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POPULATION BIOLOGY OF THE GHOST SHRIMP *SERGIO TRILOBATA* (BIFFAR 1970) (CRUSTACEA: DECAPODA: THALASSINIDEA)

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ABSTRACT *Sergio trilobata* is a common burrowing crustacean found in Tampa Bay, Lemon Bay, and Miami, Florida, where it inhabits mainly intertidal soft sediments (Biffar 1971, Manning and Lemaitre 1993). Although *S. trilobata* is a dominant member of the benthic community, very little is known about population dynamics and reproduction of these thalassinideans. The population biology of this ghost shrimp was examined over a period of a year and a half to gain understanding of its life history. Seasonal variation in the proportion of individuals in each size class was observed during the study, suggesting that there may be environmental factors affecting the ghost shrimp. Additionally, a life span of approximately two years is indicated by the seasonal variation in the proportion of individuals in each size class. The population was biased toward females with a 1:1.81 male:female ratio, and the mean total length of females (68.2 mm) was larger than the males collected (54.6 mm) ($P = 0.0001$). Collection of ovigerous females were directly correlated with an increasing ovary width of females during the preceding months, and the total length of *S. trilobata* was positively correlated with the number of eggs produced. Mean number of eggs per female *S. trilobata* was 197 with a maximum of 412 eggs.

INTRODUCTION

Ghost shrimp are decapod crustaceans that construct and inhabit burrows predominantly in shallow intertidal regions containing a soft sediment base (Felder and Manning 1997, Kevrekidis et al. 1997, Berkenbusch and Rowden 1999). These thalassinideans also commonly inhabit regions with a high content of organic matter (Felder and Manning 1997) which has been known to trigger settlement in some species of ghost shrimp (Strasser and Felder 1999). Ghost shrimp are frequently found in both tropical and temperate regions (Berkenbusch and Rowden 1999), and are an important component of the ecosystem due to their bioturbating activities, which impact nutrient cycling (Nates and Felder 1998), sediment turnover rates (Felder and Griffis 1994), benthic community structure (Dittmann 1996) and commercial industries such as aquaculture (Davey et al. 1990, Lemaitre and Rodrigues 1991, Lafferty and Kuris 1996, Nates and Felder 1998, Berkenbusch and Rowden 2000, Felder 2001).

Sergio trilobata (Biffar 1970) is a common burrowing crustacean in Tampa Bay that inhabits mainly shallow intertidal soft sediment habitats (Biffar 1971) and dominates the benthic community in mid to lower bay regions. *S. trilobata* was described from Tampa Bay but has also been reported from Miami and Lemon Bay, Florida (Biffar 1971, Manning and Lemaitre 1993). Collections of this species have been made in Tampa Bay at a water depth of approximately 2–4 meters (Biffar 1971). *S. trilobata* is also thought to thrive in

regions of high organic content and construct a thicker burrow wall than do other species of thalassinidean shrimp in South Florida (Biffar 1971).

Environmental conditions such as temperature and salinity have been recognized to impact intertidal decapod crustaceans (Tamaki et al. 1997, Berkenbusch and Rowden 1999). Low temperatures may cause shrimp to be relatively inactive, resulting in a decrease in sediment turnover rates, decreasing the impact of these organisms on their environment (Berkenbusch and Rowden 1999). Salinity may also be a factor in the distribution of this species, since *S. trilobata* is usually found in mid to high salinities and is then replaced by *Lepidophthalmus louisianensis* in areas of low or more fluctuating salinities (Felder 1978, Felder and Rodrigues 1993) and higher sedimentary organic content (unpublished data).

Members of the genus *Sergio* are considered to be diverse ecologically and may vary with respect to reproductive and life history characteristics such as development and dispersal activities (Nates et al. 1997). It is known that varied symbiotes such as copepods, pea crabs, caridean shrimp, clams, and gobiid shrimp are commonly found in the burrows of ghost shrimp (Jackson 1996). Although *Sergio trilobata* is a dominant member of the benthic community, very little is currently known about this species. The present study undertakes observations of population dynamics and reproductive characteristics in this poorly known but dominant member of the Tampa Bay benthic community.

MATERIALS AND METHODS

Monthly collections of *Sergio trilobata* were made on an intertidal sand flat located on the southwest end of the Gandy Bridge in Tampa Bay, Florida (27.87N, 82.60W) from April 2000 to August 2001. Specimens were obtained by extracting animals from randomly chosen burrow holes in a sub-area of the intertidal sand flat using yabby pumps to extract samples, which were then washed over 1-mm mesh sieves (Felder 1978). At least 15 animals were collected during each collection. Each individual organism was placed in a clean whirl pack® plastic bag and returned to the laboratory for examination. The proportion of individuals in each size class (10 mm increments) was examined on a seasonal basis, with three months being included in each season: spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February).

The sex of the animal, total length (TL, measured from the tip of the rostrum to the posterior end of the telson in live specimens), and carapace length (CL, measured from the tip of the rostrum to the posterior end of the carapace) were recorded for each individual. All measurements were made to the nearest millimeter. Although specimens as small as 10.5 mm TL were collected, individuals below approximately 30 mm in total length could not be sexed and were classified as juveniles. Female ovary width was measured on the second abdominal segment at the widest point visible through the transparent dorsal integument of the second abdominal somite, and the number of eggs was also recorded for each female when ovigerous. Females thought to be releasing eggs during the time of collection were excluded because it was thought they would bias the results. Females classified as thought to be releasing eggs were those that had a small number of well developed eggs remaining on the pleopods and had obviously released the remainder of the brood. This resulted in the exclusion of a maximum of 10–15 specimens throughout the entire study. Eggs were also categorized according to their color (red orange, orange, yellow orange, or yellow) and whether or not they contained visible eyespots. After measurements were recorded, specimens were archived in 70% ethanol.

RESULTS

The proportion of individuals in each size class varied seasonally (Figure 1). In spring 2000 the population was dominated by individuals in the larger size

classes of 60–89 mm and included only a very small proportion of individuals in the smaller size categories of 20–39 mm (Figure 1A). Samples in summer of 2000 exhibited a larger proportion of the population in the smaller size categories, but most individuals were still in the 60–79 mm size range (Figure 1B). During the fall, no organisms were present in the largest size class (80–89 mm). Also in this period, the 60–69 mm size class contained the highest proportion of the population, which may represent individuals recruited into the population during the previous spring (Figure 1C). In winter 2000 and spring 2001, there were no individuals present in the smallest size class, and the highest proportion of the population was again in the 60–79 mm size classes (Figures 1D and 1E). A bimodal distribution is present in both of these seasons, which may again represent the presence of two distinct generations. As in the previous year, in summer 2001 the highest proportion of individuals was observed in the 70–79 mm size category, and there is an increase in the proportion of larger individuals in the 80–89 mm size category (Figure 1F). Although collections in the fall of 2001 were limited to September and October, once again, no organisms in the largest size class of 80–89 mm were represented in the sample.

The population of *S. trilobata* was biased toward females with a ratio of 1:1.81. Males ranged in total length from 31 to 82 mm with a mean ($\pm$ SE) of 54.6 ± 5.4 . Females had a mean ($\pm$ SE) length of 68.2 ± 2.2 , ranged in total length from 34 to 88 mm, and were significantly larger than males ($P = 0.0001$) when compared with a Mann Whitney U Test. Although variable, this difference in size was consistent over the entire sampling period (Figure 2) with the exception of October 2000.

Ovigerous females were collected from April through October 2000, and March through August 2001 (Figure 3A). During the months of April and May in both years, the proportion of ovigerous females collected was larger than during the rest of the year. The time period during which ovigerous females were present can be directly correlated with the ovary width of the females during the preceding months. During the months of November 2000 to February 2001, when no ovigerous females were collected, a peak in mean ovary width of females was observed. There was also a decline in mean ovary width starting in March and continuing through June, when the highest proportion of ovigerous females were collected (Figure 3B).

The average number of eggs collected per female was 197 ± 18.1 eggs, and a positive correlation existed

Figure 1. Seasonal variation in the proportion of *Sergio trilobata* in each of six 10-mm total length size categories: A) Spring 2000; B) Summer 2000; C) Fall 2000; D) Winter 2000; E) Spring 2001; F) Summer 2001.

between number of eggs per female and its total length ($r^2 = 0.929$, $n = 56$) (Figure 4). The highest fecundity observed was 412, although this may be an underestimate of potential fecundity as some eggs may be lost in the collection process. Eggs ranged in color from red-orange immediately after release from the ovary to a pale yellow containing distinct eyespots in the days prior to hatching. The smallest female found to be ovigerous was 48 mm in total length with 62 eggs, and the smallest female collected with developed ovaries was 41 mm in total length with ovaries 2 mm wide.

DISCUSSION

Seasonal variation in the proportion of individuals in each size class was observed during the study suggesting that there may be environmental factors affecting the ghost shrimp. Additionally, a life span of approximately two years is indicated by the seasonal variation in the proportion of individuals in each size.

The bimodal distribution of the population in winter 2000 and spring 2001 indicate the presence of two generations in the burrowed population. Maturity of those recently recruited then follows the next year as ovigerous females are most commonly found in the spring and summer. These observations along with the apparent mortality in the largest size classes in fall 2000 and 2001 suggest the life span of these organisms may be limited to two years. The life span of thalassinidean shrimp is variable, but there are some that have comparable life spans of two years, such as with *Lepidophthalmus louisianensis* (Felder and Lovett 1989), *Callinassa japonica* (Tamaki et al. 1997), and *Callinassa kraussi* (Forbes 1977). Some other thalassinidean shrimp exhibit a longer life span of approximately 3–4 years such as *Upogebia pusilla* (Kevrekidis et al. 1997), *Sergio mirim* (Pezzuto 1998), and *Callinassa filholi* (Berkenbusch and Rowden 2000). The seasonal variation in the proportion of individuals in each size class in the population is also related to the

Figure 2. Mean total length ($\pm$ SE) of male ($n = 138$) and female ($n = 297$) *Sergio trilobata* during each month of collection (April 2000 to August 2001).

fecundity of the organisms and recruitment of juveniles into the population. Fecundity and recruitment may be affected by temperature or salinity fluctuations, although the exact cause of these variations warrants further study. Salinity was found to range from 25 to 38‰ but does not seem to impact the reproductive output of *S. trilobata* as the fluctuations in salinity did not mirror trends in reproduction. Although exact temperatures were not recorded on a regular basis, seasonal temperature changes were the most likely cue for reproduction since data collected does indicate a seasonal trend in ovary size and egg production of females. However, even if surface water temperatures were collected, they might have been misleading since the water temperature in the burrows is often lower than the surface water temperature.

The population of ghost shrimp was found to be biased toward females with a 1: 1.81 male:female ratio. Sex ratios have been found to be variable in other thalassinidean shrimp; for example, *Sergio mirim* (Pezzuto 1998), *Lepidophthalmus louisianensis* (Felder and Lovett 1989, Felder and Griffis 1994) *Lepidophthalmus sinuensis* Lemaitre (Nates and Felder

1999), *Callianassa filholi* (Devine 1966, Berkenbusch and Rowden 2000), *Callianassa japonica* Ortmann (Tamaki et al. 1997), *Callichirus armatus* (Vaugelas et al. 1986), and *Callichirus islagrande* (Felder and Griffis 1994) exhibit a female biased sex ratio. The sex ratio has also commonly been reported as male biased in other species such as with *Callichirus kraussi* (Forbes 1977) and *Callianassa subterranea* (Rowden and Jones 1994). The variability in the sex ratio of ghost shrimp can be attributed to many factors including seasonal variation and variation between species (Berkenbusch and Rowden 2000). The variability may also have a behavioral basis; for example, females with eggs are often found closer to the burrow entrance than males, which would make them more susceptible to collection (Nates and Felder 1999).

The mean TL of females was larger than the males collected from April until October 2001, with the noted exception of October 2000. Populations in which females are larger than males is comparable with other thalassinidean shrimp such as *Callianassa filholi* (Berkenbusch and Rowden 2000) and *Sergio mirim* (Pezzuto 1998) in which the females collected were also

Figure 3. Reproductive data for *Sergio trilobata* from April 2000 to August 2001: A) Proportion of female sample ovigerous during each month of collection; B) Mean ovary width ($\pm$ SE) of females during the collection period.

Figure 4. Mean number of eggs per females of *Sergio trilobata* in each of six 10-mm total length (TL) size category.

TABLE 1

Comparison of the mean and maximum number of eggs of female thalassinidean shrimp in selected studies. (–) indicates no value was provided in reference.

Species	Mean Egg No.	Maximum Egg No.	Reference
<i>Sergio trilobata</i>	197	412	present study
<i>Lepidophthalmus sinuensis</i>	251	958	Nates and Felder 1999
<i>Callianassa tyrrhena</i>	270	1188	Thessalou-Legaki and Kiortsis 1997
<i>Callianassa japonica</i>	331	962	Tamaki et al. 1997
<i>Lepidophthalmus louisianensis</i>	598	–	Nates et al. 1997
<i>Sergio mirim</i>	–	6586	Pezzuto 1998
<i>Callichirus major</i>	–	8710	Pohl 1946

larger in mean size than the males in the population. There are, however, many thalassinidean shrimp in which the males exhibit a larger mean TL than the females such as *Upogebia pusilla* (Kevrekidis et al. 1997) and *Callianassa japonica* Ortman (Tamaki et al. 1997). In many cases when males are larger than females in the population, the size difference can be attributed to male to male competition. However, in this case males were found to be smaller than females providing no evidence of intrasexual selection or sex-related mortality which would cause the female biased population.

The increased proportion of ovigerous females can be directly correlated with an increasing ovary width of the females during the preceding months. During the summer months, the proportion of ovigerous females increases as the mean ovary width decreases. Correlations between the mean ovary width and the proportion of ovigerous females in populations of ghost shrimp has also been observed in other thalassinidean shrimp such as *Lepidophthalmus louisianensis* (Felder and Griffis 1994), *Lepidophthalmus sinuensis* (Nates and Felder 1999), *Callianassa japonica* (Tamaki et al. 1997) and *Neotrypaea californiensis* (Dumbauld et al. 1996). The total length of *S. trilobata* was also found to be positively correlated with the number of eggs produced, which is similar to results found with many other ghost shrimp species such as *Callianassa tyrrhena* (Thessalou-Legaki and Kiortsis 1997), *Callianassa filholi* (Berkenbusch and Rowden 2000), and *Sergio mirim* (Rodrigues 1971) (Pezzuto 1998). The mean and maximum number of eggs per female *S. trilobata* (mean = 197, max. = 412) was slightly lower than other species of ghost shrimp, although the mean number of eggs per female in thalassinidean shrimp can be highly variable (Table 1). A low number of eggs per female is indicative of year round reproductive activity or multiple broods

produced per female annually, as well as large egg size (Thessalou-Legaki and Kiortsis 1997, Nates and Felder 1999, Berkenbusch and Rowden 2000). Although year round reproductive activity is not likely in *S. trilobata*, due to the apparent seasonal trends in reproduction, the possibility that *S. trilobata* produces multiple broods in a given breeding season cannot be eliminated. Additionally, although egg size was not measured in this study, eggs were found to be much larger than that of a sympatric species of ghost shrimp, *Lepidophthalmus louisianensis* (personal observation). Egg size has been directly correlated with larval development in many species of ghost shrimp in which species with larger eggs exhibit abbreviated development in larval stages (Forbes 1973). The egg size and number of broods produced annually would be of significance in determining the fecundity and the development of larval stages of *S. trilobata* and therefore warrant further study.

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