends in both carapace lengths and sex ratios for the overall four-year span of the study were analyzed by linear-linear piecewise polynomial regression to define slope transition points. Percentile data for the sex ratios were arcsine-transformed prior to these analyses. In order to remove effects of morphologically anomalous postreproductive and senescent individuals, animals >18.0mm CL (two females and three males) were excluded from analyses of relative growth. Linear-linear piecewise polynomial analysis of untransformed data was used to optimize positioning of ontogenetic transition points (±0.05 mm) in all relative growth comparisons. Except for this alternative method of iteratively locating slope transitions, methods complied with the recommended practice of fitting regressions to untransformed data above and below transition points by reduced major axis (Lovett and Felder, 1989). Standard allometric coefficients (Huxley, 1932) were also determined from regressions of log-transformed data by least squares estimate, with data subdivided at the previously estimated transition points. All statistical analyses were performed with NCSS® (Number Cruncher Statistical System) 6.0 software (Hintz, 1995).

Because generic revisions have yet to address many of the confamilial taxa that are treated in our comparative discussions, it was necessary in comparative discussions to refer to some species under *Callianassa sensu lato* (s.l.), while acknowledging that *Callianassa sensu stricto* has been restricted to a few eastern Atlantic populations (see Manning and Felder, 1991).

Results

Sex ratio

Except for January to June 1992, March 1993, and February 1995, sex ratios were significantly female-biased over the four years of sampling (Fig. 1A). Over the entire study period, the mean sex ratio was 2.4 ±0.3 females per male, with the lowest mean ratio (1.1) occurring in February 1992, and the highest ratio (5.1) in October 1993. Trends in mean CL of the population (Fig. 1B) generally tracked those in sex ratios, as defined by piecewise regression analysis. Slopes over the first two years revealed declining relative abundance and increasing mean CL of males, patterns that differed significantly from those of the last two years of monitoring. An iteratively optimized transition point for sex ratios occurred at 23 months, whereafter mean sex ratios remained

near asymptotic. Analysis over the full study period also defined an optimized transition point or peak in CL of males at 23 months, beyond which male CL was asymptotic. The CL of females, however, peaked late in the first year of monitoring.

Mean size of both males and females increased slightly but significantly from the first through fourth quarter of each year except for 1994, a year in which the presence of first quarter recruits was offset by a cohort of large individuals surviving from the previous year (Fig. 2). When treated separately, mature-sized individuals (>11 mm CL) of both male and female populations increased in mean CL over the year, usually peaking in the fourth quarter prior to maximum abundance of ovigerous females in the following year (Fig. 3, B and D). Mean CL of males appeared to exceed slightly that of females over the full study period, and males dominated large size classes (Figs. 1B, 2, 3B). Only 4.3% of the collected females were >15.0 mm CL, whereas 12.4% of males attained this size. The largest animal collected was a 20.7-mm-CL male. Detection of recruits <8–10 mm CL was sporadic throughout the study (Fig. 3E), and tracking of growth in recruitment cohorts was not possible.

Ovigerous females

Among all ovigerous females collected during the study (*n*=444), size ranged from 7.04 mm CL to 16.8 mm CL. However, 38.3% of all these were in the 13.0 to 13.9 mm CL size class and <1.5% of ovigerous females were <11.0 mm CL (Fig. 4). The single ovigerous specimen <9.8 mm CL was an apparently precocious individual taken in August 1994, while the population of ovigerous females was low (Fig. 3D). During peak abundances of ovigerous females (February to June, Fig. 5B), 64.3% of females in the 13.0 to 13.9 mm CL size class were ovigerous (Fig. 2).

Ovigerous females were found in all months of the four-year study (Figs. 2 and 3D). However, percentages were lowest in the third quarters of 1992, 1993, and 1995, and the fourth quarter of 1994, whereas the highest percentages occurred in the first or second quarter of each year. Peak abundance of ovigerous females coincided with the highest quarterly salinity in 1992, 1994, and 1995 but was less defined in 1993 when the fourth quarter salinity did not fall to a typical low value (Fig. 3, A and D). When monthly samples were pooled over the entire study, highest percentages of ovigerous individuals among all females were evident during the high salinity period from February to June; a maximum was found in May (35.7%), three months after peak development of the ovaries (Fig. 5, A–C).
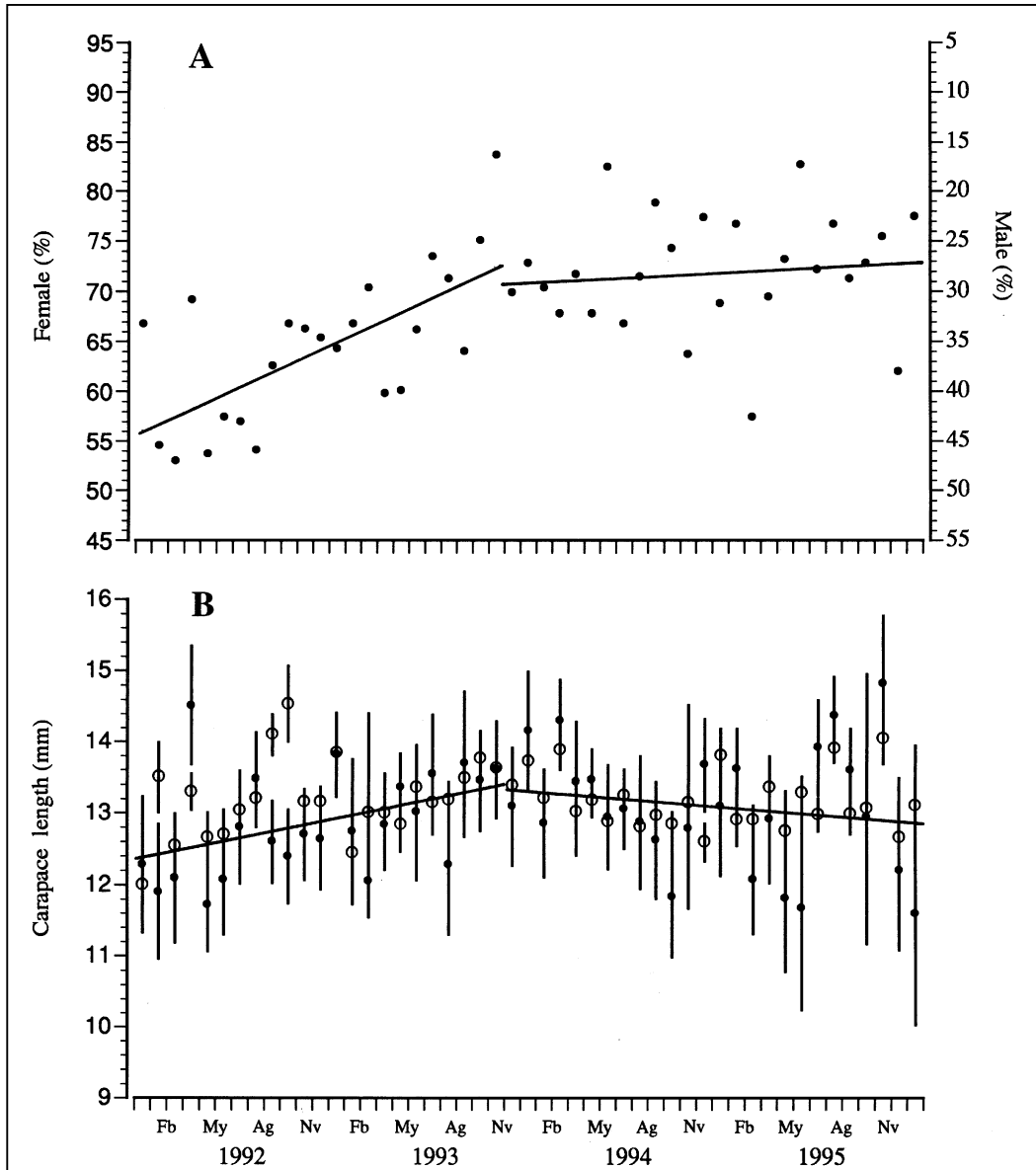
Figure 1

Sex composition (**A**) and mean carapace length (CL) (**B**) in sampled Colombian populations of *Lepidophthalmus sinuensis*, December 1991 through December 1995. Mean CL is shown separately for males (closed circles) and females (open circles); vertical lines define 95% CI. The transition point at which data are subdivided, estimated by piecewise linear-linear polynomial regression, was selected to minimize the sum of squares of residuals.

Development of ovaries reached maxima in the quarter prior to peak occurrences of ovigerous females and either coincided with or immediately followed the quarter in which lowest ambient salinities occurred (Fig. 3, A, C, and D). Examined as a monthly value pooled over the three years that it was monitored (Fig. 5C), this index of ovarian development was at minimum values in June and July when ovaries of many spent and immature females, al-

though evident for the full length of the abdomen, were limited in width to narrow translucent-yellow strands. Ovaries became deep yellow to yellow-orange as relative ovarian width began to increase markedly in August, concurrent with an annual decline in ambient salinity. By October, ovaries of most mature females were somewhat lobate in shape and yellow-orange to reddish orange in color, and ovarian index reached high values that persisted through
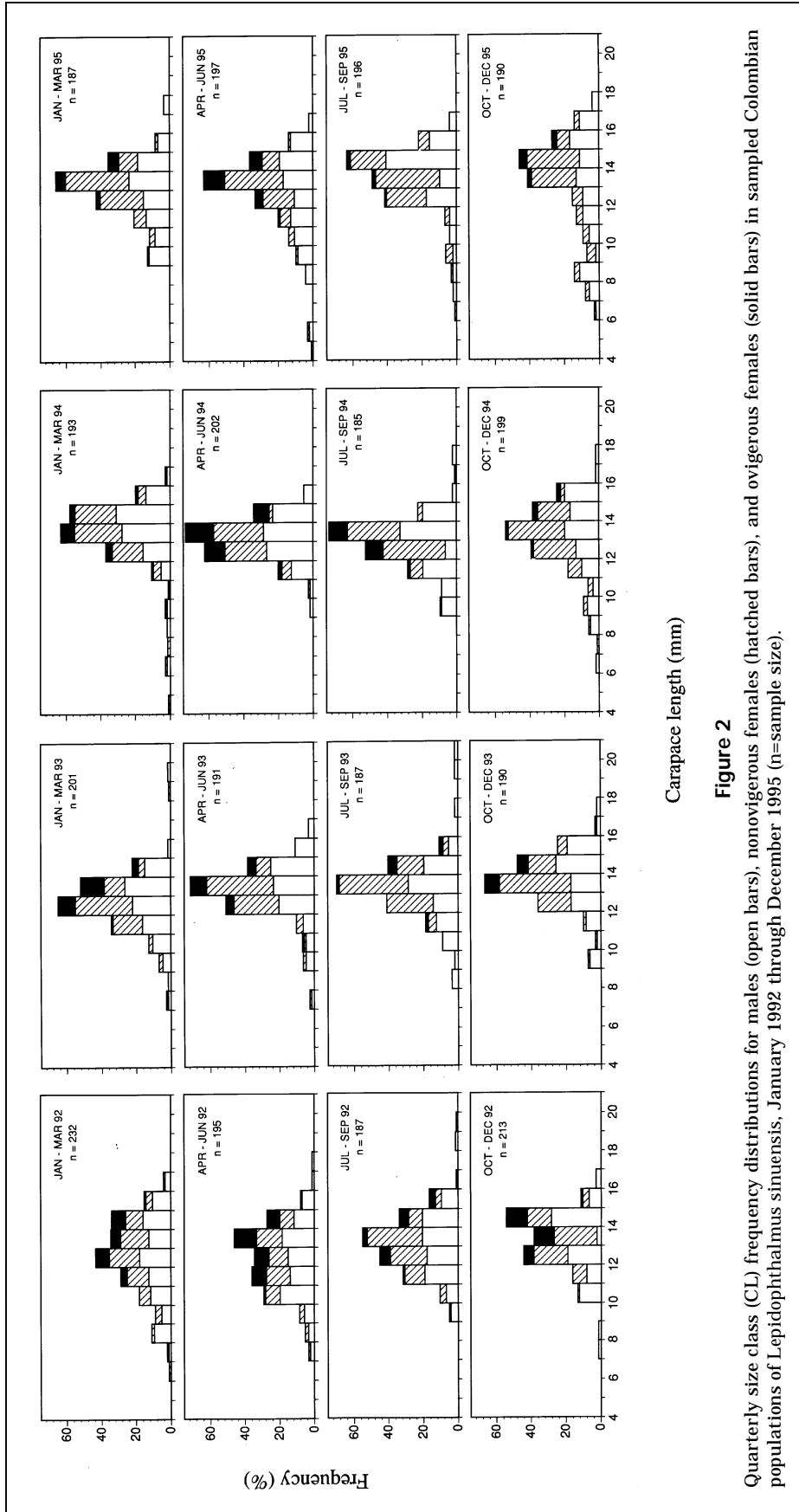
Figure 2

Quarterly size class (CL) frequency distributions for males (open bars), nonovigerous females (hatched bars), and ovigerous females (solid bars) in sampled Colombian populations of Lepidophthalmus sinuensis, January 1992 through December 1995 (n=sample size).

February. Highest values for the ovarian index, in February (0.139 ±0.012), were significantly greater than were preceding values in December or those that followed in March through May. Decreasing measures of relative ovarian width during April through June (Figs. 3C and 5C) were coincident with the second quarter maxima in abundance of ovigerous females (Fig. 3D and 5B) because many of those females had spent ovaries.

Shape of the eggs was almost spherical in recently deposited pale yellow to yellow-orange clutches and became more oblong as color faded to translucent gray-brown in late-stage eggs just prior to hatching. Mean egg volume in live late stage eggs was 0.81 ± 0.07 mm^3 (n=76 eggs, from 5 different females), and the coefficient of variation in volume within a single egg clutch was 5.09% (n=30); mean dimensions were 1.22 ± 0.04 mm by 1.05 ± 0.02 mm. The total number of eggs per female ranged from 182 ± 44 in small females (<12.0 mm CL; n=30) to 301 ± 36 in large females ($\leq$14.0 mm CL; n=141). The overall mean number of eggs for all ovigerous females collected was 251 ± 18 (n=444), and the maximum number found on any single female was 958 on a specimen of 14.2 mm CL. Monthly egg counts per ovigerous female, pooled over the study (Fig. 5D), revealed peak abundances in February–April, followed by significantly lower numbers in June–July. Thus, the overall rate of egg production, when considered as a product of both abundance of ovigerous females and egg

abundance per clutch (Fig. 5, B and D), was maintained at particularly elevated levels from February through at least April and perhaps May.

Growth and sexual maturation

Size at sexual maturation in both males and females of the sampled population was evident in relative growth changes of the major chela. Asymmetry of the first pereopodal chelae was clearly evident in both sexes and did not show bias for right or left handedness in random subsamples (left:right handedness 23:27 for males, 25:25 for females; n=50 per sex). The value of this feature as a secondary sex character was suggested initially by the much heavier general appearance of the appendage in large males than in females of approximately the same size, and sexual differences in allometric growth were documented subsequently by regression analyses of morphological measurements (Fig. 6; Tables 1 and 2).

Relative growth rate in the chela width of males increased in animals that had reached a mean carapace length of at least 11.3 mm, as estimated by linear-linear piecewise polynomial regression analysis (Fig. 6A). Independent regression analysis of males larger and smaller than this size by reduced major axis revealed significant differences in slopes for those data sets (Table 1), even though the two values for this positive allometric growth did not differ significantly when compared as allometric coefficients (Table 2). When fitted by reduced major axis, regression slopes for both prematuration and postmaturation phases of growth in female chela width (Fig. 6B) differed significantly from those for both growth phases in males, although there was far greater difference between the sexes in the postmaturation phase. Relative growth in the chela width of females
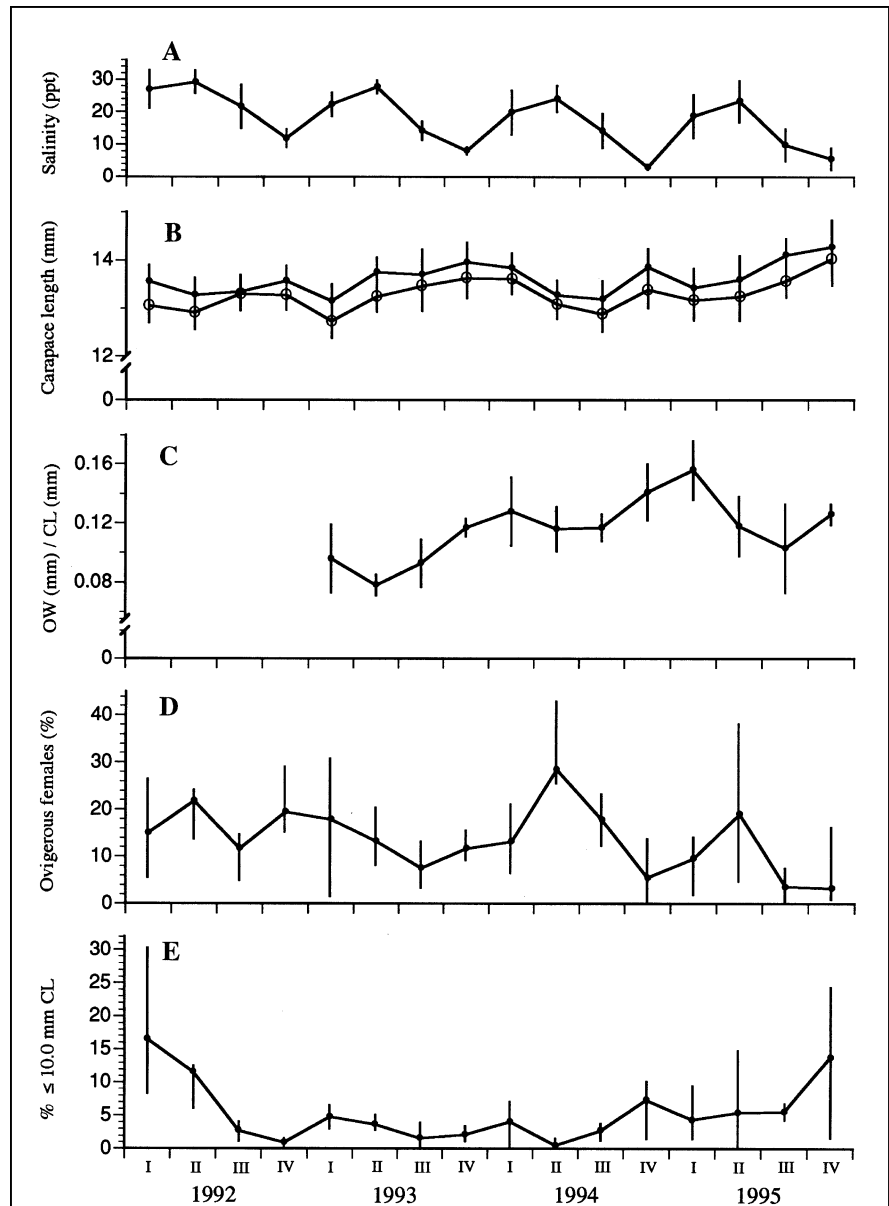

Figure 3

Quarterly measures of salinity, growth, and reproductive indices in sampled Colombian populations of *Lepidophthalmus sinuensis*, January 1992 through December 1995; for A–C, vertical lines define 95% CI; for D–E, vertical lines define range. (**A**) Morning surface salinity (ppt) at the farm intake pump station in the upper estuary, expressed as mean of daily measures throughout each quarter; (**B**) mean CL of mature (>11 mm CL) males (closed circles) and females (open circles) in sampled populations; (**C**) relative ovarian development (OW/CL); (**D**) percentage of ovigerous individuals among females; (**E**) percentage of juveniles (≤10.00 mm CL).

became significantly less positive beyond a carapace length near 10.8 mm. The negative allometric growth (coefficient <1) for this postmaturation phase in females (Table 2) differed significantly from the strongly positive allometric growth in postmaturation males.

Analysis of relative growth in major chela height for males (Fig. 6C) and females (Fig. 6D), when scaled to carapace length, produced remarkably similar results to that for relative growth in chela width, suggesting some interdependency of those measures. Transition points were optimally located at a mean carapace length of 11.0 mm for males and 11.2 mm for females, and postmaturation growth differed significantly between the sexes (Table 1). On the basis of allometric coefficients (Table 2), positive prematuration allometric growth once again did not differ between the sexes, whereas negative postmaturation growth in females differed significantly from the strongly positive allometric growth in postmaturation males. Analysis of chela width scaled to chela height in both sexes did not indicate significant prematuration differences between males and females, and growth in both sexes was isometric or nearly so (Tables 1 and 2). However, following transition to the postmaturation phase in males, relative growth in chela width exceeded that of height. The opposite effect was seen in postmaturation females; negative allometric growth was seen in chela width, when compared to chela height.

Analysis of total length scaled to carapace length revealed large measures of error (Tables 1 and 2), as expected in size measurements that include the length of a soft, stretchable abdomen. Allometric coefficients indicated that slopes did not significantly differentiate prematuration growth from an isometric pattern in either sex, whereas postmaturation growth on the basis of this parameter appeared to be negatively allometric but similar in rate for both males and females.

Large measures of error associated with wet weight measurements in relation to carapace length, especially at small sizes, limited detection of possible sex differences in allometric coefficients based upon this parameter and did not resolve significant differences between growth phases of either sex (Table 2). Only in the postmaturation phase were allometric coefficients based upon wet weight significantly more positive in males than in females. The more sensitive analyses of wet weight based upon regressions by reduced major axis (Fig. 7, A and B; Table 1) detected highly significant differences between postmaturation males and females, regardless of whether ovigerous females were included or excluded from the analysis, and also resolved significant differences
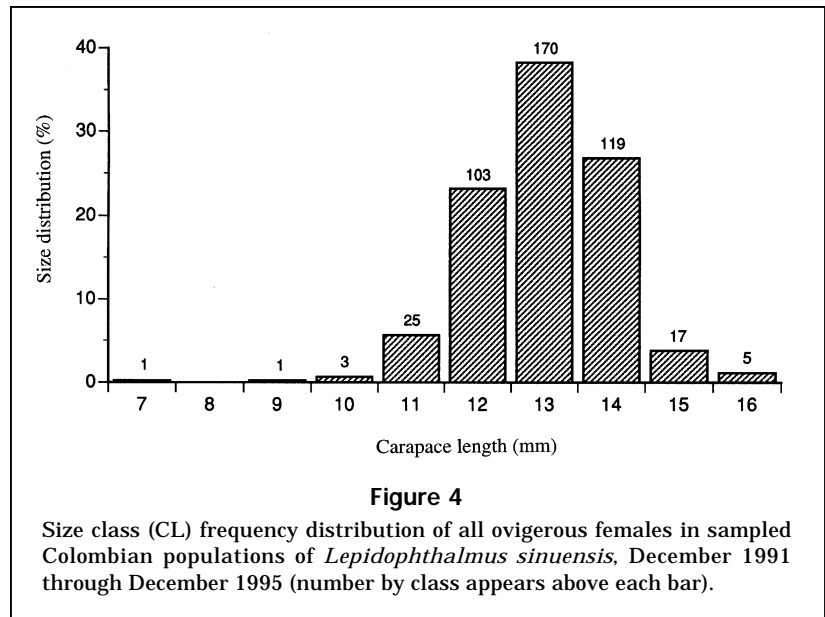

Figure 4

Size class (CL) frequency distribution of all ovigerous females in sampled Colombian populations of *Lepidophthalmus sinuensis*, December 1991 through December 1995 (number by class appears above each bar).

in rates of mass accumulation between prematuration and postmaturation growth phases. Optimized transition points in piecewise regression analyses of wet weight to length relationships were near 9.8 mm CL for females and near 11.3 mm CL for males. These regression breaks suggest that maturation in males occurs at slightly higher wet weights (1.5 to 2 g) than in females (usually near 1 g).

Dry weights and ash free dry weights were determined for limited subsets of our sample and were not subjected to regression analysis. The proportional relation of dry to wet weight in ovigerous females (0.47 ±0.06; n=8) was slightly but significantly higher than in nonovigerous females (0.36 ±0.03; n=76) and males (0.33 ±0.05; n=12), whereas the relation of ash free dry weight to wet weight in ovigerous females (0.052 ±0.003; n=8) was not significantly different from that of either nonovigerous females (0.059 ±0.011; n=41) or males (0.055 ± 0.003; n=2).

Discussion

Sex ratio

Strongly female-biased sex ratios in the monitored population of *Lepidophthalmus sinuensis* are in marked contrast to those reported in intertidal populations of *L. louisianensis* on the Mississippi coast in the northern Gulf of Mexico (Felder and Griffis, 1994), which were variable but averaged near 1:1. However, female-biased ratios have been reported in populations of *L. louisianensis* from the Louisiana coast in the northern Gulf of Mexico (Felder and

Lovett, 1989), as well as in populations of western Pacific intertidal thalassinideans such as *Trypaea australiensis* Dana (Hailstone and Stephenson, 1961), *Callianassa* s. l. *filholi* Milne Edwards (Devine, 1966), and sexually mature adult populations of *Neotrypaea californiensis* (Dana) and *Upogebia pugettensis* Dana (Dumbauld et al., 1996). Populations were male-biased in sampled populations of *Callianassa* s. l. *subterranea* Montagu from subtidal European waters (Rowden and Jones, 1994).

Observance of skewed sex ratios in thalassinidean samples may reflect actual bias in the population or an artifact of collecting methods that do not sample sexes equally within the vertical profile of burrows or across horizontal beach transections, especially when collections must be restricted to readily accessed reaches of shoreline sediments. Movement of ovigerous females toward the surface for egg release or to optimally ventilate eggs could lead to greater probability of their capture when burrows are aspirated with yabby pumps. Likewise, sampling restricted to shorelines may reflect differential positioning of sexes within the burrow along tidal or wave agitation clines. Such effects could account for previous observations in which populations of *Callichirus islagrande* were female-biased on high wave-energy beaches but not on nearby protected beaches, or for ratios that differed markedly from month to month in some populations of *L. louisianensis* from the Gulf of Mexico (Felder and Griffis, 1994). In the present study, mudflats along margins of drainage canals were fully accessible to sampling during periods of low pond discharge, samples were not limited to shorelines, and burrows were not as deep as reported
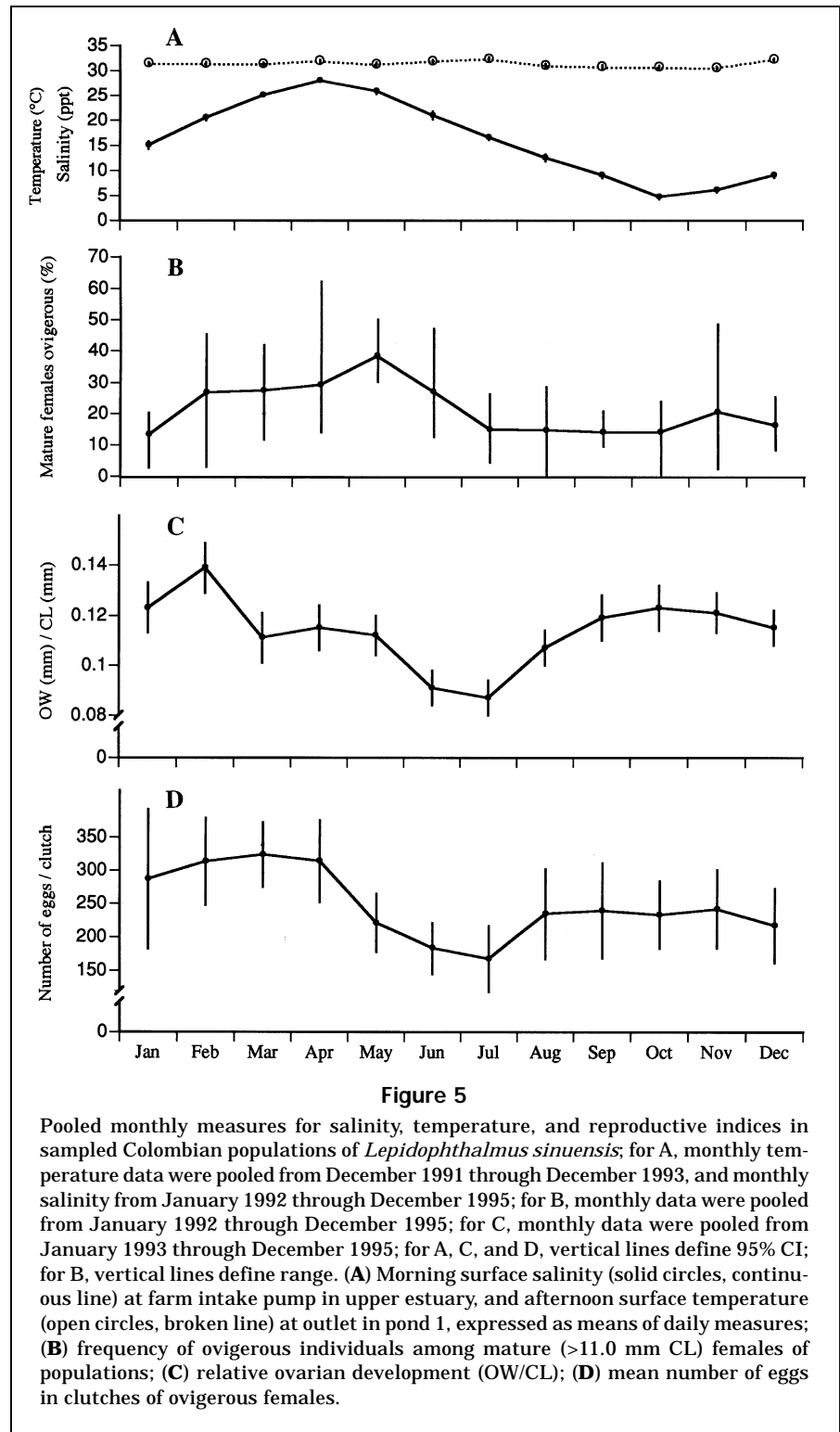

Figure 5

Pooled monthly measures for salinity, temperature, and reproductive indices in sampled Colombian populations of *Lepidophthalmus sinuensis*; for A, monthly temperature data were pooled from December 1991 through December 1993, and monthly salinity from January 1992 through December 1995; for B, monthly data were pooled from January 1992 through December 1995; for C, monthly data were pooled from January 1993 through December 1995; for A, C, and D, vertical lines define 95% CI; for B, vertical lines define range. (**A**) Morning surface salinity (solid circles, continuous line) at farm intake pump in upper estuary, and afternoon surface temperature (open circles, broken line) at outlet in pond 1, expressed as means of daily measures; (**B**) frequency of ovigerous individuals among mature (>11.0 mm CL) females of populations; (**C**) relative ovarian development (OW/CL); (**D**) mean number of eggs in clutches of ovigerous females.

for above mentioned populations of *C. islagrande* and *L. louisianensis*. From resin casts (Fig. 4 in Nates and Felder, 1998), it was observed that almost all burrows were <1 m in depth, thus encompassing water volumes readily extractable with yabby pumps.

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), chela width on chela height (ChW:ChH), total length on carapace length (TL:CL), and wet weight on carapace length (WW:CL) for male and female populations of *Lepidophthalmus sinuensis* sampled at the Agrosoledad S. A. shrimp farm, upper Cispata estuary, Colombia, from December 1991 through December 1995. Regressions were calculated for entire data set (All) and for data subdivided at the transition point (yielding separate regressions for data points $\leq X$ and data points $>X$, where X = size at onset of sexual maturity estimated by piecewise linear-linear polynomial regression), n = sample size, r^2 = coefficient of determination, 95% CI = confidence interval of slope.

	n	r^2	Formulae	95% CI
ChW:CL				
Males				
All	985	0.69	$ChW = (0.612 \times CL) - 3.474^{a}$	±0.021
$\leq X$	218	0.47	$ChW = (0.618 \times CL) - 3.179^{b}$	±0.061
$>X$	767	0.49	$ChW = (0.789 \times CL) - 5.974^{a,b}$	±0.039
Females				
All	1998	0.35	$ChW = (0.273 \times CL) - 0.519^{a,b}$	±0.009
$\leq X$	125	0.62	$ChW = (0.454 \times CL) - 1.925^{a,b}$	±0.049
$>X$	1873	0.12	$ChW = (0.304 \times CL) - 0.943^{a,b}$	±0.013
ChH:CL				
Males				
All	987	0.74	$ChH = (0.991 \times CL) - 4.843^{c}$	±0.031
$\leq X$	192	0.47	$ChH = (1.063 \times CL) - 5.012^{d}$	±0.111
$>X$	795	0.57	$ChH = (1.198 \times CL) - 7.761^{c}$	±0.054
Females				
All	1998	0.49	$ChH = (0.513 \times CL) - 0.425^{c,d}$	±0.016
$\leq X$	177	0.64	$ChH = (0.842 \times CL) - 3.345^{c,d}$	±0.075
$>X$	1821	0.20	$ChH = (0.513 \times CL) - 0.425^{c,d}$	±0.021
ChW:ChH				
Males				
All	987	0.94	$ChW = (0.618 \times ChH) - 0.482^{e,f}$	±0.009
$\leq X$	274	0.85	$ChW = (0.605 \times ChH) - 0.354^{g}$	±0.028
$>X$	713	0.88	$ChW = (0.655 \times ChH) - 0.831^{e,g}$	±0.017
Females				
All	2000	0.71	$ChW = (0.532 \times ChH) - 0.292^{e,g}$	±0.013
$\leq X$	71	0.88	$ChW = (0.550 \times ChH) - 0.175^{f}$	±0.046
$>X$	1929	0.53	$ChW = (0.588 \times ChH) - 0.646^{e}$	±0.018
TL:CL				
Males				
All	1007	0.80	$TL = (4.349 \times CL) - 1.033^{h,i,l}$	±0.121
$\leq X$	737	0.77	$TL = (4.693 \times CL) - 4.695^{h,l}$	±0.161
$>X$	270	0.15	$TL = (6.374 \times CL) - 32.918^{h,j}$	±0.703
Females				
All	2158	0.64	$TL = (4.641 \times CL) - 3.186^{i,j,k}$	±0.117
$\leq X$	1006	0.64	$TL = (5.419 \times CL) - 11.495^{h,i,j}$	±0.201
$>X$	1152	0.22	$TL = (5.766 \times CL) - 19.813^{k}$	±0.293
WW:CL				
Males				
All	937	0.70	$WW = (0.751 \times CL) - 6.431^{l,m,o}$	±0.026
$\leq X$	200	0.22	$WW = (0.679 \times CL) - 5.250^{n}$	±0.084
$>X$	737	0.60	$WW = (0.998 \times CL) - 9.927^{l,n,s}$	±0.046
Females (including those with eggs)				
All	1933	0.49	$WW = (0.613 \times CL) - 5.053^{l,p}$	±0.019
$\leq X$	50	0.32	$WW = (0.508 \times CL) - 3.195^{m,q}$	±0.122
$>X$	1883	0.42	$WW = (0.698 \times CL) - 6.204^{l,p,q}$	±0.024
Females (excluding those with eggs)				
All	1542	0.53	$WW = (0.581 \times CL) - 4.680^{o}$	±0.019
$\leq X$	41	0.42	$WW = (0.472 \times CL) - 2.933^{l,n,r}$	±0.119
$>X$	1501	0.44	$WW = (0.662 \times CL) - 5.767^{o,r,s}$	±0.024

a–s = allometric coefficients with same superscript are significantly ($P<0.05$) different from each other.

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), chela width on chela height (ChW:ChH), total length on carapace length (TL:CL), and wet weight on carapace length (WW:CL) for male and female populations of *Lepidophthalmus sinuensis* sampled at the Agrosoledad S. A. shrimp farm, upper Cispata estuary, Colombia, December 1991, through December 1995. Coefficients were determined for entire data set (All) and for data subdivided at the transition point (yielding separate regressions for data points $\leq X$ and data points $>X$, where X = size at onset of sexual maturity estimated by piecewise linear-linear polynomial regression), 95% CI = confidence interval of coefficient. * *= allometric coefficient significantly ($P<0.05$) different from 1.0. a–u = allometric coefficients with same superscript are significantly ($P<0.05$) different from each other.

	ChW:CL		ChH:CL		ChW:ChH		TL:CL		WW:CL	
	Allom. coef.	95% CI	Allom. coef.	95% CI	Allom. coef.	95% CI	Allom. coef.	95% CI	Allom. coef.	95% CI
Males										
All	1.577**[a]	±0.059	1.457**[e]	±0.047	1.085**[i]	±0.017	0.928**[m,q]	±0.027	3.094**[s]	±0.118
$\leq X$	1.525**[b]	±0.162	1.440**[f]	±0.122	1.061**[j]	±0.039	0.968[n,r]	±0.035	2.762**	±0.747
$>X$	1.608**[c]	±0.129	1.477**[g]	±0.110	1.106**[k]	±0.033	0.618**[m,n,o]	±0.164	3.056**[t]	±0.118
Females (including those with eggs)										
All	0.820**[a,b,c,d]	±0.039	0.869***[e,f,g,h]	±0.033	0.934**[i,j,k,l]	±0.021	0.895**[n,o,p]	±0.025	2.476***[s,t]	±0.090
$\leq X$	1.625**[d]	±0.210	1.470**[h]	±0.160	1.096[l]	±0.116	1.031[m,o,p]	±0.052	3.458**[u]	±1.102
$>X$	0.441***[a,b,c,d]	±0.053	0.491***[e,f,g,h]	±0.045	0.864**[i,j,k,l]	±0.033	0.693**[p,q,r]	±0.051	2.064***[s,t,u]	±0.122

This observation suggests that the detected sex bias accurately characterizes the population sampled.

In the course of previously reported observations on populations of *C*. s. l. *filholi,* it was noted that the sex ratio was near 1:1 only when small animals were included in the sample (Devine, 1966). For *L. sinuensis* there is also a correlation between mean size of animals in the monitored population and sex ratio over the four years of monitoring. As noted for *C*. s. l. *filholi*, samples of smaller mean CL were nearer 1:1 in sex ratio than were samples of larger mean CL. The trend toward increasing frequency of females reached an approximate asymptote after 23 months of observation, simultaneous with the trend in increasing CL of males, and may indicate a point at which increasing numbers of larger males established a sexual equilibrium by displacing small males from a limited habitat or maintained territory. This increase corresponds roughly to the time when burrow densities within ponds on the farm began exponential increase and when detrimental effects on water quality and penaeid production became evident (equals month 38 in Figure 1 of Nates and Felder, 1998). Sex ratios and mean carapace lengths may thus serve to forecast potential for rapid increases in infesting populations.

Both the large body size and the robust chelipeds of mature males could be of advantage in competition for limited space and available females wherever *L. sinuensis* occurs in dense, mature aggrega-

tions. Such behaviors have been suggested previously to account for large numbers of possibly displaced juvenile males of *L. louisianensis* observed periodically in plankton samples (Felder and Lovett, 1989; Felder and Rodrigues, 1993). Similar intraspecific competition for space, in which juveniles are expelled to the surface, has also been postulated to occur in some populations of *Callianassa* s. l. *japonica* (Ortmann), along with possible immigration of juveniles to other habitats (Tamaki and Ingole, 1993). While not documented to occur in *L. sinuensis*, colonization of mariculture ponds by such displaced juvenile males pumped in with estuarine waters could account for higher percentages of males observed early in our study. Such recruitment of juveniles could potentially supplement larval settlement within ponds to rapidly build early infestation densities.
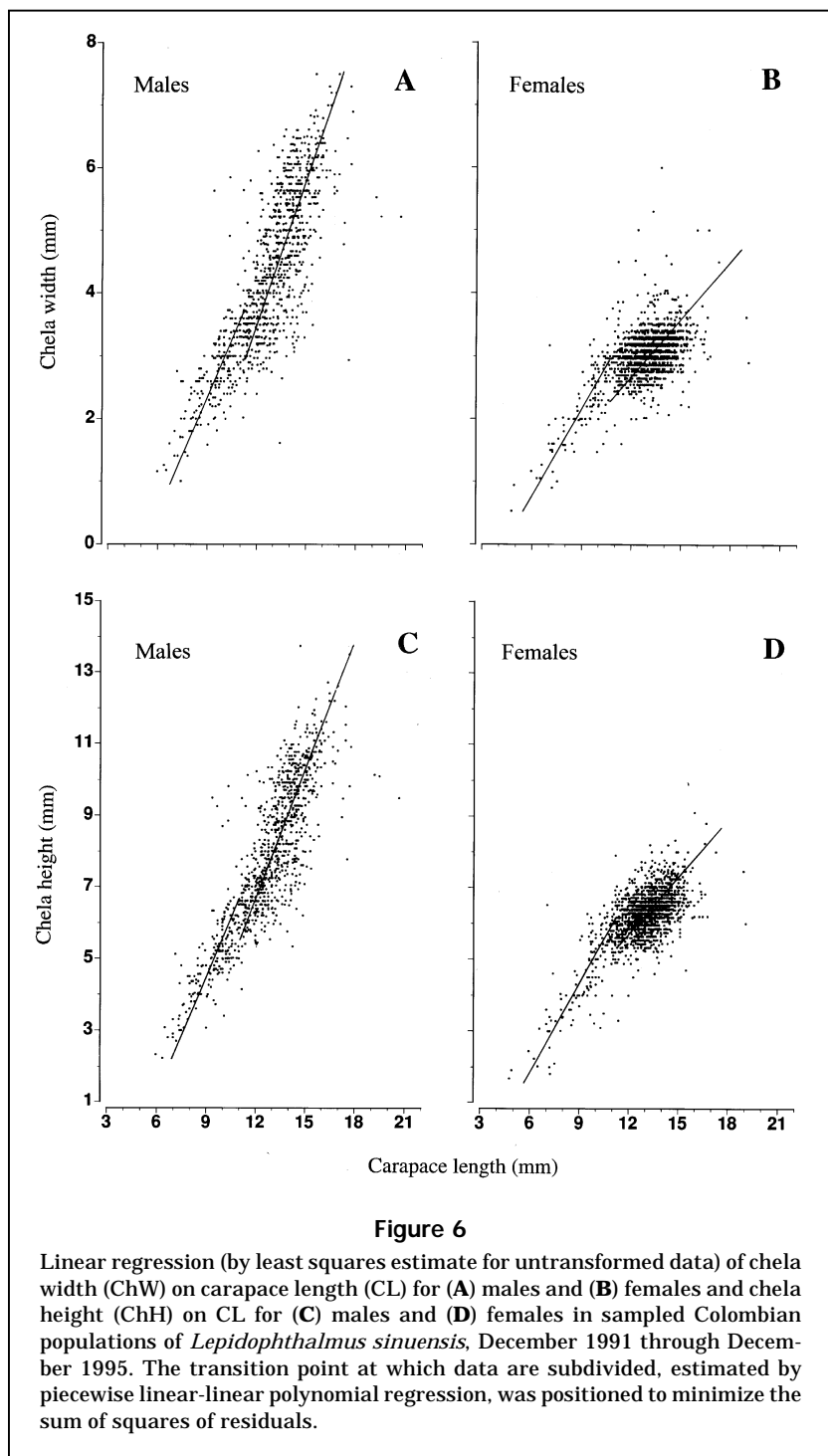
Ovigerous females

The abbreviated life cycle in *L. sinuensis* includes only two brief zoeal stages, large numbers of which occur in nocturnal plankton samples taken at the study site (Nates et al., 1997). The eggs of this species and its congener *L. louisianensis* are comparable in size to those of *Callianassa* s. l. *kraussi* Stebbing, another estuarine species that exhibits markedly abbreviated development (Forbes, 1973), and are larger than those of many thalassinids with longer larval histories and wider planktonic dispersal (see

Pohl, 1946; Forbes, 1973; Tunberg, 1986), with some clear exceptions (see de Vaugelas et al., 1986). Given abbreviated development in *L. sinuensis* and the likelihood of almost immediate settlement by decapodids into the vicinity of our sample site, we expected to detect distinct cohorts of small recruits, from which we could estimate rates of growth to maturation. However, unlike the population of the warm temper-

ate species *L. louisianensis* from the Gulf of Mexico (Felder and Lovett, 1989), tropical populations of *L. sinuensis* included ovigerous females in every month of sampling. This potential for continuous recruitment over the annual cycle, coupled with our limited success in consistently capturing small individuals, limits clear definition of reproduction and growth cycles from collections of recruits.

Figure 6

Linear regression (by least squares estimate for untransformed data) of chela width (ChW) on carapace length (CL) for (**A**) males and (**B**) females and chela height (ChH) on CL for (**C**) males and (**D**) females in sampled Colombian populations of *Lepidophthalmus sinuensis*, December 1991 through December 1995. The transition point at which data are subdivided, estimated by piecewise linear-linear polynomial regression, was positioned to minimize the sum of squares of residuals.

Vitellogenesis in *L. sinuensis* was evident in coloration and size changes of ovaries viewed through a translucent region of the cuticle, as in other thalassinid species (Hailstone and Stephenson, 1961; Forbes, 1977; Felder and Lovett, 1989). The pattern of change in *L. sinuensis* over the course of maturation is as much as that reported for *L. louisianensis*, with ovaries becoming more massive and opaque as maturation advances (Felder and Lovett, 1989). However, when tracked as an annual index of reproductive activity, relative ovarian width in *L. sinuensis* at no point reached the highest mean values reported for *L. louisianensis* (even after correcting misplaced decimals in the y-axis of Fig. 1 of Felder and Lovett [1989]). We suggest that this reflects year-round reproductive activity in *L. sinuensis*, rather than investment in a more punctuated temperature-modulated event as might be expected in temperate latitudes. It may also account for a greater number of eggs on ovigerous females of *L. louisianensis* (598 ±212; $n=4$) than on ovigerous females of the year-round reproducing *L. sinuensis* (251 ±18; $n=444$) (Nates et al., 1997). Even so, significant fluctuations in mean values for relative ovarian width did occur over the three years that we monitored this value in *L. sinuensis*, with highest values preceding maximum abundance of ovigerous females by two to three months.

In tropical nearshore decapods, it is common to have extended periods of reproduction without distinct peaks defined by seasonal temperature (Sastry, 1983; Steele, 1988; Bauer, 1992; Mouton and Felder, 1995). However, whether modulated by temperature or other factors, an-

nual cycles in availability of nutrition may determine potential for vitellogenesis and success of larvae (Zimmerman and Felder, 1991; Mouton and Felder, 1995). Although temperature was not subject to marked fluctuation in the shrimp farm habitat of *L. sinuensis*, it did vary slightly with the annual changes in rainfall patterns that determined salinity of the upper estuary (Fig. 4A). The annual decline in salinity from April through October reflected increased input of nutrient-loaded waters from the nearby Río Sinú which was reported to result in periodic elevation of penaeid shrimp growth rates on the Agrosoledad farm (Mogollón[1]). Similarly, such low salinity periods may have produced improved conditions for vitellogenesis in *L. sinuensis*. Peak development of ovaries in the first quarter of the typical year either coincided with or shortly followed lowest mean salinity during the last quarter of the pre-

Figure 7

Linear regression (by least squares estimate for untransformed data) of wet weight (WW) on carapace length (CL) for males (**A**) and females (**B**) in sampled Colombian populations of *Lepidophthalmus sinuensis*, December 1991 through December 1995. The transition point at which data are subdivided, estimated by piecewise linear-linear polynomial regression, was positioned to minimize the sum of squares of residuals.

vious year, and fell markedly just after salinity peaked. The abundance of ovigerous females peaked almost simultaneously with salinity in most years of the study and a decrease in mean ovarian width immediately followed, indicating that the abundance of females with spent ovaries was not offset by other females simultaneously undergoing vigorous ovarian development. Reduced vitellogenesis following the high salinity period was also suggested by the markedly reduced mean number of eggs per clutch found in those ovigerous females that occurred from May through July.

Growth and sexual maturation

Among callianassids and other thalassinid shrimp, the major chela is used commonly for aggressive interactions between captured individuals that are held together or among individuals encountering one another where burrows intersect in laboratory fossoria (MacGinitie, 1934; Pearse, 1945; Rodrigues, 1976; Tunberg, 1986; Felder and Lovett, 1989; Pillai, 1990;
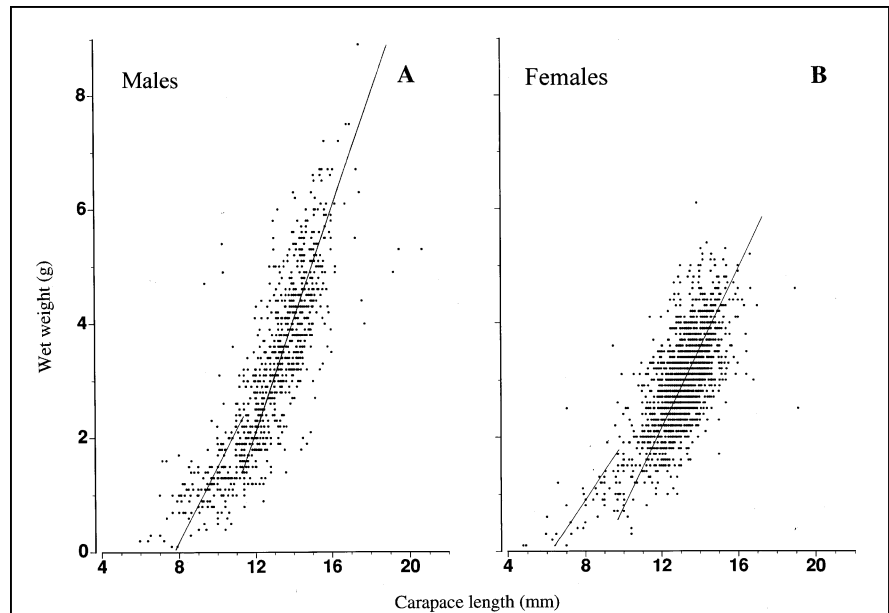
[1] Mogollón, J. V.   1995.   Agrosoledad S. A., Playa de la Artillería no. 33–36, Cartagena, Columbia.   Personal commun.

Rowden and Jones, 1994). Contrary to the case with many other genera, both males and females of *Lepidophthalmus* have one chela enlarged, but the major chela of mature males is much more strikingly developed than that of mature females (Felder and Rodrigues, 1993; Felder and Manning, 1997). Sexual dimorphism of the chelae in decapods is generally thought to reflect adaptations for their use, especially by males, in combat, display, and courtship (Hartnoll, 1974). The enlarged chela can play a role in intermale competition during the precopulatory phase of the life cycle, and marked change in its allometric growth rate is frequently related to functional sexual maturity (Grey, 1979; Aiken and Waddy, 1989; Claxton and Govind, 1994; Gu et al., 1994; Robertson and Kruger, 1994). This is likely also the case in *L. sinuensis*, even though we can only speculate as to the exact role this appendage plays in such fossorial populations.

A striking transition takes place in rate of relative growth for the major chela in *L. sinuensis,* and there is an allometric divergence between males and females in the shape of this appendage at sizes that exceed a defined, transitional carapace length. For the most part, the relationships of slopes above and below these transition or maturation points are similar to relationships previously reported in monitored

populations of *L. louisianensis* from the northern Gulf of Mexico (Felder and Lovett, 1989). In relative growth parameters of the major chela, when scaled to carapace length, males and females of both *Lepidophthalmus* species are much more similar to one another at sizes below transition points than at sizes exceeding those points.

The estimated maturational transition size in male *L. sinuensis* ranges from 11.0 to 11.3 mm CL, whether based upon regression analysis of relative growth in chela width, chela height, or wet weight. The range of these values is markedly less than that reported in *L. louisianensis* (≥15.5 mm CL), a warm-temperate congener (Felder and Lovett, 1989). In all of these measures, postmaturation growth rate in males is more positively allometric and significantly greater than postmaturation growth rate in females, as has been shown in many other decapods (Hartnoll, 1978, 1982). Although relative weight increases were positively allometric in both males and females of mature size, the positive allometry of growth in size of the major chela, accompanied by sex-dependent changes in its shape, appears to account for postmaturation rates of weight increase in males that significantly exceeding those of females. Weight accumulation due to massive but episodic development of ovaries in maturing females would appear to be somewhat offset by the simultaneous trend toward negative allometric growth of the major chela.

Estimated from the major chela measurements, the mean maturational size in female *L. sinuensis* ranges from 10.8 to 11.2 mm CL, or slightly less than that of males but very near the values reported for females of *L. louisianensis,* which ranged from 10.7 to 11.0 mm CL (Felder and Lovett, 1989). Because over 99% of the ovigerous females we collected were ≥11.0 mm CL, the general validity of this mean size estimate for maturation appears to be confirmed on an independent basis, even though two atypically small ovigerous females <10.0 mm CL, were collected (Fig. 4). Our regression analysis of wet weight indicated that the transitional maturation point for females fell near 9.8 mm CL, but error appeared to be high in values surrounding this point. A relatively large range and error in this weight-dependent value should perhaps be expected because two variables, negative allometry of the major chela and growth of the ovaries, are likely influencing it in opposite ways. We suggest that the aforementioned annual salinity variations and the simultaneous effects on nutrient loading may seasonally alter rates of ovarian growth. This could in turn contribute to the range of weight dependent values for maturation or account for occasional occurrences of small egg-bearing females by favoring early maturation of young cohorts.

Management summary

Those penaeid culture ponds on the Caribbean coast of Colombia that operate at higher salinities than those near the Río Sinú have not been found to harbor detrimental infestations of *Lepidophthalmus*. However, nutrient-rich, estuarine waters are believed to yield high rates of penaeid production, promoting location of several major penaeid farms in oligohaline habitats that harbor natural populations of *L. sinuensis*. This pest is introduced to culture ponds by pumping in larvae and perhaps migrant juveniles from the estuary. Although filtration of influent water should serve to limit entry of any migrant juveniles, it is practical to limit entry of much smaller planktonic larvae only by carefully avoiding pumping in of waters from the estuary during nocturnal hours of peak larval activity in the water column (Nates et al., 1997). Because we herein document that *L. sinuensis* reproduces year-round, this diel restriction of pumping schedules cannot be limited solely to the first annual quarter of elevated salinity when peak abundances of ovigerous females suggest that high densities of larvae might be present among nocturnal plankton. However, such periods would almost certainly present the greatest risk of larval introductions to culture ponds.

Although controlling water influx may limit colonization of ponds from surrounding environments, *Lepidophthalmus* will almost certainly over time succeed in becoming established in estuarine ponds that provide it with both richly organic muddy substrates and annual cycles of water quality that favor reproduction. Detrimental effects become obvious when densities in ponds exceed 200 burrow openings/m^2 or 66 animals/m^2 (Nates and Felder, 1998), levels we have never found in natural settings on in the Río Sinú estuary. Explosive reproduction within the ponds appears to immediately precede problem levels of infestation, and measurements of the sex ratios and CL of the population may serve to forecast the potential for such an event. Because attainment of a strongly female-biased sex ratio is roughly coincident with previously reported exponential population growth (Nates and Felder, 1998), both sex ratio and density of mature females may prove useful predictors of population growth potential. Maturity of both males and females can be determined by measures of CL and cheliped dimensions, or by inference from burrow diameters, and immediately pending episodes of egg deposition can be predicted by monitoring the ovarian index.

Dense infestations of *Lepidophthalmus* in Colombian shrimp culture ponds have to date been treated periodically by farm operators with the carbaryl pes-

ticide Sevin®, a practice unlikely to change in the absence of proven alternative management strategies. From our observations, such applications have usually been contained within drained or slightly filled culture ponds and limited only to control of excessive thalassinid densities. It is possible that reductions in frequencies of such applications can be achieved by timing of treatments to pre-empt reproductive peaks or by limiting pesticide applications only to infestations that are found to include high percentages of mature or near-mature females, such as we observed in this study most often in the fourth annual quarter. Any measure that reduces application rates and frequencies may lessen ecological risks and contribute to effectiveness of carbaryl degradation prior to flushing treated ponds into surrounding environments.

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