NATURAL HISTORY AND FACTORS INFLUENCING POPULATION STRUCTURE IN THE BANDED CORAL SHRIMP (*Stenopus hispidus*)

By

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To my Mother, Father, and Fiancé for your constant loving support and general curiosity throughout this process.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Abstract of Thesis Presented to the Graduate School
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By

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Chair: Colette St. Mary
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Understanding natural history and population dynamics of marine organisms is imperative for their management and conservation. My research documents important life history parameters of the banded coral shrimp (*Stenopus hispidus*), a popular marine ornamental shrimp, as well as estimates effects of several factors on the population structure in the Upper Florida Keys. Among the life history parameters described are 1) size at settlement, 2) molt interval, 3) growth, and 4) relative fecundity. Variation in the size at settlement of *S. hispidus* in the Upper Florida Keys was much smaller than that found in previous studies from other parts of the world. This suggests that there is large-scale spatial variation in the size at settlement of *S. hispidus*. In a laboratory study, molt interval increased as shrimp body size increased. I estimated weekly molting probability and growth increment per molt under natural conditions, for various sized individuals, with a field tagging study. These data were then incorporated into a crustacean growth model, which included discontinuous growth and natural variability in size at settlement

and growth increment, to describe expected patterns of *S. hispidus* growth. This model also allowed for the estimation of post-settlement age of *S. hispidus* in the Upper Florida Keys. Finally, I described the relationships among female body size and egg mass volume and egg number, and found that both relationships were significantly positive.

In the summer of 2002, I conduced studies that estimated to what degree 1) settlement, 2) post-settlement mortality and movement, and 3) growth contributed to the variable size-structure of *S. hispidus* populations in the Upper Florida Keys. Smaller typically immature shrimp dominated offshore reefs in the Upper Florida Keys, while larger mature shrimp dominated inshore reefs. I showed, using artificial reefs, that settlement to the offshore region was much higher than that to the inshore region. Using an extensive tagging study, I documented size-selective mortality, which was consistent between the two regions. Smaller individuals experienced much higher rates of mortality than did larger individuals. Post-settlement movement was found to be minimal, with no evidence of long distance movement between regions. Finally, growth in the offshore region was slower than that in the inshore region. These results indicate that the offshore region may be dominated by smaller shrimp because settlers rarely reach larger sizes, due to lower growth rates and increased periods of vulnerability to high mortality (possibly due to predation). Therefore, the variable size-structure of *S. hispidus* in the Upper Florida Keys is probably due to the differential growth rates between the two habitats.

CHAPTER 1
SIZE AT SETTLEMENT, GROWTH, AND FECUNDITY OF THE BANDED CORAL SHRIMP, *Stenopus hispidus*, IN THE UPPER FLORIDA KEYS

Introduction

Understanding life history of marine organisms is imperative for their management and conservation. Only when demographic features such as growth rates, size at maturity, and fecundity are better understood can reliable management practices be implemented. This is especially true in harvested species. One fishery in need of data is that of marine ornamentals, fishes and invertebrates that are harvested for the aquarium trade. It is estimated that the global trade of ornamentals and associated accessories is in excess of $7 billion/year (Andrews 1990). Current opinion is that 90% of freshwater ornamentals can be captive-bred (Andrews 1990). However, Wilson et al. (2001) report that approximately 98% of all marine species are still taken from wild populations, based on an estimate provided by Martin Moe from Green Turtle Publications. It is estimated that over 3000 species of marine fishes and invertebrates are collected from natural habitats for the marine aquarium trade (Fletcher et al. 1995). The harvest of marine ornamentals is still increasing, even with documented declines in local fish abundance and habitat quality (Andrews 1990, Fletcher et al. 1995, Tissot and Hallacher 1999).

In 1998, the trade of invertebrates for aquariums was valued at $30 million in the United States alone, and virtually all of the invertebrates in the aquarium trade are marine species (Larkin and Degner 2001). Among the marine invertebrates collected for the aquarium trade are the cleaner shrimps, consisting of over 18 species (Fletcher et al.

1995). It has been hypothesized that the harvest of cleaner shrimps from the natural environment for the aquarium trade can result in a decline in the local fish population, therefore having broader implications for the ornamental trade and reef communities (Fletcher et al. 1995).

One of the most popular cleaner shrimps in the marine ornamental trade is the banded coral shrimp, *Stenopus hispidus* (Olivier) (Zhang et al. 1998). *Stenopus hispidus* is a reef-associated cleaner shrimp (Decapoda: Stenopodidae) with a worldwide distribution. It is known to remove and consume ectoparasites, injured or dead tissues, and excess food particles from fishes (Limbaugh et al. 1961, Johnson 1977). As adults, *S. hispidus* are found in crevices or overhangs in reefs at depths ranging from <1 to 210 meters and are thought to move over an extremely limited area (<1 m^2) with males exhibiting territorial behavior within this area (Limbaugh et al. 1961, Stolen 1964, Young 1979, Fletcher et al. 1995).

Adults are typically found in reproductive pairs (Limbaugh et al. 1961, Johnson 1969, Young 1979). It is believed that juveniles form pairs and then grow up together (Limbaugh et al. 1961). Females reach sexual maturity at ~30 mm TL (Stolen 1964). Unlike many other cleaner shrimps that exhibit simultaneous hermaphroditism, *S. hispidus* shows no signs of hermaphroditism (Fletcher et al. 1995). Mating usually occurs within 12-48 hours of a female molt and can be broken into five discrete steps: 1) antennule contact (10 minutes-6 hours), 2) erection of female body, 3) grasping, 4) copulation (10 seconds), and 5) spawning (Zhang et al. 1998). Spawning typically begins within 15-25 minutes of copulation and lasts approximately 10 minutes, during which the

female deposits a blue-green egg mass on the swimmerets under the abdomen (Limbaugh et al. 1961, Zhang et al. 1998).

After spawning, eggs progress from heavily pigmented towards transparency, where darkly pigmented eyespots begin to appear. Larvae typically hatch within 16 days of fertilization at 28°C (Young 1979). Like many other members of the family Stenopodidae, newly hatched *S. hispidus* larvae go through nine larval stages before settling to the benthos (Gurney and Lebour 1941). However, compared to most Stenopodids, *S. hispidus* has a long larval duration (at least 123 days) and has shown the ability to delay metamorphosis up to as many as 210 days, until suitable nutritional or environmental conditions are encountered (Gurney and Lebour 1941, Williamson 1976, Fletcher et al. 1995). Because of its long larval duration and potential to delay metamorphosis, little progress has been made in the culture of *S. hispidus* in the laboratory, unlike many other species of cleaner shrimps (Zhang et al. 1997).

Although much is known about *S. hispidus*, several key factors of its life history are still unknown. From a management perspective, perhaps the most important aspect of *S. hispidus* biology is its growth rate. For most marine fisheries, estimates of species' growth rates is one of the most essential elements in population modeling when trying to provide estimates of sustainable harvests (Chen and Kennelly 1999). Although determining growth rates for fishes is straightforward, measuring growth in crustaceans is more difficult, due primarily to the loss of all hard parts upon molting and the discontinuous nature of crustacean growth (McCaughran and Powell 1977, Annala and Bycroft 1988, Chen and Kennelly 1999).

The overall objective of this chapter is to provide additional life history information which will aid in the management of *S. hispidus,* including estimates of 1) size at settlement, 2) molt interval across the range of sizes, 3) relative fecundity and egg number, and 4) estimates of *S. hispidus* growth based on data from a detailed tagging study, which allowed for the estimation of weekly molting probability and growth increment per molt of *S. hispidus* under natural conditions. These data were then incorporated into a crustacean model (Chen and Kennelly 1999) to describe expected patterns of S. *hispidus* growth.

Methods

Size at Settlement

Light traps and artificial settlement substrates. To quantify size at settlement of *S. hispidus* I deployed larval light traps and artificial settlement substrates in several locations in the Upper Florida Keys. Light traps were variations on the design of Meekan et al. (2001). Traps consisted of a single chamber made of clear acrylic. In the center of the chamber was a suspended dive light (Princeton Tech IMPACT) attached to a 50 cm clear plastic tube with a mirror on the opposite end to prevent light loss through the bottom of the traps. A single "funnel" (10.16 cm diameter) made of clear soda bottles (Sponaugle and Cowan 1996) was imbedded into each side of the trap, to allow photopositive organisms to enter. Once deployed, the light traps operated continuously for approximately 120 hours. Floats were attached to the top of each trap to make them positively buoyant and traps were suspended 2 m above the surface of the reef by mooring them to two, 2.37 L concrete weights.

Artificial settlement substrates were slight variations on the design of van Montfrans et al. (1995). As with those of van Montfrans et al. (1995), substrates consisted of a

plastic fibrous material, approximately 1.9 cm thick typically used as an air-conditioner filter (surface area = 0.26 m^2) formed around a cylinder of PVC pipe. However, the PVC pipe used in this study was 10.16 cm in diameter and 50.8 cm long. Substrates were secured to PVC cylinders by large rubber bands. Cylinders were equipped with internal flotation and capped at each end. The substrates were suspended vertically 2 m from the surface of the reef by mooring them to two 0.95 L concrete weights.

Previous studies with light traps indicate that marine invertebrate post-larvae are most abundant between the 3rd quarter and new moon phases of the lunar cycle (Reyns and Sponaugle 1999, Meekan et al. 2001). Therefore, traps were deployed each night beginning two nights prior to the new moon and ending two nights after new moon in May and June of 2002. Four replicate light traps and four replicate settlement substrates were deployed in both offshore and inshore reefs in the Upper Florida Keys. Traps and substrates were recovered and redeployed daily during the collection periods. Upon recovery, trap contents were emptied into 0.85 mm mesh sieves and preserved in 95% EtOH. Processing of substrate collections consisted of removing and replacing each filter with a new, clean filter. Old filters were placed into individual plastic bags for later rinsing with freshwater. This water was then sieved (0.85 mm mesh) for organisms, which were preserved in EtOH (van Montfrans et al. 1995).

Artificial reefs. Artificial reefs were also used to quantify size at settlement. On June 19, 2002, 87 small (<1 m^2) artificial reefs, each consisting of five limestone rocks from a local quarry, were deployed in a linear array (5 meters apart), approximately five meters from a natural contiguous reef, in the Upper Florida Keys. From July 25 to August 3, 2002, each reef was surveyed daily and emptied of all fishes and invertebrates (including

S. hispidus) using Eugenol (an anesthetic, also known as clove oil). All *S. hispidus* collected from these reefs were then measured (mm TL).

Surveys. A previous study by Gurney and Lebour (1941) provided descriptions and sketches of *S. hispidus* post larvae. One distinguishing characteristic among these post larvae is the presence of red on the body and legs in less distinguishable bands than that of adults. I observed similar color patterns among small *S. hispidus* in the Upper Florida Keys. Because this color pattern matched that described by Gurney and Lebour (1941), I assumed these shrimp had recently settled. Therefore, I conducted extensive surveys for *S. hispidus* of this color pattern among several reefs in the Upper Florida Keys. All shrimp encountered were collected and measured (mm TL) underwater and released.

Data analysis. A pooled mean size was calculated from all measured individuals from all three studies. I checked for possible outliers, individuals greater than three standard deviations from this mean, and then removed them. After removing outliers, a mean size at settlement was calculated from all remaining individuals.

Molt Interval

Twenty-seven shrimp, of various sizes, were purchased from a collector operating in the Upper Florida Keys (Sea Life Inc.) and maintained in a closed-system aquarium at the University of Florida, Department of Zoology from March 12 to May 3, 2002. Shrimp were housed in individual 2L containers that constantly received recycled water from a drip-bar located above each container. Water temperature fluctuated between 24 and 26°C and salinity was kept between 35-39 ppt. All shrimp were fed quartered silversides once every three days. Upon introduction to the aquaria, all shrimp were measured (mm

TL), sexed, and tagged. Daily inspections for molting events were then conducted for 52 days.

The criteria used to sex individuals were revised from those given by Stolen (1964) and Johnson (1969): (1) if a single, median spine was found on the ventral surface of the abdominal segments of a shrimp >30 mm TL, it was assumed to be a male; (2) If a shrimp >30 mm TL lacked spines, it was called a female; (3) If a shrimp carried a blue-green egg mass on the ventral surface of the abdomen or had a blue-green mass beneath the dorsal surface of the carapace, it was assumed to be female; (4) All individuals <30 mm TL (which typically have an abdominal spine) were categorized as unknown sex, unless criteria 3 was met.

Tagging consisted of an injection of non-toxic, acrylic paint just beneath the dorsal surface of the second-to-last abdominal segment with a 30 gauge, 1.27 cm hypodermic needle and 1 mL syringe. A similar method was used with juvenile and adults of a popular food shrimp (*Panaeus vannamei)* and found to result in 99.9% and 100% tag retention, respectively, after undergoing as many as 23 molts (Godin et al. 1995).

Upon molting, each shrimp was re-measured. Molt interval (i.e., the time between two successive molts) was calculated for each individual, as well as a mean interval for those individuals that molted more than once during the study. A linear regression model was fit to describe the relationship between molt interval and shrimp body size. Mean molt intervals for females and males were compared with a t-test.

Growth

To quantify growth rates of *S. hispidus*, a large scale tagging study was conducted in three inshore and three offshore sites in the Upper Florida Keys, from May 14 to July 31, 2002. The offshore sites consisted of three sections of contiguous reef. The inshore reefs

were part of a series of small patch reefs found in shallower water interspersed with beds of sea grass (*Thalassia testudinum*). Further details of these sites are presented in Table 1-1.

Quantifying growth in crustaceans is difficult because of their loss of all hard parts as a result of molting. This problem can be overcome through the use of internal tags that identify individuals and indicate if an individual has molted (Ennis 1972, Taylor and Hoenig 1990, Godin et al. 1995, Chen and Kennelly 1999).

All shrimp in each site were tagged underwater (see procedure above), measured (mm TL), and sexed (see criteria above). A total of six colors were used (black, green, blue, red, orange, and yellow) and distance between two shrimp with the same color was maximized and greater than their estimated home range (~1 m^2) (Limbaugh et al, 1961, Stolen 1964, Young 1979), so that individuals could be distinguished. I also ablated the left exopod of each shrimp. Upon subsequent molting, the ablated exopod is replaced with a new exopod, therefore indicating that a tagged shrimp had molted (Linnane and Mercer 1998). This technique was verified for *S. hispidus* in the molt interval lab study detailed above.

All holes where shrimp were found were marked with numbered flagging tape tied to a weight and mapped to PVC paper for use underwater. I then conducted extensive weekly surveys of each study site. In these surveys, I 1) recorded presence/absence of previously tagged shrimp, 2) tagged, measured, and sexed any new shrimp, and 3) re-measured and re-clipped any individuals who were missing their molt indicators. Each week, prior to surveying, the maps of each site were updated with the locations of newly tagged shrimp in order to assure all tagged individuals were included in the surveys.

Based on the results from the molt interval study (see Results) and previously published data (Johnson 1977), this study ran for 70 days, in order to maximize the probability of an individual molting twice in the duration of the study.

Time to each molt (weeks) as well as growth increments (i.e., change in length after a single molt) were measured for all tagged shrimp that were observed to molt in the tagging study. Using shrimp that molted more than once, the weekly probability of molting was estimated. Due to the relationship between shrimp size (mm TL) and molt interval (days) from the molt interval study (see Results), I expected shrimp of different sizes to have different molt intervals (weeks) in the tagging study. Therefore, I conducted a survivorship analysis (exponential model) to estimate the time to molt (T_m; weeks) as a function of shrimp size (s) as

$$T_m = e^{(a + b*s)}, \quad 1.1$$

where *a* and *b* are fitted parameters (Allison 1995). Therefore, the weekly probability, Pr(m), of a shrimp molting was estimated as

$$Pr(m) = 1/e^{(a + b*s)}. \quad 1.2$$

This weekly probability of molting, Pr(m), was then incorporated into a crustacean growth model (detailed below).

The relationship between growth increment and pre-molt size was estimated using polynomial regression (Sokal and Rohlf 1996). The best-fit model for this relationship was used to provide estimates of growth increment for a given pre-molt size, also to be used in the crustacean growth model (detailed below). Additionally, deviations from this predicted growth increment (G_d) were calculated, to provide estimates of variation in growth. These deviations were also incorporated into the growth model.

I modeled *S. hispidus* growth through the application of an approach first used by Chen and Kennelly (1999), referred to as the probabilistic stepwise growth curves (PSGC) approach. This approach generates a distribution of growth curves that mimic a discontinuous pattern of growth while incorporating intrinsic variation in the data. A simulation of a population of shrimp was generated using the following sequence of steps: (1) a size at settlement, L_1, was chosen from the observed distribution of settler sizes (see Results); (2) for each subsequent week an individual molted with probability P_1 (Equation 1.2); (3) if no molting occurred, then the same process was repeated for the next week; (4) if the individual did molt then its new size was determined as $L_2 = L_1 + \Delta L + G_d$, where ΔL is the predicted growth increment (Equation 1.3) and G_d is a random deviation from this predicted increment. This process (steps 2-4) was repeated for 100 shrimp for 100 weeks, in order to obtain a distribution of growth curves. Mean size (± standard deviation) at age was estimated from this distribution of growth curves, in order to describe growth of the average shrimp. This growth model was constructed to provide an estimate of growth for an average shrimp and, therefore, all differences in size structure among the sites used in this study (see Chapter 2) were ignored and all shrimp were treated as if from a single population.

Relative Fecundity

In May 2001, 33 gravid females were collected from various locations in the Upper Florida Keys. Additionally, in July 2002, eight gravid females were purchased from a local collector working in the Upper Florida Keys (Sea Life Inc.). Upon collection/purchase, females were measured (mm TL) and weighed (in 2001 only). Three

dimensions of the egg masses were measured, mass length (l_m), mass width (w_m), and mass height (h_m), and egg mass volume (V_m) was estimated as $4\pi(l_m*w_m*h_m/8)$.

Samples of the eggs were collected (~20 eggs per female) and preserved in 10% buffered formalin (2001) or 95% EtOH (2002). Ten eggs from each female were randomly selected and the diameter of each egg was measured (mm) with a dissecting microscope integrated with an image analysis program (Image Pro Plus). Mean egg diameter (d_e) was estimated for each female, and mean egg volume (V_e), for each female was calculated as $\pi(d_e^3)/6$ (Zhang et al. 1998). Finally, egg number (N_e) was estimated as V_m/V_e.

Because these measurements (female length, female mass, V_m, and N_e) were assumed to be allometric, they were log-transformed (base 10) and fit with linear regression models to investigate the relationships between $\log_{10}$(female length) and $\log_{10}$(wet body mass), $\log_{10}(V_m)$, and $\log_{10}(N_e)$, respectively (LaBarbera 1989).

To investigate possible influences of the egg preservation method or the effect of female length on egg size, a two-way ANCOVA was conducted to estimate the effect of $\log_{10}$(female length), preservation method, and their interaction on $\log_{10}(d_e)$.

Results

Size at Settlement

Both larval light traps and artificial settlement substrates were unsuccessful in collecting *S. hispidus* larvae. However, a total of 14 individuals were collected from the artificial reef (n=7) and survey studies (n=7). The average (± SD) TL of these individuals was 17.61 ± 2.84 mm. One individual was considered an outlier (27 mm TL). When this

outlier was excluded, mean (± SD) TL of settlers was 16.88 ± 0.89 mm, with individuals ranging from 14.8-18.4 mm TL.

Molt Interval

There were a total of 23 individuals used in this study. Of these, 14 had multiple molts, so the molt intervals were averaged for each individual. Virtually no growth was observed for individuals in this laboratory study. The overall mean (±standard error) intermolt duration was 23.18 ± 1.65 days. The molt interval was positively related to shrimp length (Linear regression: b±se=0.60 ± 0.09, $p<0.0001$, $r^2=0.6931$; Figure 1-1). There was no significant difference in the molt interval between males and females ($t_{12}=0.019$, $p=0.9851$). Mean (±SE) molt interval for females was 25.07 ± 2.52 days (n=7), whereas that for males was 25.0 ± 2.65 days (n=7). In addition, all ablated exopods were replaced upon subsequent molts, as well as 100% retention of internal tags.

Growth

Fifty-five of the 83 tagged shrimp were observed to molt over the course of the 10 week study, and 44 of these shrimp molted more than once. This resulted in 98 measurements of growth increments and 44 measurements of molt interval. In one case, a shrimp was not sampled for several weeks and later re-sighted having molted; this individual was excluded from the analysis.

Survivorship analysis revealed a significant effect of shrimp size (mm TL) on time to molt (weeks) (Wald's Chi-square: $\chi^2=6.03$, $p=0.0140$). Estimates for the fitted parameters, *a* and *b* (±SE), were as follows: a = -0.2930±0.4980 and b = 0.0333±0.0136 (to be used in Equation 1.2). The estimated weekly probability of molting decreased rapidly as shrimp size increased (Figure 1-2).

The mean growth increment (± SE) was 1.64 ± 0.23 mm, ranging from –4.2 to 7.9 mm, and varied substantially among individuals with different pre-molt sizes. The relationship between pre-molt size and growth increment was hump shaped, and best described by a quadratic model:

$$\Delta L_i = a + b(L_i) + c(L_i)^2 + \varepsilon_i, \quad 1.3$$

where ΔL_i is the growth increment after a molt, L_i is the pre-molt size, and ε_i is an error term (Polynomial Regression: $F_{2,95}$=8.72, p=0.0003; Figure 1-3), compared to a linear (Linear Regression: $F_{1,96}$=8.31, p=0.0049) and cubic model (Polynomial Regression: $F_{3,94}$=5.76, p=0.0012). The quadratic model provided parameter estimates (± SE) of *a*=-2.5265 ± 2.05, *b*=0.32 ± 0.13, and *c*=-0.0051 ± 0.002 (Figure 1-3). However, growth was highly variable, with pre-molt size accounting for only 15.5% of the variance in growth.

Growth simulations showed that size increased rapidly during the first 40 weeks, gradually slowing, and essentially stopping after approximately 60 weeks (1.15 years). Shrimp reached maximum size (~53 mm TL) by approximately 62 weeks (1.19 years) (Figure 1-4). Variation in size at age increased as age increased until about 35 weeks (0.67 year), when it began to decrease slightly.

Relative Fecundity

There was no effect of preservation method on $\log_{10}(e_d)$ (ANCOVA: $F_{1,37}$=0.83, p=0.3669). Therefore, all females were included in the regression analyses. Averaged across the entire sample, female length (TL) was 46.80 ± 0.91 mm (n=41), wet body mass was 3.01 ± 0.28 g (n=33), egg mass volume was 292.48 ± 37.98 mm^3 (n=41), egg diameter was 0.617 ± 0.014 mm (n=41), egg volume was 0.131 ± 0.009 mm^3 (n=41), and EN was 2,557 ± 337 eggs/brood (n=41) (± SE). Most of these variables covaried

positively with one another. Log_{10}(wet body mass) was significantly related to log_{10}(female length) (Linear Regression: a±SE=-6.08 ± 0.30, b±SE=3.89 ± 0.18, $F_{1,31}$=474.28, p<0.0001, n=33, r^2=0.94). Given the high association of these two variables, I focused on relationships with TL, although they can be readily converted to wet body mass.

As log_{10}(female length) increased, $log_{10}(V_m)$ increased (Linear Regression: a±SE=-4.99 ± 1.10, b±SE=4.40 ± 0.66, $F_{1,39}$=44.42, p<0.0001, n=41, r^2=0.53; Figure 1-5) and $log_{10}(N_e)$ increased (Linear Regression: a±SE=-4.21 ± 1.29, b±SE=4.48 ± 0.78, $F_{1,39}$=33.41, p<0.0001, n=41, r^2=0.46; Figure 1-6). There was no significant relationship between $log_{10}(d_e)$ and log_{10}(female length) (ANCOVA: log_{10}(female length), $F_{1,37}$=0.70, p=0.4073; interaction, $F_{1,37}$=0.83, p=0.3670).

Discussion

Size at Settlement

Previous estimates of size at settlement for *S. hispidus* are highly variable, ranging from last larval stage measurements of 21-31 mm to post larva measuring 10-31 mm (Gurney and Lebour 1941, Williamson 1976, Fletcher et al. 1995). A portion of the substantial difference in last and post larval length can be attributed to the rostrum of the last larval stage, accounting for as much as 31% of its total body length (Gurney and Lebour 1941). It has been hypothesized that it may be possible for larvae in the last stage to change to another practically identical larval stage and continue to grow to a larger size, due to extended periods of feeding in the water column (Gurney and Lebour 1941, Zhang et al 1998). With the presence of delayed metamorphosis in *S. hispidus* (Fletcher et al. 1995), this hypothesis may be supported, thus possibly contributing to the high

variability in the measurements of last larval size. All individuals encountered in this study were of the post larval stage and within the size range of those described in Gurney and Lebour (1941) and Williamson (1976). However, the variation in the size of individuals from this study was much smaller than those from Gurney and Lebour (1941) and Williamson (1976). This may be due to differences in environmental factors such as temperature or depth in the regions studied. Gurney and Lebour (1941) only collected individuals from Bermuda, sometimes at great depths (300 m), while Williamson (1976) collected individuals from the Indian Ocean. This suggests that there may be extensive spatial variation in the size at settlement of *S. hispidus*. However, Gurney and Lebour (1941) and Williamson (1976) only vaguely describe those shrimp that they considered post-larvae and, therefore, it is possible that they included larger juveniles. Further studies are needed to describe spatial variation in *S. hispidus* size at settlement.

Molt Interval

Previously, the only published data on molt interval of *S. hispidus* was for mature females. The results from this study indicate that younger smaller shrimp molt more frequently than larger older individuals. This relationship has also been documented in other crustacean species (Tremblay and Eagles 1997, Chen and Kennelly 1999, Comeau and Savoie 2001). This shift in molt interval may be due to the onset of sexual maturity, and, in females, the brooding of eggs. Because molting and brood development are related in *S. hispidus*, the increased molt interval may be required to assure sufficient time for embryo development (16 days) and oocyte maturation. What maintains male molting frequency is unknown at this point. Since male molt interval is not different from that of females, it is possible that the cycle of female molts is what maintains male molting frequency.

Growth

The time period between molts was estimated as the time between tagging with the molt indicator and the time at which the exopod was replaced. This estimation assumes that shrimp molted just once before being re-measured and re-tagged. This assumption may introduce additional error in modeling the weekly probability of molting. However, the molt interval study (Figure 1.1) indicated that the minimum time interval between successive molts was 9 days. Therefore, surveys were conducted at weekly intervals in order to minimize this error.

The relationship between growth increment and pre-molt size indicated that smaller shrimp have smaller growth increments, which then increase until approximately the size at maturity (30 mm TL) when they gradually begin to decrease again (Figure 1.3). Given that larger shrimp tend to molt less frequently and their growth increment begins to decline, it is apparent that growth rates tend to decline as shrimp size increases. This is supported by the growth curves generated by the PSGC approach.

Similar to Chen and Kennelly (1999), pre-molt size only accounted for 15.5% of the variation in growth increment. It is apparent that other external factors may influence growth increment. Both abiotic and biotic factors, including temperature, depth, and food supply, may also be influencing growth increments (Annala and Bycroft 1988, Chen and Kennelly 1999, Hartnoll 2001). Further studies are needed to identify the effects of these factors and to potentially model growth of individuals from different habitats separately (see Chapter 2).

The growth curves generated in this study indicate that the average female reaches sexual maturity (30 mm TL) 4 weeks after settlement. Variation in mean size seemed to decrease by approximately 50 weeks, at about 50 mm TL. This is probably due to a

decreased growth increment at this size (Figure 1.3). Finally, it is worth noting that this model is based on growth data taken during the summer. Therefore, the growth rates generated by this study may be an overestimation of annualized growth, due to the warmer temperatures in the summer months. Also, since there were differences in the size-structure of the populations used in this study, I re-constructed this model for each population (inshore and offshore) based on their growth increments (see Chapter 2).

Since the tagging study used all sized individuals in the prediction of growth increments and each run started with a settler, the mean growth curve (Figure 1.4) is based on true post-settlement age, and thus, provided a means of ageing *S. hispidus*. Previously, the most reliable method for ageing crustaceans was through the measurement of the concentration of lipofuscin deposits, irregular yellow-fluorescing granules found in the post-mitotic tissues of senescing animals (Sheehey et al. 1994). However, this method is only possible in species that can be reared in the laboratory, in order to use known-aged individuals to devise a statistical model that predicts age from lipofuscin concentration (Sheehey 1990, Sheehey et al. 1994). Sheehey et al, (1994) concluded that lipofuscin concentration was more accurate in predicting crayfish age than a model using body size measurements. However, the model that Sheehey et al. (1994) used in predicting age from body size measurements was a von Bertalanffy growth model. The von Bertalanffy growth model is commonly used in describing fish growth, which is assumed to be continuous (Chen and Kennelly 1999), whereas crustacean growth is discontinuous. Since the PSGC approach produces growth curves that mimic discontinuous growth and incorporates intrinsic variation, it may provide a more realistic means with which to age crustaceans than the von Bertalanffy model. Therefore, the

PSGC approach may provide comparable estimates of age as a model predicting age from lipofuscin concentration. Further studies are needed to test this assumption.

Relative Fecundity

The positive, linear relationship between female wet body weight and total length is consistent with observations made for *S. hispidus* (Zhang et al. 1998). However, the slope produced by this study (b±SE=3.89 ± 0.18) was significantly different (t_{53}=-64.74, $p<0.0001$) from that of Zhang et al. (1998) (b±SE=3.12 ± 0.14; Figure 1-7) (Zar 1996). This may be due to different sized females used in each study. For example, as mentioned earlier, the mean female mass for this study was 3.01 g, whereas that for Zhang et al. (1998) was 1.40 g.

This study shows that total length is a good predictor of fecundity, also consistent with previous observations (Zhang et al. 1998). However, $\log_{10}(V_m)$ seems to be a better measure of relative fecundity than $\log_{10}(N_e)$, when regressed against $\log_{10}$(female length). One explanation for this may be variation in measuring egg diameters (critical for egg number estimations), since not all eggs were perfectly spherical. This argument is supported by the non-significant effect of $\log_{10}$(female length) on $\log_{10}(d_e)$. Further studies are needed to identify the true size at sexual maturity for both males and females, possibly through the use of histology.

Conclusion

The results of these studies begin to provide valuable information for the possible future management of *S. hispidus* for the marine ornamental trade. I provide a method for ageing *S. hispidus*, and possibly other crustacean species, without the need of successful larviculture. In addition, I provide an easily attainable measurement of

relative fecundity (V_m) with minimal disturbance. With additional research, particularly to investigate: 1) the influence of environmental factors on *S. hispidus* growth, 2) estimation of the true size at maturity, and 3) physical and environmental factors that contribute to population dynamics and demographics, managers can begin to develop management plans based on its life history.

Table 1-1. Details of sites used in the growth tagging study.

Region Site	Depth (m)	Distance from shore (km)	Reef type	Coordinates
Offshore				
Davis Deep	14.6	7.60	contiguous	24° 55.461'N, 80° 30.019'W
Crocker Deep	14.6	7.02	contiguous	24° 54.279'N, 80° 31.681'W
Crocker Shallow	6.71	6.69	contiguous and patch	24° 54.454'N, 80° 31.672'W
Inshore				
Rock 1	3.05	1.63	patch	24° 56.548'N, 80° 33.666'W
Rock 2	3.66	1.60	patch	24° 56.991'N, 80° 33.157'W
Rock 3	5.79	2.04	patch	24° 57.256'N, 80° 32.774'W

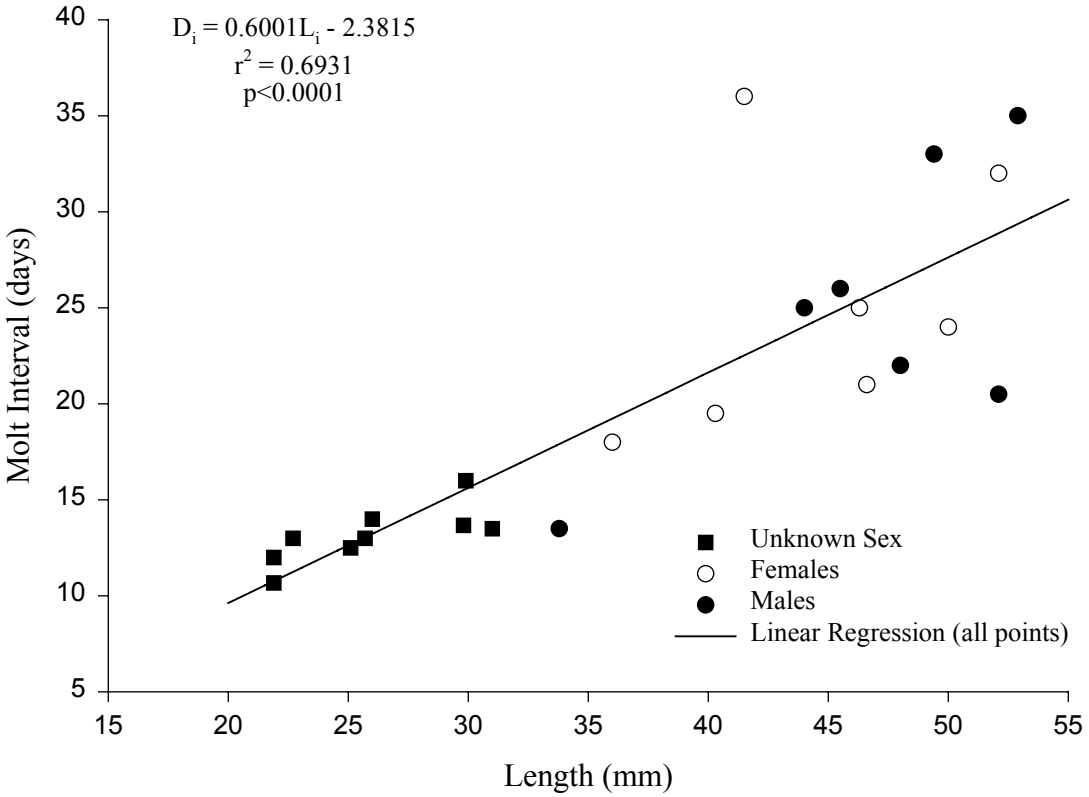

Figure 1-1. Linear regression (solid line) of mean molt interval (days) on body size (mm TL) of all *S. hispidus*. Closed squares represent individuals of unknown sex, open circles are females, and closed circles are males. D_i is the molt interval and L_i is initial length. Sample sizes are as follows: unknown, n=9; female, n=7; male, n=7.

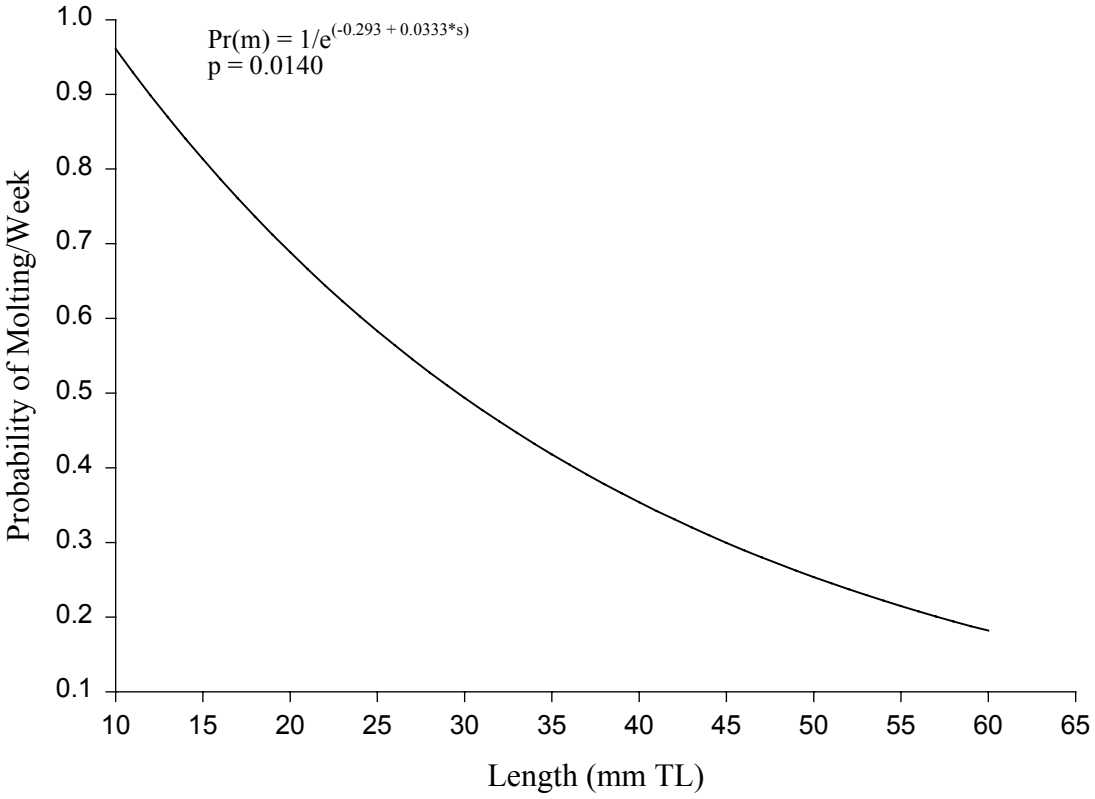

Figure 1-2. Estimated weekly molting probability as a function of shrimp size (mm TL) based on survivorship analysis (exponential model). Parameter estimates for *a* and *b* (Equation 1.2) are provided above, where Pr(m) is the estimated weekly molting probability and s is shrimp length (mm TL) (n=44).

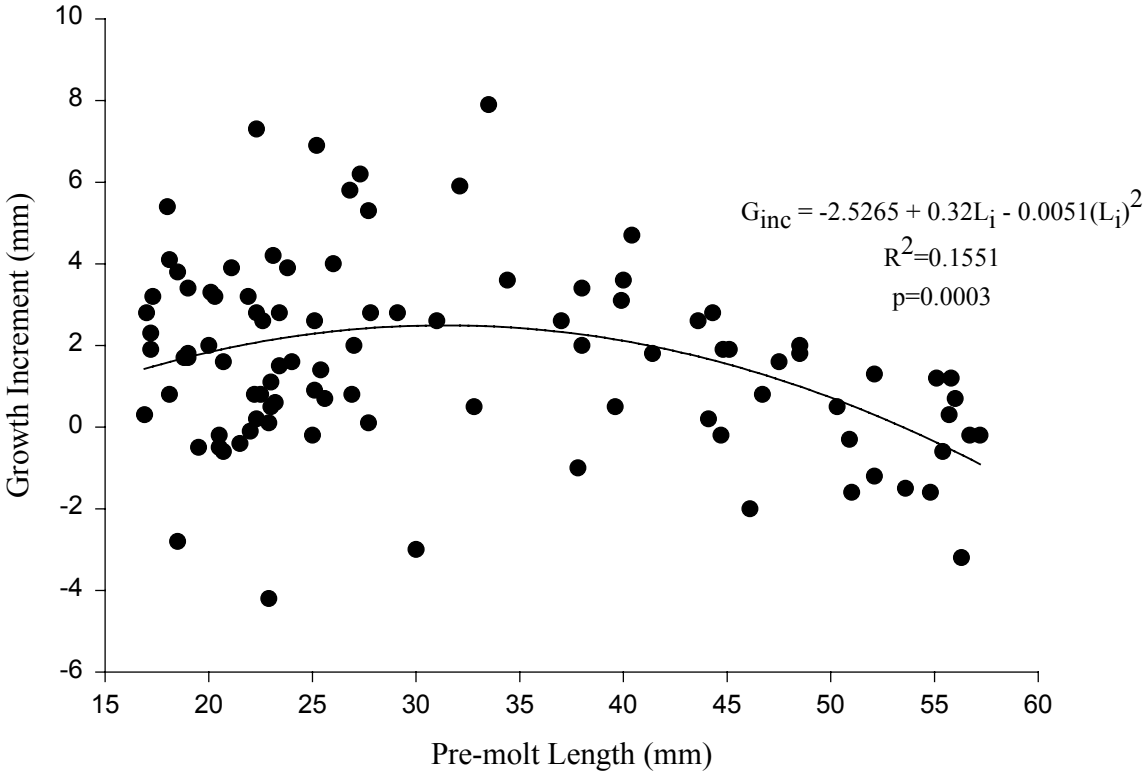

Figure 1-3. Polynomial regression (solid line) of growth increment (mm) on pre-molt length (mm TL) of *S. hispidus*. Parameter estimates for *a*, *b,* and *c* (Equation 1.3) are provided in the above regression equation, where G_{inc} is the growth increment and L_i is the pre-molt length (n=98).

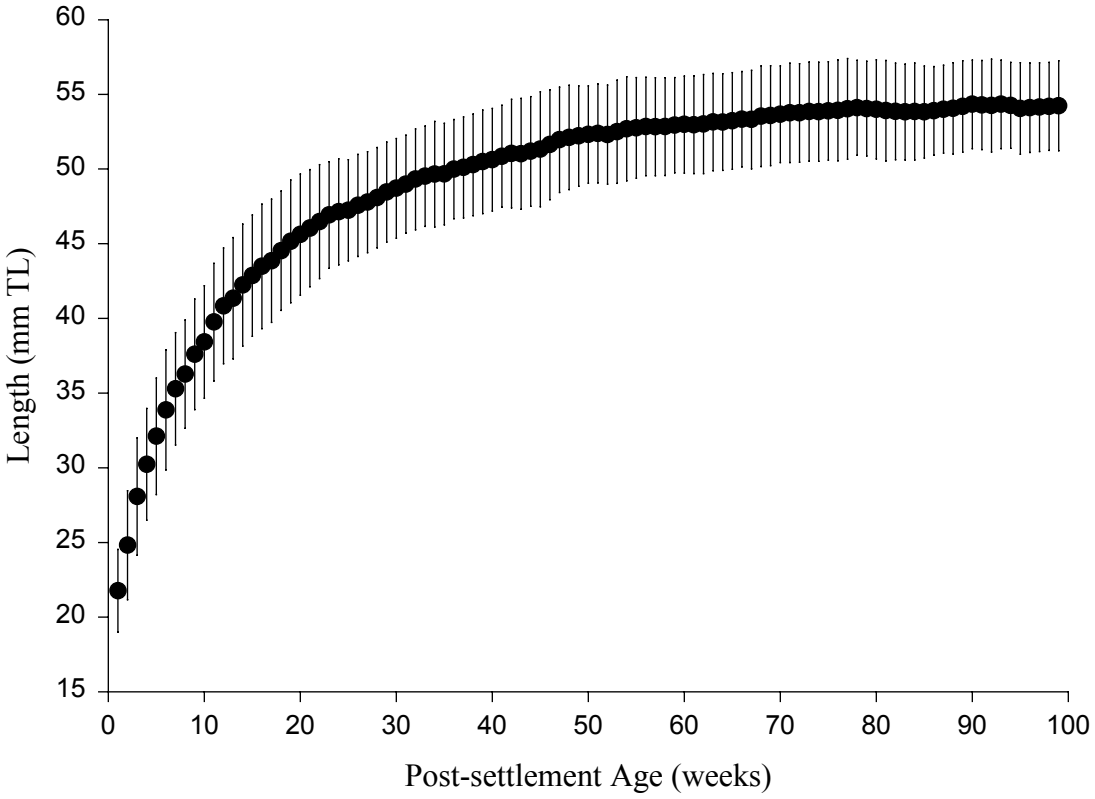

Figure 1-4. Mean (dots) and standard deviations (error bars) of length (mm TL) at post-settlement age (weeks) resulting from 100 simulations of the growth model.

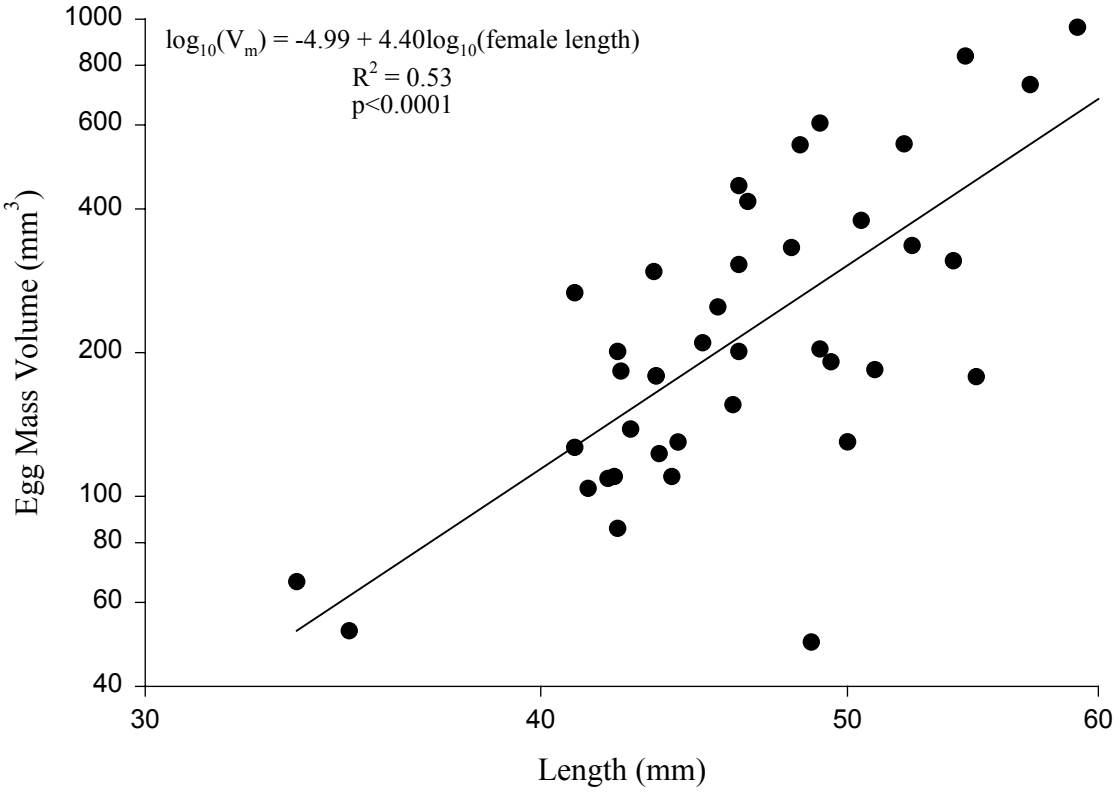

Figure 1-5. Relationship between female length (mm TL) and egg mass volume (mm^3) in *S. hispidus* (n=41). Equation and regression line (solid line) represent linear regression of $\log_{10}$(female length) (mm TL) on $\log_{10}(V_m)$ (mm^3) where V_m is egg mass volume.

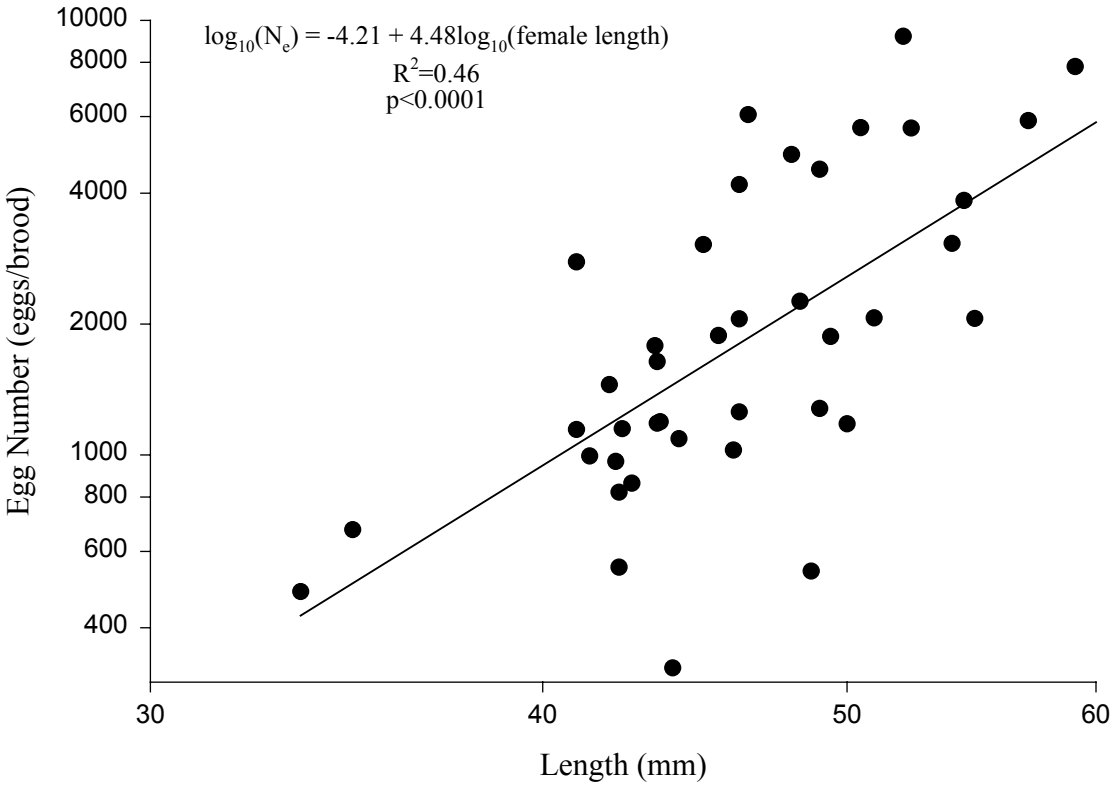

Figure 1-6. Relationship between female length (mm TL) and egg number (eggs/brood) in *S. hispidus* (n=41). Equation and regression line (solid line) correspond to linear regression of $\log_{10}$(female length) (mm TL) on $\log_{10}(N_e)$ (eggs/brood) where N_e is egg number.

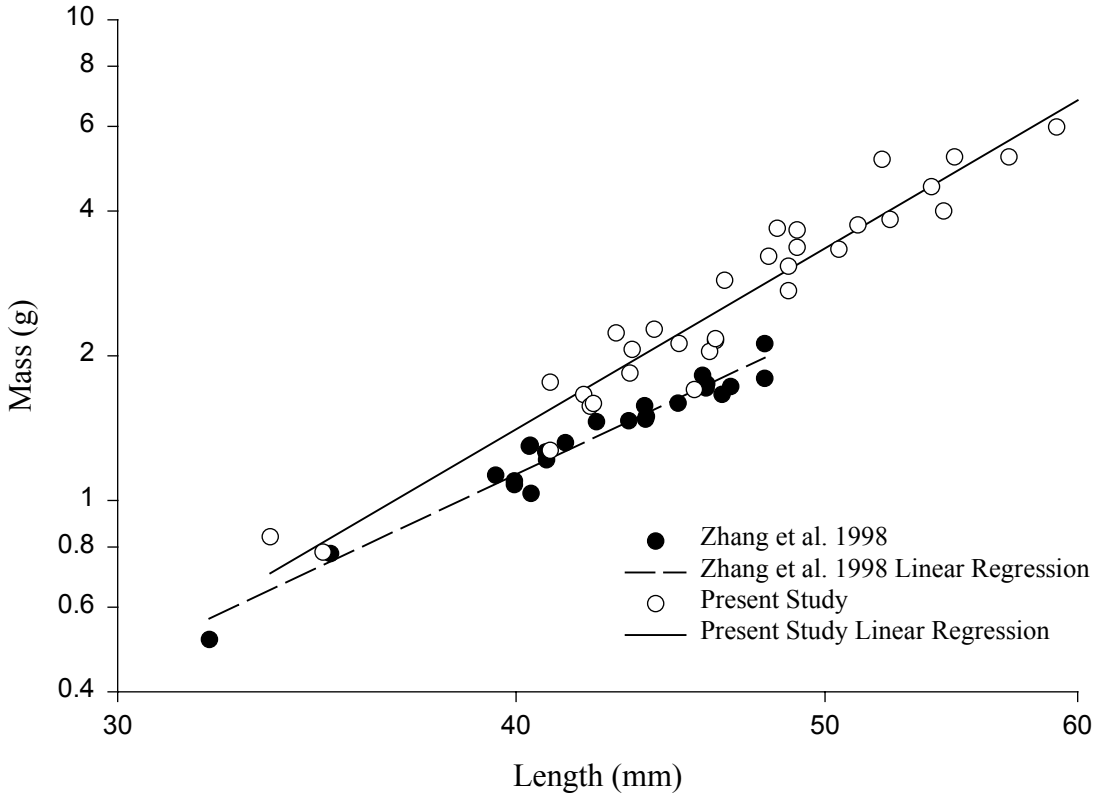

Figure 1-7. Relationship between female length (mm TL) and female wet body mass (g) in *S. hispidus* from Zhang et al. (1998) (closed circles) and present study (open circles). Dotted line represents regression of $\log_{10}$(female length) on $\log_{10}$(female mass) from Zhang et al. (1998), solid line represents that of present study. Sample sizes are as follows: Zhang et al. (1998), n=24; Present Study, n=33.

CHAPTER 2
EFFECTS OF SETTLEMENT, POST-SETTLEMENT MORTALITY, AND GROWTH, ON THE POPULATION SIZE-STRUCTURE OF THE BANDED CORAL SHRIMP, *Stenopus hispidus,* IN THE UPPER FLORIDA KEYS

Introduction

Spatial variation in population structure among marine invertebrate populations has been well documented (von Montfrans et al. 1995, Miron et al. 1999, Pascual et al. 2001). Typically, studies of this variation focus on one phenomenon (e.g., settlement, growth, movement, or post-settlement mortality). However, the structure of marine invertebrate populations probably does not depend on any one process alone, but rather on several processes acting together.

Population structure is often linked to the settlement rates and larval supply to a habitat (Minchinton and Scheibling 1991). For instance, it has been argued that the number of larvae settling to a habitat determines the number of older individuals found in that habitat (Sale 1991). However, concentrating on settlement by itself may cause one to dismiss other processes that are equally likely to affect population structure, such as post-settlement survival, movement, or growth. If spatial variation in post-settlement mortality exists between two habitats that receive equal levels of settlement, the two habitats will not be structured similarly (Rochette and Dill 2000, Pascual et al. 2001). Furthermore, if one fails to detect a relationship between adult numbers and settlement, post-settlement movement or mortality may contribute to this lack of correlation (Robertson 1988). Most studies that identify post-settlement mortality as the primary

factor contributing to populations often fail to quantify post-settlement movement (but see Frederick 1997) and thus confound these two processes.

Finally, differential growth rates between habitats may contribute to differences in population structure. Kube et al. (1996) found that the growth rates of two species of marine bivalve were considerably lower in a brackish sublittoral zone of the Southern Baltic Sea, compared to growth rates from a full marine environment. Another environmental factor to which differential growth rates are often attributed is temperature, especially in crustaceans (Hartnoll 2001). Clearly, two habitats that share similar settlement, post-settlement mortality, and movement rates, but differ in temperature, possibly due to depth, might be expected to differ in population structure as a result.

These processes can also interact to affect the population structure of an organism. For example, in a species of fish in which size-selective mortality was present, Werner et al. (1983) found that smaller fish underwent lower growth rates in the presence of a predator, due to behavioral responses. In fish, it has been hypothesized that lower growth rates, coupled with size-selective mortality, could prolong the period of increased vulnerability to predators (Leggett and DeBlois 1994), increase mortality (Werner et al. 1983), and/or increase the amount of time it takes for an individual to reach a size-refugia and sexual maturity (Miller et al. 1988, Bailey and Houde 1989, Werner et al. 1983). Thus, differential growth rates between habitats, whether through differential food availability, temperature, or behavioral responses to predation can give rise to spatial variation in population size-structure between the habitats.

Understanding which processes affect the population structures of marine organisms, and to what degree, is critical for understanding the dynamics of these systems. With a better understanding of the population dynamics of these organisms, management practices can be tailored for particular areas or habitats. One fishery in need of information for the development of management practices is the marine ornamental trade. The marine ornamental trade is growing at a high rate, with documented declines in local fish abundances and habitat quality, due to current practices (Tissot and Hallacher 1999).

Over 18 species of cleaner shrimps are collected for marine aquaria (Fletcher et al. 1995). In addition to concern about over-harvesting and harvest effects on habitat quality, it has been hypothesized that the removal of cleaner shrimps might also lead to declines in the local fish populations (e.g., via increased local fish diseases) (Fletcher et al. 1995, Zhang et al. 1997), therefore having broader implications for the ornamental trade and reef communities.

One of the most popular cleaner shrimps in the marine ornamental trade is the banded coral shrimp, *Stenopus hispidus* (Olivier, 1811) (Zhang et al. 1998). *Stenopus hispidus* is a reef associated cleaner shrimp (Decapoda: Stenopodidae) with a worldwide distribution. As adults, *S. hispidus* are found in crevices or overhangs in reefs at depths ranging from <1 to 210 meters and are extremely limited in post-settlement dispersal (<1 m^2) with males exhibiting territorial behavior within this area (Limbaugh et al. 1961, Stolen 1964, Young 1979, Fletcher et al. 1995). Adults are typically found in reproductive pairs (Limbaugh et al. 1961, Johnson 1969, Young 1979), possibly formed as juveniles (Limbaugh et al. 1961). After a molt, the female typically mates with her long-term mate, and a mass of blue-green eggs is deposited on the swimmerets (Zhang et

al. 1998). As the larvae develop, the blue-green eggs begin to lose this pigmentation and darkly pigmented eyespots begin to appear. Hatching typically occurs within 16 days of spawning (Young 1979). *Stenopus hispidus* larvae have a highly variable larval duration (17-30 weeks) and are capable of delaying metamorphosis until suitable habitat is encountered (Fletcher et al. 1995). It is still unknown what settlement cues *S. hispidus* may use.

The overall objective of this chapter is to 1) compare the size-structure of populations of *S. hispidus* in different habitats and 2) examine the mechanisms that produce spatial variation in population size-structure. In particular, I examine i) settlement, ii) post-settlement movement and mortality, and iii) growth rates in inshore and offshore habitats of the Upper Florida Keys.

Methods

Population Structure

During the summers of 2001 and 2002 (May-August), I conducted surveys in both inshore and offshore regions of the Upper Florida Keys (Table 2-1) to quantify spatial and temporal variation in *S. hispidus* abundance and size-frequency distributions. The surveys consisted of thoroughly searching each reef and surrounding rocks for *S. hispidus*. Every shrimp encountered was collected, measured (mm TL), and sexed (male, female, and unknown) underwater, and released. Sex was assigned using a modification of criteria given by Stolen (1964) and Johnson (1969): (1) if a single, median spine was found on the ventral surface of the abdominal segments of a shrimp >30 mm TL, it was assumed to be a male; (2) If a shrimp >30 mm TL lacked spines, it was called a female; (3) If a shrimp carried a blue-green egg mass on the ventral surface of the abdomen or had a blue-green mass beneath the dorsal surface of the carapace, it was assumed to be

female; (4) All individuals <30 mm TL (which typically have an abdominal spine) were categorized as unknown sex, unless criteria 3 was met.

For all reefs that were surveyed in both 2001 and 2002 (three inshore and two offshore), I evaluated the effects of region, site, year, and their interactions on shrimp total length (log-transformed) using a nested-ANOVA model with site nested within region. In the case of a significant year effect in this analysis, separate nested-ANOVA models were run for each year, testing for region and site effects, again with site nested within region. All sites for a given year (2001: five sites, 2002: 10 sites) were included in these analyses, including those that were not surveyed both years. In the case when a significant site effect was found, post-hoc comparisons of means were conducted to see which sites differed within and between regions (Younger 1998).

Larval Settlement

To quantify spatial variation in settlement of *S. hispidus* in the Upper Florida Keys, I used artificial reefs that were cleared of all fishes and invertebrates on a weekly basis. In the summer of 2001, two arrays of five artificial reefs were deployed in each of the inshore and offshore regions. All artificial reefs consisted of small boulders of limestone, taken from a single quarry in Miami, Florida. Reefs were deployed within a few days of one another, in June 2001, and were approximately 1 m^2 in basal area. In the summer of 2002 (May-July), I conducted 10 weekly surveys and collections from each artificial reef. Collections consisted of removing all fishes and invertebrates using Eugenol (an anesthetic, also known as clove oil), and preserving them in 95% EtOH for later identification and measuring.

To check for possible outliers (i.e., migrants) among the settlers collected, I used estimates of size at settlement of *S. hispidus* from a separate study (see Chapter 1). This

process involved estimating a mean size at settlement, and removing all individuals who were greater than three standard deviations from this mean. Individuals collected in this study that were larger than that upper limit (26.11 mm TL) were considered migrants and removed from the analysis. No migrants were found in this study.

Counts of shrimp collected, for each array of reefs on each collection day, were square-root-transformed and analyzed with a repeated measures ANOVA, to test for the effect of site, transect (nested within site), and week (the repeated factor) on the number of settlers in each region.

Post-settlement Mortality and Movement

Tagging study. To quantify spatial and temporal variation in natural post-settlement mortality rates of *S. hispidus*, I conducted a tagging study at three inshore and two offshore sites in the Upper Florida Keys during the summers of 2001 (July-August) and 2002 (May-July). These sites were among the same sites used in the growth study from Chapter 1, and the population structure study above (Table 2-2).

Shrimp in each site were tagged (Chapter 1; Godin et al. 1996), measured (mm TL), and sexed. To keep track of individuals, a total of six colors were used (black, green, blue, red, orange, and yellow) and distance between two shrimp with the same color was maximized and always greater then their estimated home range (~1 m) (Limbaugh et al, 1961, Stolen 1964, Young 1979). Holes where shrimp were found were marked with numbered flagging tape tied to a weight and mapped onto PVC paper for use underwater. I then conducted extensive weekly surveys of each study site. In these surveys, I: 1) recorded presence/absence of previously tagged shrimp, 2) tagged, measured, and sexed any newly encountered shrimp, and 3) in 2001, measured the distance moved (when an individual moved from its original site). Each week, prior to surveying, the maps of each

site were updated with the locations of newly tagged and relocated shrimp in order to assure all tagged individuals were included in the surveys.

Since each shrimp was individually tagged, the time to disappearance of an individual was known. These times were analyzed using a survivorship analysis (Cox' Proportional Hazards Model), which allows for the estimation of the effects of covariates in shrimp disappearance (Barbaeau et al. 1994, Allison 1995). Because of the small home range reported for this species, I assumed that disappearances were the result of mortality rather than movement. To eliminate tagging induced mortality from estimates of mortality, I excluded all shrimp that died within the first week of tagging. Covariates considered in the survival analysis included shrimp size (mm TL), region (inshore or offshore), site (five sites used in the study), and year (2001 or 2002). I report significant effects in the model as well as estimates of the hazard ratio, which can be converted to estimate the percent change in survivorship for each one-unit increase of quantitative covariates (i.e., body size) as

$$Pr(s) = 100*(1-h), \qquad 2.1$$

where h is the hazard ratio (Allison 1995).

I compared distances that shrimp moved in inshore vs. offshore sites using a t-test. Analyses were based on mean movement distances (per week) for each shrimp. Analyses were repeated after excluding all weekly movement of 0 m. Finally, I compared the proportion of movements (>0 m) from the two regions through the use of a Chi-square test.

Tethering experiments. To further investigate spatial variation in predation and size-selective mortality, I conducted a tethering experiment from August 5-8, 2002, using the

five sites from the tagging study. In previous studies, I found that translocating shrimp, without tethering, resulted in the disappearance of all individuals within 24 hours, due to unknown causes. Therefore, tethering was necessary for this study, to assure no translocation-induced movement. All naturally occurring shrimp were removed from the study sites prior to experimentation. Seventy shrimp were purchased from a local collector operating in the Upper Florida Keys (Sea Life Inc.). None of these shrimp were collected in any of the study sites. Shrimp were sexed, measured, and separated into two size categories; small: ≤30 mm TL and large: ≥40 mm TL. Each shrimp was tethered to an 85 g weight with a 250 mm length of 2.72 kg test monofilament line by securing a loop of the monofilament line to the carapace with a drop of cyanoacrylate glue (Pile et al. 1996, Acosta and Butler 1999). Tethered shrimp were then held in a closed aquarium system, in individual containers, until deployment the next day. A total of 40 shrimp were randomly assigned to the offshore region (10 of each size category in each of 2 sites) and 30 to the inshore region (4-6 of each size category in each of 3 sites). Experimental shrimp were placed into holes where a shrimp had previously been encountered. As with the tagging study, a survivorship analysis (Cox Proportional Hazards Model) was used to test for the effects of region (inshore or offshore), site (five reefs used in study), and size category (small or large) on survival.

Typically, tethering studies include a caged treatment of tethered individuals in the field to control for potential tethering effects (Peterson and Black 1994, Rochette and Dill 2000). However, caging tethered shrimp in the wild was not possible. Therefore, a separate lab experiment was conducted to assess the tether effect (Pile et al. 1996). Forty shrimp were purchased from the same local collector. Shrimp were measured and placed

into one of the two size categories (as above). Ten shrimp of each size category were then randomly assigned a treatment, un-tethered or tethered (as described above although with 100 mm tethers). Shrimp were then randomly assigned to a holding tank (in individual containers) and monitored for a week for mortality and molting activity. Survivorship analysis (Cox Proportional Hazards Model) was used to test for the effects of tethering (tethered or non-tethered), size category (small or large), and tank (tank 1 or tank 2) on the survivorship of individuals.

Predator abundance. To characterize variation in predator abundance in the two regions, I surveyed each of the five sites by counting all possible predators (including invertebrates) within a 1 m radius of each marked hole from the tagging study. Fish predators surveyed were among the following families: Haemulidae, Lutjanidae, Serranidae, Scorpiaenidae, Tetraodontidae, Synodontidae, Kyphosidae, Pomacentridae, Labridae, and Sciaenidae. The only invertebrate predators encountered were mantis shrimps (Order: Stomatopoda). The abundance of each predator from each hole was square-root-transformed and analyzed with a k-means cluster analysis (STATISTICA 1999) to see if the clusters generated corresponded to the designated regions. Two clusters were generated in this analysis.

Growth

Tagging study. The 2002 tagging study was modified to compare shrimp growth between the inshore and offshore regions. The left exopod of each shrimp's uropod was clipped. Since all hard parts are replaced at molting (Chapter 1; Linnane and Mercer 1998), I could identify tagged shrimp that had molted by the presence of the left exopod. All tagged shrimp with an intact left exopod were re-measured and re-clipped.

A mean pre-molt length (mm) and mean growth increment (mm) was calculated for each individual that was observed to molt during the course of this study. One individual was missed and later rediscovered. Since the number of molting events that occurred in this interval could not be assigned, the growth increment associated with this interval was excluded from the analysis. A two-way ANCOVA tested for the effects of region and mean pre-molt length on mean growth increment. In the case that mean pre-molt length was found to significantly effect mean growth increment, separate linear regression analyses for each region were conducted to describe this relationship.

As mentioned earlier, temperature has been known to affect crustacean growth, typically causing faster growth at higher temperatures (Hartnoll 2001). Because the inshore and offshore regions used in this growth study differed in depth, and temperature is generally negatively correlated with depth (Lee et al. 1992), I measured bottom temperature in each of the two regions, several times throughout the summer. Mean temperatures were calculated for each region and compared with a t-test.

Growth model. Once growth in each region was evaluated in the above study, I applied a crustacean growth model (Chapter 1; Chen and Kennelly 1999) in order to model the growth of shrimp in each region. To do this, I used the same distribution of settlers when choosing a start size, as well as the same weekly probability of molting (Pr(m)) as described in Chapter 1 (Equation 1.2; Figure 1-2). However, the estimated growth increment for a given pre-molt size was based on the linear regression analyses conducted to describe the relationship between mean pre-molt length and mean growth increment for each region. Therefore, the equations for estimated growth increment for each region were

$$\Delta L_i = a + b(L_i) + \varepsilon_i, \quad 2.2$$

where ΔL_i is the growth increment after a molt, L_i is the pre-molt size, *a* and *b* are parameter estimates provided by the linear regression models of each region, and ε_i is an error term. As in Chapter 1, deviations (G_d) from the predicted growth increment for each region were calculated, to provide estimates of variation in growth. These deviations were also incorporated into the growth models. Using the same sequence of steps as in Chapter 1, I applied this growth model to each region for 100 individuals for 100 weeks each. Mean size (± standard deviation) at age was estimated from the distribution of growth curves for each region, in order to compare the growth trajectories between the two regions.

Results

Population Structure

A total of 261 shrimp were measured among the sites surveyed in both in 2001 and 2002. Region (Nested ANOVA: $F_{1,251}$=317.62, p<0.0001) and year (Nested ANOVA: $F_{1,251}$=13.90, p=0.0002) had significant effects on shrimp size, although there was no effect of site or any of the interactions (Nested ANOVA: all F<1.94, all p>0.1325). The year effect was strong in the offshore region but no so much in the inshore region (Figure 2-1). Overall, shrimp inshore were approximately 18 mm larger than those offshore.

Due to the significant year effect, and differences in the sites sampled in 2001 vs. 2002, each year was analyzed separately. In 2001, the five sites yielded 111 shrimp. Regions differed significantly in shrimp body size (Nested ANOVA: $F_{1,106}$=146.97, p<0.0001), but there was no significant variation among sites (Nested ANOVA: $F_{3,106}$=1.55, p=0.2057; Figure 2-1). In 2002, the 10 sites yielded 236 shrimp. There were

significant differences among regions (Nested ANOVA: $F_{1,226}$=178.29, p<0.0001) and among sites within regions (Nested ANOVA: $F_{8,226}$=2.97, p=0.0035; Figure 2-1). Also in 2002, among the three sites that had both shallow and deep areas surveyed, only one (Crocker) exhibited a significant difference in mean shrimp size between the two depths (p=0.0392), where the mean (± standard error) total length in the deeper area was 19.97±1.03 mm and that for the shallow area was 22.28±1.05 mm (Figure 2-1).

Larval Settlement

One shrimp was collected from the inshore artificial reefs, whereas 43 were collected offshore. Using the criteria outlined above, no migrants were found in either region. The average size (± SE) of all the settlers collected was 17.38±0.19 mm TL (range: 14.0-20.8 mm). There were significantly more settlers offshore than inshore (Repeated measures ANOVA: $F_{1,2}$=64.08, p=0.0152) but the number of settlers was unaffected by week and transect within region (Repeated Measures ANOVA: all F<1.81, all p>0.1) (Figure 2-2).

Post-Settlement Mortality and Movement

Tagging experiment. To evaluate the patterns of mortality that were observed in the tagging study, a full survivorship model was considered that included effects of region, site, year, and shrimp size. Only the effect of shrimp size on survival was significant (Wald's Chi-square: χ^2=12.18, p=0.0005), so the model was simplified to include only shrimp size. This simplified model provided a more precise estimate of the hazard ratio. Smaller shrimp had much lower survivorship than larger shrimp (Figure 2-3). Specifically, for each 1mm increase in total length, the probability of survival increased by 5.8% (Equation 2.1).

Overall, shrimp in both regions moved similarly (t_{57}=1.599, p=0.115) with an average (± SE) displacement of 0.34±0.10 m (range: 0-9.33 m). With 0m movements eliminated, shrimp still moved similarly between the regions: 1.18±0.35 m (Range: 0.20-9.33 m) pooled across regions. Finally, there was no significant difference in the proportion of movements (>0m) between the inshore and offshore regions (χ^2=3.50, df=1, p>0.05).

The results from the tethering experiments identified no effects of tethering or body size and no regional or site-specific difference in survival. In the laboratory control experiment there were no differences in the survivorship of the tethered or un-tethered individuals (Wald's Chi-square: χ^2=0.3099, df=1, p=0.5777). In addition, neither body size (Wald's Chi-square: χ^2=1.23, df=1, p=0.2670) nor tank (Wald's Chi-square: χ^2=1.5481, df=1, p=0.2134) affected shrimp survival (Figure 2-4). Similarly, in the field experiment, neither shrimp size nor region significantly affected survivorship (Wald's Chi-square: χ^2=0.4622, df=2, p=0.7936; Figure 2-5).

Predator abundance. In all, 94 holes were surveyed for this study and 24 predator species identified. Sixty-six of these holes were surveyed in the offshore region and 28 from the inshore region. Overall, the two clusters generated by the k-means clustering analysis did separate the holes from the two regions. Cluster 1 (inshore) consisted of 19 of the surveyed holes, all of which were found inshore. Only eight predator species were found in this cluster, which was dominated by three predator species: 1) *Haemulon plumieri*, 2) *Anisotremus virginicus*, and 3) *Haemulon parra* (descending order of mean abundance; Figure 2-6). Cluster 2 (offshore) consisted of 75 surveyed holes, all 66 from the offshore region and 9 from inshore. This cluster was not dominated by any one

predator in particular, but instead was made up of low abundances of all the predators surveyed (except *Kyphosus sectatrix* and *Lutjanus apodus*; Figure 2-6).

Growth

Tagging study. Fifty-five shrimp molted during the course of this study. Both region (ANCOVA: $F_{1,52}$=14.05, p=0.0004) and mean pre-molt length (ANCOVA: $F_{1,52}$=18.72, p<0.0001) had significant effects on mean growth increment. The least-squares means (± SE) for the growth increment in the two regions were 3.18±0.52 mm inshore and 0.27±0.39 mm offshore (Figure 2-7). There was no significant relationship between mean pre-molt length and mean growth increment in the offshore region (Linear Regression: $F_{1,31}$=0.48, p=0.4942; Table 2-3; Figure 2-8). However, in the inshore region, there was a significant negative relationship between mean pre-molt length and mean growth increment (Linear Regression: $F_{1,20}$=30.71, p<0.0001; Table 2-3; Figure 2-8).

The mean bottom temperatures differed significantly between the two regions (t_{27}=2.77, p=0.0101). Overall, the mean temperature (±SE) of the inshore region was 27.64±0.32°C, whereas that for the offshore region was 26.48±0.27°C.

Growth model. The linear regression models to describe the relationship between mean pre-molt length and mean growth increment for each region provided estimates of *a* and *b* for Equation 2.2 (Table 2-3). With these parameter estimates, the growth models revealed that the expected growth trajectories for the two regions differed substantially (Figure 2-9). Consistently, the shrimp in the inshore region reached particular sizes approximately four times faster than those in the offshore region. For example, the inshore shrimp reached sexual maturity (approximately 30 mm TL) in approximately 4

weeks (post-settlement), whereas those offshore did not reach sexual maturity until approximately 16 weeks (post-settlement).

Discussion

The significant spatial variation in *S. hispidus* size structure is consistent with observations made by local collectors in the Upper Florida Keys (Ken Nedimyer, personal communication). Generally, this difference must stem from regional differences in settlement and/or subsequent survivorship, movement, or growth.

Often, observed spatial variation in settlement is attributed to oceanographic processes (Sponaugle and Cowen 1996, Balch and Scheibling 2000). Here I have shown significant and temporally consistent differences in the supply of settlers to the inshore and offshore regions. This difference may be due to oceanographic processes. In mid-late April, a cold cyclonic gyre forms seaward of the middle and lower Keys, where the Florida Current shifts from an eastward to northward flow (Lee et al. 1992). Prevailing easterly winds circulate over this gyre and cause a convergence of Ekman flow, which facilitates an inshore transport of pelagic larvae from the Florida Current to the fringing reefs (Lee et al. 1992, Ogden 1997). This inshore transport of larvae to the fringing reefs could cause larvae to reach the offshore study sites before those inshore, thus potentially depleting larval supply to the inshore region. Other studies have identified tidal currents and wind stress as factors influencing larval settlement (Sponaugle and Cowen 1996, Paula et al. 2001). Further studies are needed to quantify the effects of tidal currents and wind stress to the settlement of organisms in the Upper Florida Keys.

Spatial variation in settlement has also been attributed to larval habitat selection (Miron et al. 1999, Paula et al. 2001). In addition, several studies have found that the larvae of many marine organisms prefer to settle to habitats where conspecifics are found

(Sweatman 1985, Raimondi 1988, Sweatman and St. John 1990, Wellington 1992). As mentioned earlier, it is unknown what settlement cues *S. hispidus* may be using. It is possible that *S. hispidus* larvae may be using chemical cues from conspecifics on the reefs as settlement cues. The offshore reefs were observed to have higher abundances of *S. hispidus*, and therefore, may contribute higher amounts of a chemical settlement cue. However, further studies are needed to identify precisely what cues *S. hispidus* larvae are using for settlement.

The tagging study documented significant size-selective mortality in *S. hispidus*, in the Upper Florida Keys. Furthermore, the pattern of size-specific mortality did not differ between sites or regions. Smaller individuals have much higher mortality rates than do larger individuals. These results are consistent with other studies in which size-selective mortality has been observed in marine invertebrates (Barbeau et al. 1994, review in Peterson and Black 1994, Pile et al. 1996, Moksnes et al. 1998). However, such studies typically used tethering as a means of investigating differential mortality rates between different sized individuals. Tethering studies are used to study potential predation rates because investigators are concerned with post-settlement movement, which may be confused with mortality.

Consistent with previous studies, the movement results from the present study indicate that *S. hispidus* is extremely limited in post-settlement dispersal. Furthermore, the majority of the post-settlement movements recorded were by larger inshore shrimp. Since mostly larger shrimp were moving, one would suspect that the estimates of their mortality might be inflated, not that of the smaller individuals. Thus, the higher mortality rates of smaller individuals were likely not due to movement. Also, no tagged

individuals were encountered in regions where they were not expected, in either year. In fact, five tagged individuals from the 2001 study were found in the same location at the beginning of the 2002 study, approximately eight months later. These observations suggest that there is no evidence for long distance movement between habitats. Therefore, it is safe to assume that the size-selective mortality identified in the tagging study is actual, and not simply an artifact of the study.

Also, during the tagging study, I observed several instances when a mature individual (usually male) would move back and forth between rocks up to nine meters away, to be found with different individuals of the opposite sex. This suggests that *S. hispidus*, although pair bonded, may not be completely monogamous.

Despite strong evidence for size-selective mortality in the tagging study, there seems to be no evidence of it from the tethering study. However, these results may be inconclusive because of inherent difficulties with this experiment. Although tethering did not seem to effect survivorship in the control, additional stresses or biases, inherent of the field experiment, may have caused increased mortality in the field study. These stresses and biases include: 1) drastic temperature increases associated with introducing shrimp to sites, 2) depleted oxygen concentration in holding containers as the day went on, and 3) predators taking notice to divers putting shrimp down. Survivorship fell drastically in the first day but seemed to slow down by day two, where it became somewhat stable to the end of the experiment (Figure 2-5). This is evidence for an increase in mortality due to the experimental manipulation itself.

Based on the predator surveys, it is clear that the regions differ substantially in the assemblage of potential predators. There is no information available about the feeding

rates of any of these species on *S. hispidus*. I did, however, see some of the predator species feeding on *S. hispidus* in the context of the tethering study and population structure surveys (e.g., *Haemulon plumieri*, *Ephinephelus cruentatus*, and Stomatopoda). Further studies are needed to categorize actual *S. hispidus* predators and characterize feeding rates, in order to better define and compare the predator assemblages between the two regions.

The significant difference in bottom temperature between the inshore and offshore region may contribute to the differential growth rates between the two regions. However, the two regions only differed by 1.16°C. Although previous studies have documented a significant change in growth from small temperature differences (Wyban et al. 1995, reviewed in Hartnoll 2001), it is difficult to ascertain whether the temperature difference between the inshore and offshore regions was large enough to cause the difference in growth between the two regions. In order to do this, further studies are needed to quantify the effect of temperature on the growth of *S. hispidus* of different sizes

In addition to temperature, food availability has been shown to affect the growth rates of crustaceans. Specifically, a reduction in food supply causes a reduction in growth rates, through an extension of molt interval and/or a reduction in growth increment (reviewed in Hartnoll 2001). Observations of the inshore and offshore habitats indicate that there may be a difference in food availability between the two. There seems to be a much higher concentration of algae and other plant material in the inshore regions, thus potential higher productivity in this habitat. In addition to cleaning fishes of parasites, *S. hispidus* are most likely opportunistic feeders, picking food particles from the reefs and

possibly grazing on algae. Therefore, it may be that the higher growth rate in the inshore region was due to increased food availability in that region.

Conclusion

This study has shown: 1) more larvae settle in the offshore region than the inshore region, 2) there is strong evidence of size-selective mortality that does not differ between the two regions, and 3) offshore shrimp grow approximately four times slower than their inshore counterparts. With these results it is possible to imagine a scenario that would explain the differences in *S. hispidus* population structure between inshore and offshore regions of the Upper Florida Keys. It is probable that the offshore population is dominated by smaller individuals because settlers never reach larger sizes, due to lower growth and increased periods of vulnerability to high predation. In contrast, although settlement inshore is much lower, settlers are able to reach larger sizes and, therefore, escape mortality more quickly, due to their higher growth.

Table 2-1. Details of sites used in population size-structure study. Site codes (in parentheses) for each site correspond to those used in Figure 2-1.

Region Site	Depth (m)	Distance from shore (km)	Reef type	Coordinates	Year(s) surveyed
Offshore					
Alligator Deep (AD)	16.2	7.23	contiguous	24° 50.526'N, 80° 37.464'W	2002
Alligator Shallow (AS)	7.62	6.74	contiguous	24° 51.221'N, 80° 36.823'W	2002
Davis Deep (DD)	14.6	7.60	contiguous	24° 55.461'N, 80° 30.019'W	2001 and 2002
Davis Shallow (DS)	9.45	7.15	contiguous	24° 55.029'N, 80° 30.614'W	2002
Crocker Deep (CD)	14.6	7.02	contiguous	24° 54.279'N, 80° 31.681'W	2001 and 2002
Crocker Shallow (CS)	6.71	6.69	contiguous and patch	24° 54.454'N, 80° 31.672'W	2002
Inshore					
Rock 1 (R1)	3.05	1.63	patch	24° 56.548'N, 80° 33.666'W	2001 and 2002
Rock 2 (R2)	3.66	1.60	patch	24° 56.991'N, 80° 33.157'W	2001 and 2002
Rock 3 (R3)	5.79	2.04	patch	24° 57.258'N, 80° 32.774'W	2001 and 2002
Shrimp Rock 1 (SR1)	3.66	1.47	patch	24° 56.909'N, 80° 33.251'W	2002

Table 2-2. Details of sites used in post-settlement mortality tagging study.

Region Site	Depth (m)	Distance from shore (km)	Reef type	Coordinates
Offshore				
Davis Deep	14.6	7.60	contiguous	24° 55.461'N, 80° 30.019'W
Crocker Deep	14.6	7.02	contiguous	24° 54.279'N, 80° 31.681'W
Inshore				
Rock 1	3.05	1.63	patch	24° 56.548'N, 80° 33.666'W
Rock 2	3.66	1.60	patch	24° 56.991'N, 80° 33.157'W
Rock 3	5.79	2.04	patch	24° 57.256'N, 80° 32.774'W

Table 2-3. Parameter estimates and test statistics from linear regression models to estimate the growth increment for shrimp from the inshore and offshore region, as in Equation 2.2. Graphical representations for these parameter estimates can be seen in Figure 2-8.

Region	Parameter Estimates		Test Statistics			
	$a \pm$ SE	$b \pm$ SE	F-value	$df_{n,d}$	Pr > F	r^2
Inshore	8.32 ± 1.25	-0.153 ± 0.027	30.71	1,20	<0.0001	0.61
Offshore	2.42 ± 1.60	-0.047 ± 0.067	0.48	1,31	0.4942	0.02

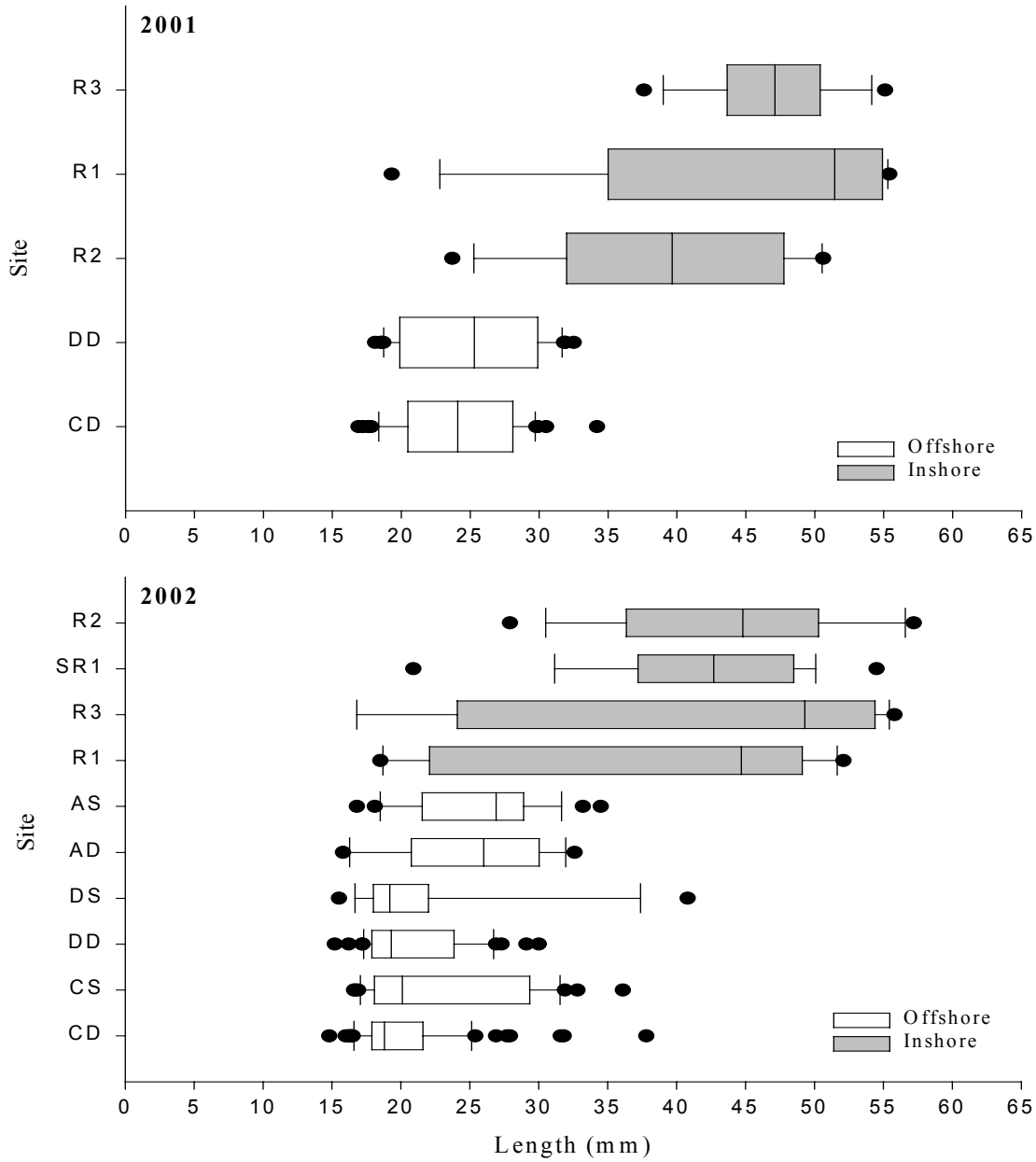

Figure 2-1. Box plots of total length (mm) for all sites surveyed in each of 2001 and 2002. Shaded boxes represent inshore sites, white boxes represent offshore sites. Site symbols correspond to those presented in Table 2.1. Boxes contain 50% of the sample values (1st sample quartile-3rd sample quartile). The two whiskers extend within a range of 1.5 times the interquartile range. Dots represent outliers. A vertical line in each box represents the median of each sample. Sample sizes are as follows: 2001 CD, n=43; 2001 DD, n=38; 2001 R2, n=12; 2001 R1, n=10; 2001 R3, n=8; 2002 CD, n=74; 2002 CS, n=29; 2002 DD, n=44; 2002 DS, n=14; 2002 AD, n=9; 2002 AS, n=20; 2002 R1, n=9; 2002 R3, n=14; 2002 SR1, n=14; 2002 R2, n=9.

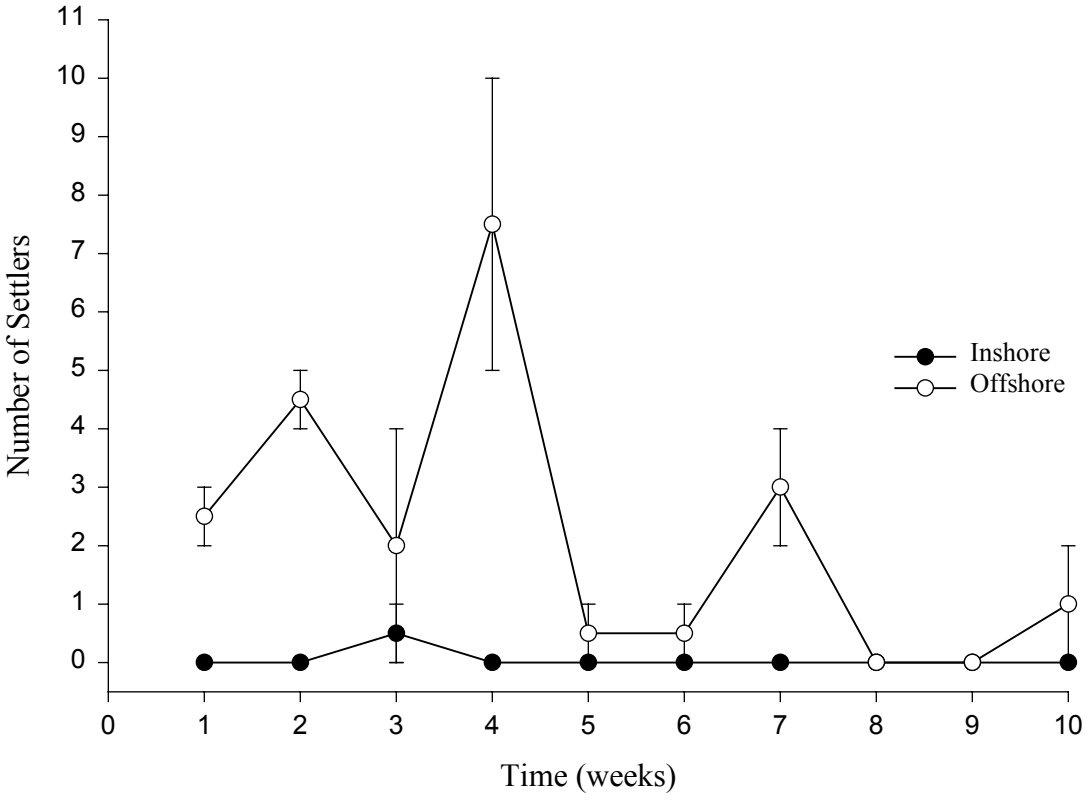

Figure 2-2. Mean (±SE) number of settlers to inshore and offshore artificial reefs in each of ten weekly surveys.

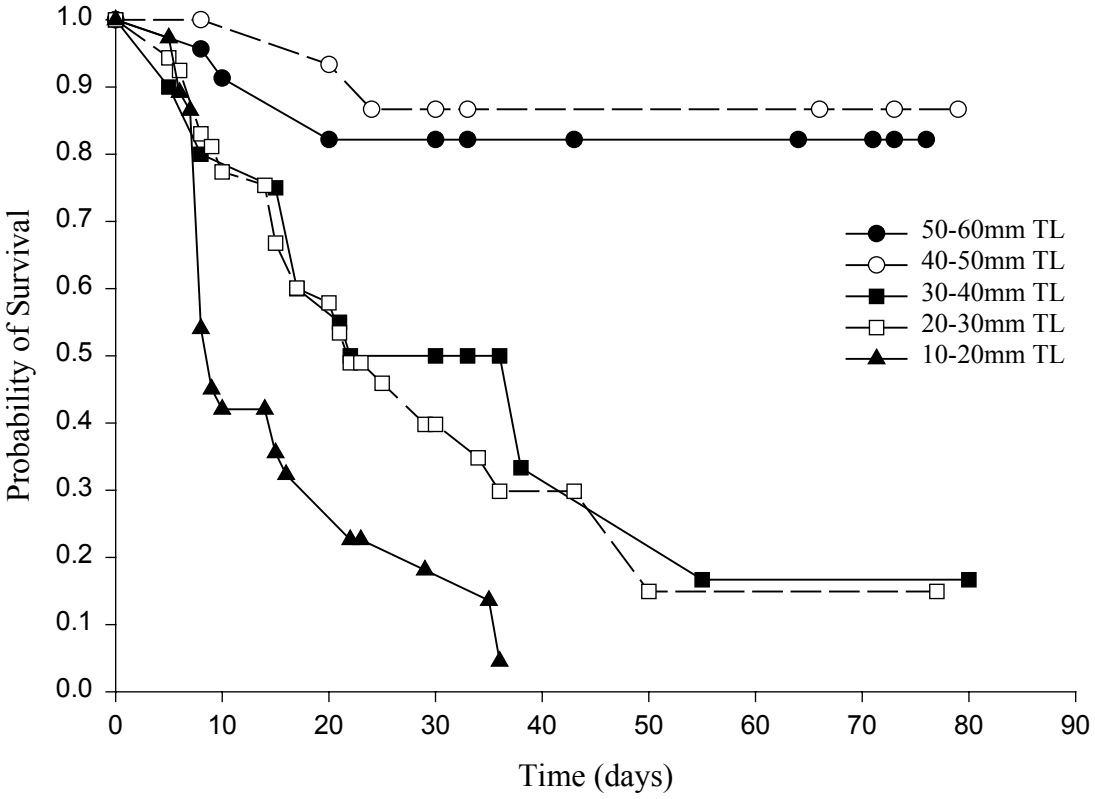

Figure 2-3. Survivorship curves of five size-classes of *S. hispidus* for 2001 and 2002 and all sites combined. Note that 10-20mm individuals have different survivorship than those of 20-30mm and 30-40mm, which have different survivorship than those of 40-50mm and 50-60mm TL. Sample sizes are as follows: 50-60mm, n=23; 40-50mm, n=16; 30-40mm, 20; 20-30mm, n=53; 10-20mm, n=37.

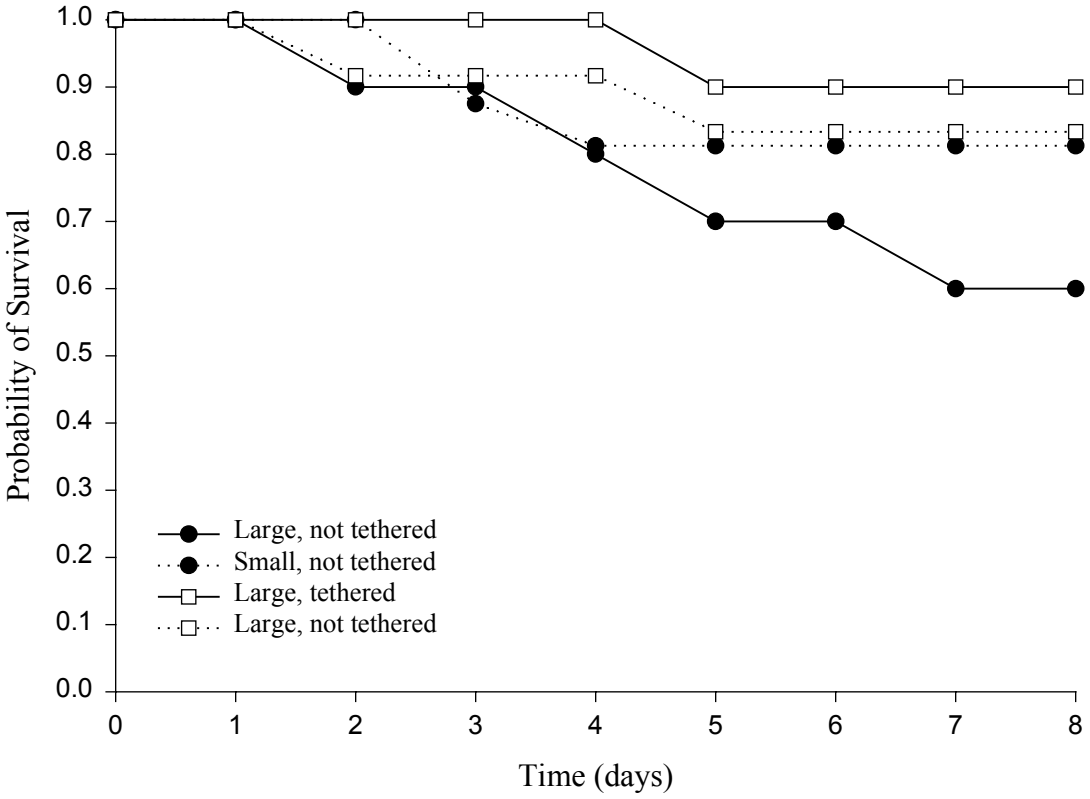

Figure 2-4. Survival of small and large, tethered and un-tethered individuals in the laboratory control tether experiment. There is no difference in survivorship in any of the four treatments. Sample sizes are 10 for all treatments.

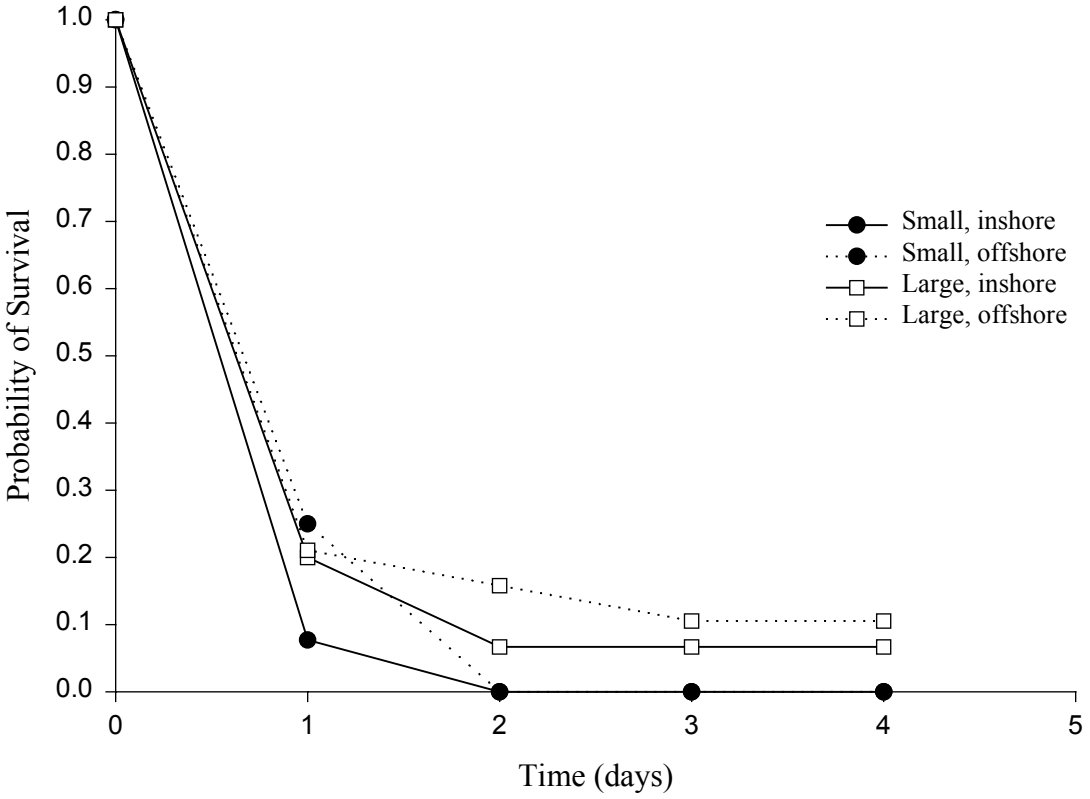

Figure 2-5. Survivorship of small and large, inshore and offshore tethered individuals in the field tether experiment. There is no difference in survivorship between any of the four treatments. Sample sizes are as follows: small inshore, n=13; small offshore, n=12; large inshore, n=15; large offshore, n=19.

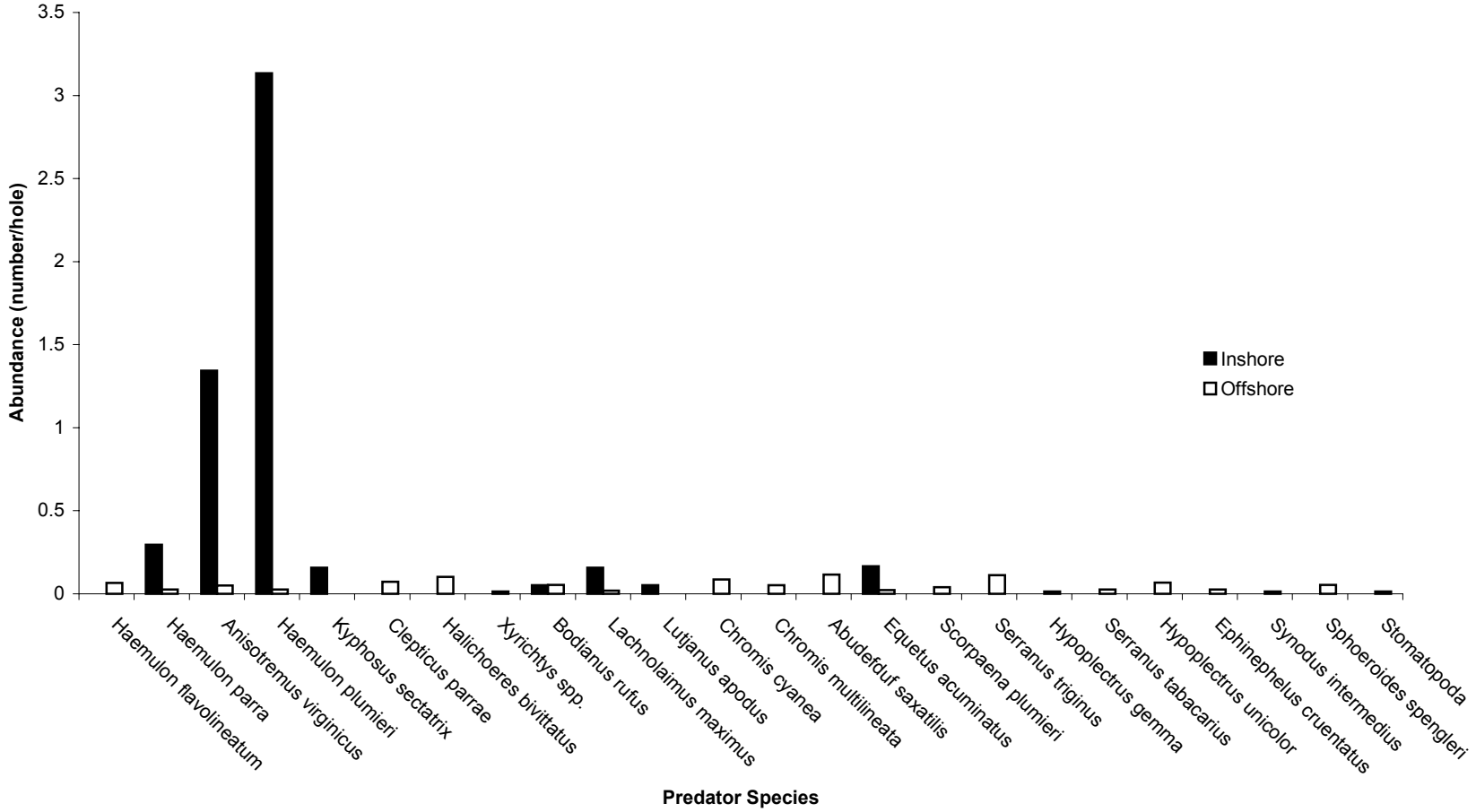

Figure 2-6. Mean abundance (number/3.14m^2) of predators in each of the clusters generated by a k-means clustering analysis.

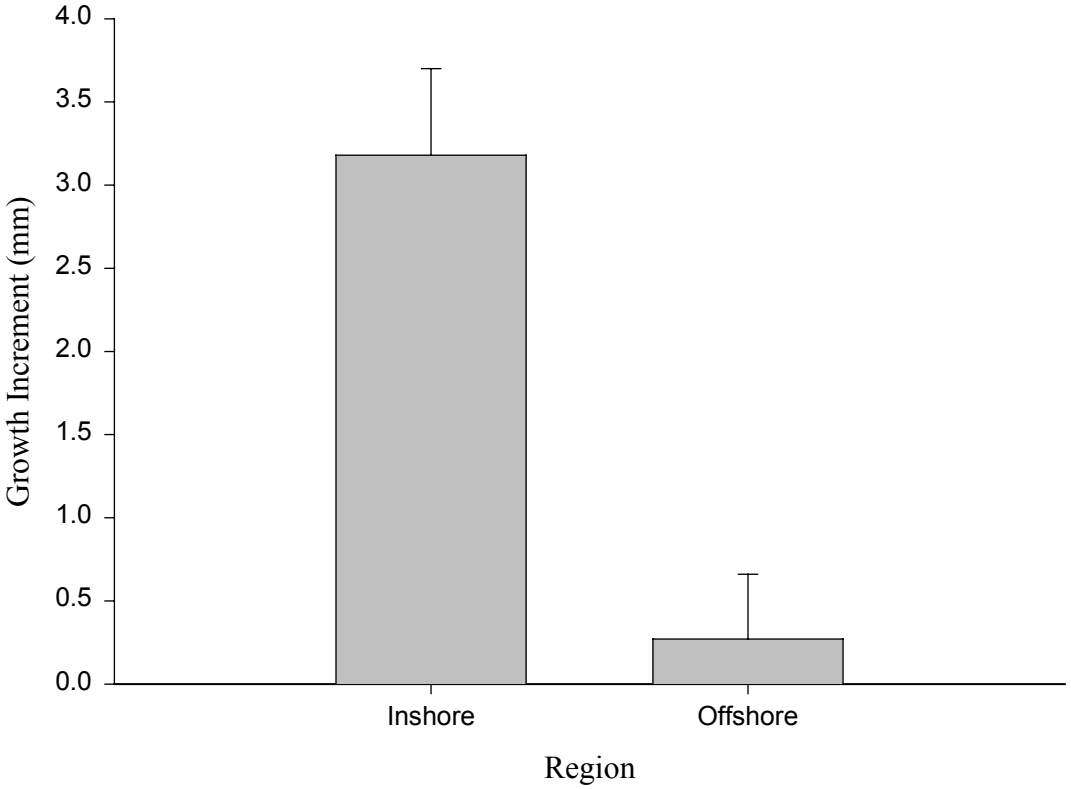

Figure 2-7. Adjusted mean (+ SE) growth increment for inshore and offshore populations of *S. hispidus* from ANCOVA. Sample sizes are as follows: inshore, n=22; offshore, n=33.

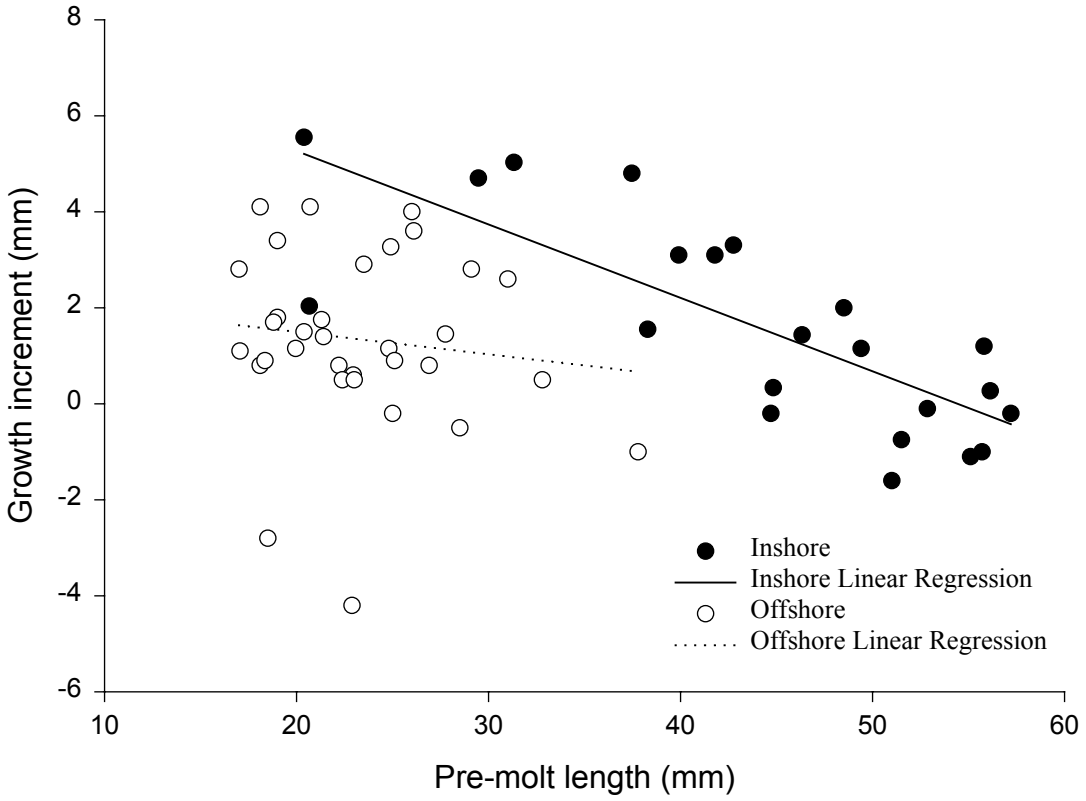

Figure 2-8. Linear regression of mean pre-molt length (mm) on mean growth increment (mm) for inshore and offshore populations of *S. hispidus*. Sample sizes are as follows: inshore, n=22; offshore, n=33. Parameter estimates for regression lines can be found in Table 2-3.

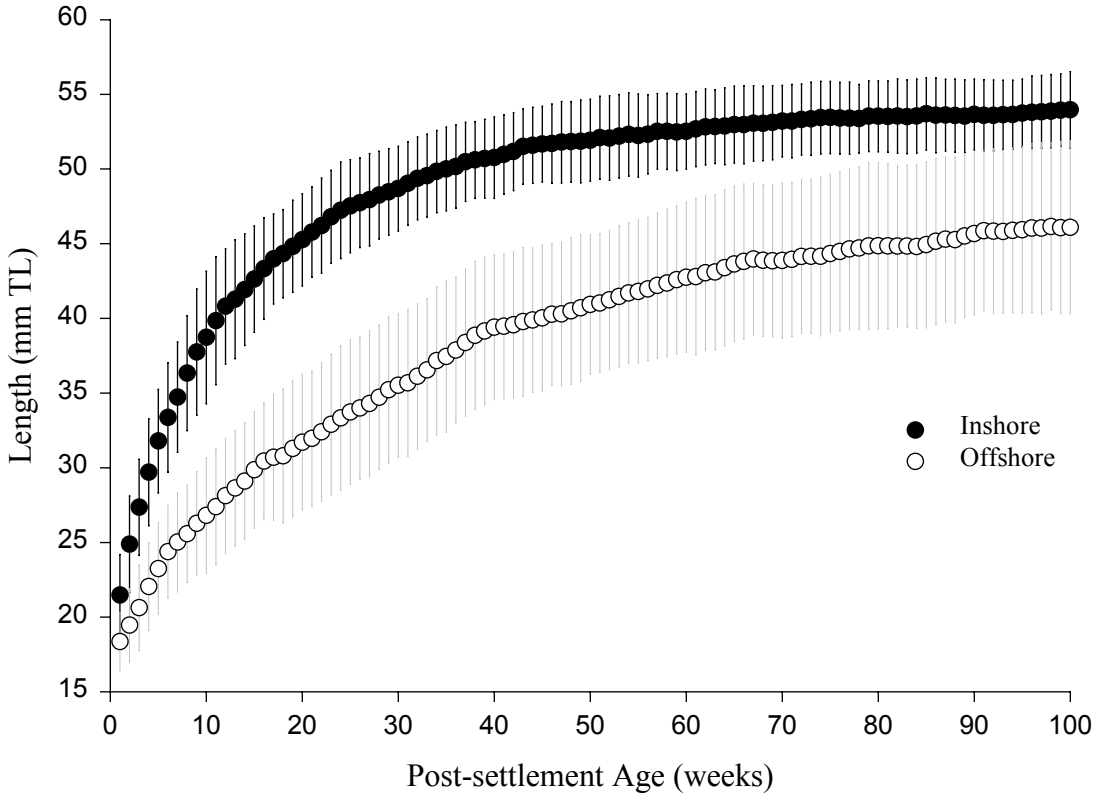

Figure 2-9. Mean and standard deviations (error bars) of shrimp length (mm TL) at post-settlement age for inshore (closed circles) and offshore (open circles) regions. These means and standard deviations result from 100 simulations of the crustacean growth model for each region. Note the only overlap in the standard deviations of the two populations is for the first 2 weeks and last 13 weeks, post-settlement.

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BIOGRAPHICAL SKETCH

Brandon Rae Chockley was born on May 4, 1978, at Andrews Air Force Base, MD. He received his Bachelor of Science in marine biology from Auburn University in Auburn, Alabama, in Spring 2000. During his last year at Auburn University, he was an undergraduate teaching assistant for two general biology classes (Principles of Biology and Animal Biology). Brandon completed an independent research project under the supervision of Dr. Jon Armbruster, in which he described a new species of armored catfish (*Panaque changae*) from eastern Peru. Partial funding for this project came from an Auburn University Undergraduate Research Award that Brandon received in June 1999. The manuscript from this project has recently been published.

Prior to Brandon's graduate career at the University of Florida, he worked as a laboratory and field teaching assistant at the Oregon Institute of Marine Biology (University of Oregon) for the Invertebrate Zoology class. He began attending the University of Florida for his Master of Science in zoology in the fall of 2000, in Dr. Colette St. Mary's lab. While at the University of Florida, he has been a teaching assistant (Principles of Biology and General Ecology) and a research assistant (under Dr. Craig Osenberg). Brandon started the fieldwork for his master's research in the Florida Keys in the summer of 2001 and continued in the summer of 2002. Brandon has received funding from the University of Florida (Grinter Fellowship, 2000-2002) and PADI Project AWARE (2002) for his master's research.