

THE RELATIVE VALUE OF SEAGRASS, MARSH EDGE, AND OYSTER
HABITATS TO THE BRACKISH GRASS SHRIMP, Palaemonetes intermedius,
ALONG THE GULF COAST OF FLORIDA

By

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Abstract of Thesis Presented to the Graduate School
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Palaemonid shrimp are abundant and important components of estuarine faunas throughout much of the world, resulting in considerable interest in their ecology. Studies of the relative value of habitats to these animals have primarily used measures of relative abundance or habitat selection by individuals as indicators of habitat quality. However, these have produced varied and conflicting results. As such, new techniques are needed for investigating the relative quality of habitats for grass shrimp.

This study examined the relative value of seagrass beds, marsh edge habitats, and oyster bars to the brackish grass shrimp, Palaemonetes intermedius, using a variety of metrics that either directly measure, or provide surrogate measures for, fecundity, mortality, and growth rates. These metrics were compared with measures of relative abundance to determine whether abundance might be an effective indicator of habitat quality. Sampling was done during July, August, and November 2002, and February,

May, July, and August 2003, in the St. Martin's Marsh Aquatic Preserve (SMMAP) near Crystal River, Florida. This provided an assessment of temporal variability in the quality of these habitat types as well as their overall relative value. In August 2003, the study was broadened to include the Weeki Wachee and Steinhatchee estuaries in order to assess the degree of regional variability in the quality of these habitats for grass shrimp.

In contrast with several other studies, P. intermedius was never collected from oyster habitat. In the SMMAP, seagrass beds provided higher quality habitat for grass shrimp than marsh edges in the July/August, November, and May, when seagrass beds had greater abundances of shrimp, as well as higher proportions of gravid females than marsh edges. In February 2003, the two habitats were determined to be of similar value to grass shrimp. As in the SMMAP, seagrass beds in Weeki Wachee provided a higher quality habitat than marsh edges for grass shrimp. Within the Steinhatchee estuary, however, the quality of marsh edge habitats was similar to, or marginally higher than, that of seagrass beds. Differences in seagrass characteristics, species composition specifically, may account for the lower abundance of P. intermedius in the sampled seagrass beds within the Steinhatchee estuary. In general, however, grass beds were determined to provide higher quality habitat than adjacent marsh edges in the broad study area.

INTRODUCTION

Grass shrimp (Palaemonetes spp.) are abundant components of coastal benthic communities throughout much of the world, including along the Gulf and east coasts of the United States (Rozas and Minello 1998, Lewis and Foss 2000, Glancy et al. 2003). They are important consumers of organic detritus, and in turn serve as prey for a myriad of commercially and recreationally important fish. As such, there has been substantial interest in their ecology, and in particular, their use of habitats. A habitat should be defined as high quality if the animals inhabiting it have increased fitness relative to those in an alternative habitat, as indicated by measures of fecundity, mortality, and growth rates (Anderson and Gutzwiller 1996, Davenport et al. 2000, Franklin et al. 2000, Lin and Batzli 2001, Luck 2002, Walters et al. 2002, Ross 2003). Delineation of high quality habitats is, therefore, an important step toward the effective management and conservation of animals, including grass shrimp.

There have been numerous attempts by ecologists to determine the relative quality of estuarine habitats for grass shrimp (Sheridan 1992, Knowlton et al. 1994, Khan et al. 1995, Eggleston et al. 1998, Rozas and Minello 1998, Bass et al. 2001). The vast majority of these studies have used relative abundance, density, or habitat selection by individuals as indicators of habitat quality. These studies have substantially increased our understanding of many aspects of the relationship between grass shrimp and their habitats. For example, it has been demonstrated that congeneric species may select different habitat types when given a choice in experimental and field settings (Knowlton

et al. 1994, Khan et al. 1995, Sheridan 1992), and that paleomonid shrimp can occur in greater abundance in adjacent, but alternative habitat types within a given ecosystem (e.g. Eggleston et al. 1998, Rozas and Minello 1998, Glancy et al. 2003).

Findings in some studies suggest, however, that grass shrimp are more abundant in seagrass beds (e.g. Glancy et al. 2003), whereas others suggest that grass shrimp are more abundant in marsh habitats (e.g. Rozas and Minello 1998). Others have shown seasonal shifts in the relative abundance of grass shrimp between habitat types (Eggleston et al. 1998). These inconsistencies imply that the processes determining habitat quality for, and relative abundance of, grass shrimp may be fairly complex and variable over both time and space and that new approaches are needed to investigate the relative quality of estuarine habitats for grass shrimp.

Van Horne (1983) noted that there are several levels of increasing sophistication by which managers delineate habitat for species of concern, but that most often, especially for nongame species, relative density or abundance are used as indicators of habitat quality. As noted above, these indicators are often used when investigating habitat use by grass shrimp. However, as Van Horne (1983) pointed out, and as is apparent from other studies, e.g., Schantz (1981), density and abundance are not always correlated with habitat quality. In fact, density and habitat quality may be decoupled in six specific types of situations: (1) when habitat use changes seasonally, (2) when social dominance interactions result in large densities of subdominant individuals in suboptimal habitats, (3) when resources and other environmental conditions are temporally unpredictable within habitats, (4) when the species have high reproductive capacity, which can result in population sizes that poorly reflect the carrying capacity of the environment over the

short term, (5) when there is spatial habitat patchiness and (6) when the species in question is a habitat generalist, which can cause the spatial distribution of habitats to have a greater influence over the distribution of populations than the relative quality of those habitats.

Interestingly, none of the papers cited in Van Horne's review were of studies from estuarine or marine systems, or of invertebrates. Also, none of the studies of grass shrimp, cited above or otherwise encountered, examined any potential indicators of habitat quality other than relative abundance or habitat selection by individual shrimp. Nonetheless, many life history and ecological characteristics of grass shrimp comply with Van Horne's criteria. Seasonal shifts in habitat use by grass shrimp have been documented (Kneib 1987, Eggleston et al. 1998), grass shrimp live in estuarine environments that exhibit pronounced variability, and also invest significantly in reproduction (Vernberg and Piyatitivorakul 1998). Moreover, there is considerable patchiness in the distribution and species composition of seagrass beds (Hovel et al. 2002), one of the primary habitats in which grass shrimp are found (Glancy et al. 2003). Finally, grass shrimp are generalists, tolerating wide ranges in many physiochemical parameters (e.g. temperature and salinity) and utilizing multiple food sources (Vernberg and Piyatitivorakul 1998).

In combination, these life history characteristics and ecological attributes suggest that the primary methods used by estuarine ecologists to investigate the relative value of habitats for grass shrimp, i.e., preference and relative abundance, may be inadequate. Ideally, the relative quality of habitats for a species should be measured via comparison of population densities or relative abundance and demographic parameters such as

fecundity, mortality, and growth rates. This was done by Chockley and St. Mary (2003), who identified and monitored individual banded coral shrimp (Stenopus hispidus), and showed that low density, inshore populations produced more eggs per area of habitat than high density, offshore populations, which implied that the inshore areas were higher quality habitats despite the fact that they supported lower shrimp abundances.

In an attempt to extend this type of habitat assessment to grass shrimp, this study looks more closely at the relative values of key habitats to the brackish grass shrimp, Palaemonetes intermedius, in terms of abundance and other measures that should indicate relative fitness of the shrimp within those habitats, termed individual shrimp fitness (ISF) variables. These ISF variables include measures of fecundity, growth, and several surrogate measures of mortality which were selected based on relevant literature. Abundance estimates were then compared to the ISF measures of habitat quality to determine whether or not abundance was an effective indicator of habitat quality for grass shrimp.

STUDY AREA

Sampling was conducted primarily at three sites within the St. Martin's Marsh Aquatic Preserve (SMMAP), along Florida's northeast Gulf coast in Citrus county (28° 53' N, 82° 41' W). These three sites are the same as those previously described and sampled by Glancy et al. (2003), and the close proximity of oyster bar, seagrass, and marsh edge habitats at these sites allow a comparison of habitat quality in similar environments, as characterized by water temperature, salinity, and dissolved oxygen concentrations.

In brief, this estuary is a complex mosaic of seagrass beds, salt marshes, oyster bars, tidal channels, bays, and sandy flats. Seagrass beds are primarily comprised of turtle grass (*Thalassia testudinum*), shoal grass (*Halodule wrightii*), and manatee grass (*Syringodium filiforme*). Intertidal oyster habitats are dominated by the eastern oyster (*Crassostrea virginica*), are low relief, and typically have a substrate of sand, mud, and shell fragments overlying a limestone base. Salt marshes are dominated by cordgrass (*Spartina alterniflora*) and black needle rush (*Juncus roemarianus*), but are interspersed with small stands of black (*Avicennia germinans*) and red (*Rhizophora mangle*) mangroves. As a whole, the estuary receives freshwater input from freshwater springs and the spring-fed Crystal River.

In August 2003, additional sites were sampled in the Weeki Wachee and Steinhatchee estuaries to determine if patterns similar to those observed within the SMMAP occur at other Florida Gulf coast locations. The Weeki Wachee estuary is located at approximately 28° 32.5' N, 82° 39.5' W, and is characterized by a similar

mosaic of habitats to SMMAP, although with a decreased prevalence of intertidal oyster bars. As a result, no oyster habitats were sampled in this estuary. Salt marsh and seagrass flora are typically the same as in the SMMAP (Frazer et al. 1998 and 2003), and the major input is from the spring-fed Weeki Wachee River. Three sites were sampled within this estuary, with selection based on similarities in size, water flow, and depth to the sites at SMMAP, as well as the close proximity of salt marsh and seagrass habitats.

The Steinhatchee estuary is located at approximately 29°39.5' N, 83° 25.5' W, and is also characterized by a similar mosaic of habitats to SMMAP, although with a decreased prevalence of intertidal oyster habitats in close proximity to seagrass beds. The seagrass beds at the sites in this estuary tended to be even more heavily dominated by turtle grass and manatee grass than the other two estuaries, and to have a decreased prevalence of shoal grass relative to the other estuaries. Salt marshes here also tended to have a decreased prevalence of both black and red mangrove trees, and to be found predominantly along the coasts rather than occurring as islands. The Steinhatchee estuary receives freshwater primarily from the Steinhatchee River, which is fed by more surface water runoff, and fewer spring inputs, than the Crystal or Weeki Wachee Rivers. Seven sites were sampled in this estuary. Three of these had a close association of seagrass and marsh edge habitats and were selected based on similarity in size, water flow, and depth to the sites sampled in other estuaries. Three of the sites in this estuary only contained seagrass, but were similar to the others in all other respects. The seventh site contained only intertidal oyster habitat.

METHODS

Field and Laboratory Methods

Sampling within SMMAP was conducted during July, August, and November 2002, and February, May, July, and August 2003. As there were no statistically significant within year or among year differences in any of the variables measured during July and August sampling periods in 2002 and 2003, summer sample data were pooled and are hereafter referred to simply as the July/August sampling periods.

After the May 2003 SMMAP sampling period, it was clear that the only sampling period during which all the ISF and abundance variables used in this study could be estimated in all habitats was July/August, which the data suggested was the primary breeding season, a conclusion that was expected based on relevant literature. Therefore, in August 2003, the sampling was broadened to include the Weeki Wachee and Steinhatchee estuaries to determine whether the patterns observed at SMMAP were representative of the Gulf coast region as a whole during the grass shrimp breeding season. Sampling of seagrass vegetation (see below) was also intensified during this period.

Sampling, at all times and locations, was performed within 3 h of low tide to minimize the variability associated with changes in habitat use due to tidal fluctuations. This schedule facilitated comparisons to data collected and reported by Glancy et al. (2003) who also sampled during low tides.

Seagrass beds, oyster bars, and marsh edges were sampled at each study site in each time period with ten 5-m sweeps with a standard D-frame sweep net 25 cm high by 35 cm wide. Sweep net sampling has been previously used in several estuarine habitat types to compare the relative abundances of fauna (e.g. Young et al. 1976, Young and Young 1978, Posey and Hines 1991, Townshend 1991, and Posey et al. 1999), and controlled tests for potential habitat bias using the sweep net collection method indicate that the method is appropriate for the habitats samples in this study (T.K. Frazer and M.H. Posey, pers comm.). Locations of sweeps in seagrass beds and in oyster habitats were chosen in an unbiased manner by taking a random number of paces (between 1 and 30) at a random bearing from the end of the previous sweep. Marsh edge sweeps were located similarly, but did not include a random bearing, as the edge of an island is measurable only in one dimension. The initial sweep in each habitat type was selected haphazardly by sighting a location in the habitat from the boat. All Palaemonetes spp. individuals caught in each sweep were put in a sealable plastic freezer bag, placed on ice, and transported to the lab for further analysis.

In seagrass beds, after every third sweep, a 0.25 m² quadrat was placed on the benthos to estimate the percent areal cover of each vascular plant species present, as well as total grass coverage. This was primarily done looking down at the benthos from above the water line, but when water clarity was too poor for the bottom to be seen, or species to be easily identified, a mask and snorkel was used. In August 2003, the plant survey sample size was increased to 10; estimates of percent areal cover were made at the end of every sweep. In August 2003, a small ponar grab was used to take ten 625 cm² bottom samples from each habitat/site, to an approximate sediment depth of 8 cm. Samples were

individually bagged in sealable plastic freezer bags and brought back to the lab for analysis. A YSI electronic meter model 650 was used to measure salinity, temperature, and dissolved oxygen (DO) concentrations in each habitat type within each site at a depth of approximately 0.25 m below the surface.

All grass shrimp within each of the bagged sweep samples were enumerated to allow for estimates of relative abundance. Subsequent processing of shrimp collected in the sweep nets was carried out with a random subsample of 50 individuals. The shrimp for the subsample were selected randomly by counting all shrimp from the 10 sweeps associated with a given habitat/site/sampling period and assigning each a number. Then 50 random numbers between 1 and the total number of shrimp counted were selected and those shrimp were selected for the subsample. This subsample size was determined to be sufficient to detect differences between samples in all variables after measuring the variability associated with measurements from the first 200 shrimp. If less than 50 shrimp were caught from a specific habitat type within any given time period, all shrimp were processed as described below. Shrimp were identified as either Palaemonetes pugio or P. intermedius, according to Abele and Kim (1986). The relative proportion of P. intermedius in each of the subsamples was multiplied by the total Palaemonetes counts from the respective sweep samples to estimate the abundances of P. intermedius.

In the laboratory, all subsampled P. intermedius were measured for total length. In addition, the sex, reproductive condition (gravid/not gravid), and clutch size of gravid females was recorded. The total length of each shrimp, as well as telson lengths of the first 200 shrimp, was measured using a WILD M3Z dissecting microscope fitted with a KR 221 120-increment optical micrometer. Measurements were recorded to the nearest

0.15 mm. Shrimp were considered female if they were gravid, or if developing ovarian tissue could be observed through the translucent body of the individual. If these indicators were not observed, then the second pleopod of the shrimp was examined to determine if it bore an appendix masculina, a male characteristic (Berg and Sandifer 1984). Shrimp without this modification of the second pleopod were counted as female. Shrimp with a total length less than 12 mm were not included in estimates of sex ratio or fecundity values as shrimp this small may not have been sexually mature, in which case the appendix masculina may not have developed. The clutch size of gravid females was determined by teasing apart egg masses with a fine metal probe and counting individual eggs with the aid of a dissecting microscope.

For the bagged vegetation samples from the ponar grabs, the above-ground vegetative portions were separated from the mud, detritus, rhizomes, and roots by hand. The below-ground portion, as well as nonliving material, was discarded. Seagrass shoots were then counted and total number of shoots for each seagrass species recorded. Above-ground biomass (wet weight) of each species of seagrass in the ponar samples was recorded and weighed with a Pesola 1000 g hanging scale and measurements recorded to the nearest 10 g.

An instantaneous growth rate technique similar to that employed by Quetin and Ross (1991) was used to estimate shrimp molting rates and growth increments in SMMAP during November 2002, and February, May, and August 2003 in SMMAP only. *P. intermedius* from each habitat/site in each sampling period were collected with sweep nets and/or a beach seine. The target sample size for each habitat/site combination was 100 shrimp. When shrimp densities were too low to collect 100 shrimp, the number of

shrimp caught in approximately 1.5 h was used. Individual shrimp were placed in pre-labeled 265-ml glass jars with mosquito-netting tops secured by rubber bands. The jars were placed in plastic tubs and left immersed in a readily accessible nearshore area that had similar salinity, temperature, and DO values as the sites from which the shrimp were collected. These jars were monitored every 12 h for 3 d, and the shrimp that molted, as well as their exuviae, were preserved in a solution of 90% ETOH and 5% glycerin, and brought back to the lab for analysis.

The number of shrimp that either escaped from the jars or died in any given experiment ($< 3\%$ in all experiments) was subtracted from the original number of total shrimp that were used. This number was further adjusted to estimate the total number of P. intermedius that were used throughout the experiments by multiplying it by the proportion of P. intermedius in the subsample from the sweep net samples which were collected in the same location during the same sampling period. The number of P. intermedius that were directly observed to molt during the course of the 3-d experiment was then divided by the estimated total number of P. intermedius, to calculate a molting frequency per 3 d. Intermolt period (IMP) was then calculated as the reciprocal of molting frequency, and expressed as days molt^{-1} .

In the laboratory, telson lengths of the preserved shrimp and their molts were measured. Species, sex, and reproductive condition of female shrimp were also recorded. The growth increment of molting shrimp (mm) was calculated as the difference between the estimated total lengths of the post-molt shrimp and their molts. Total lengths of the molts and post-molt shrimp were estimated using measured telson lengths and

Equation 1, which was derived from a linear regression analysis between measured telson and total lengths for the first 200 shrimp from the sweep net subsamples ($p < 0.0001$, $r^2 = 0.87$).

$$\text{total length} = 1.92 + (7.36 * \text{telson length}) \quad \text{eq. (1)}$$

Growth rate was defined as the average growth (mm/day) for an individual P. intermedius within a sample population, and was calculated by dividing the average growth increment (mm) by the IMP (days) for each habitat/site/sampling period combination. This provided an estimate of continuous growth which was a population-wide average, individual shrimp growth is incremental. The estimated values for IMP, growth increment, and growth rate were assumed to be indicative of the sample population as a whole for the time period in which the experiment took place.

The combination of field, laboratory and mathematical techniques described above resulted in estimates for a variety of variables which provide information about P. intermedius. These fall into two general categories. (1) measures of abundance, and (2) those variables that provide information about the relative fitness of shrimp (individual shrimp fitness, or ISF, variables). The latter include measures of fecundity (proportion of gravid females and fecundity), and surrogate measures of mortality and nutritional stress (sex ratio, size distribution, and growth rates).

These surrogate measures were necessary because the mortality of a high density, small-bodied, mobile species such as P. intermedius, is extremely difficult to measure directly in an open estuarine habitat. The validity of these surrogates is supported by the results of previous investigations. Females have been shown to respond to decreased food availability with increased mortality relative to males (Reinsel et al. 2001). Also,

population size structure has been shown to be shifted towards smaller shrimp in ecosystems with increased predation on P. pugio and with increased mortality due to nutritional stress (Cross and Stiven 1999, Bass et al. 2001, Reinsel et al. 2001). In addition, reduced food availability can result in decreased intermolt growth increments and increased intermolt periods in crustaceans in general (Hartnoll 2001). As such, population size and sex structure, as well as growth rates, were used as the surrogate measures of relative mortality and nutritional stress for shrimp. In addition, histograms of size distributions of the shrimp from each habitat/time period were created to further explore the relationships between life history, habitat quality, and shrimp size.

Statistical Methods

Within each sampling period and estuary, one way Analyses of Variance (ANOVAs) were performed with each of the numerical variables (abundance, size, clutch size, growth increment, total growth, as well as percent cover, biomass, and shoot density of seagrass and individual seagrass species) as dependent variables and habitat type as the independent variable (MINITAB Release 14). When necessary, variables were \log_{10} transformed to achieve normality and homoscedasticity and all tests were assumed significant at $p < 0.05$. Tukey's post-hoc test was used to determine where significant differences existed when ANOVAs detected significant effects (MINITAB Release 14). Student's t-tests were used when only 2 habitats were compared within a particular season (MINITAB Release 14). When the assumptions of normality and homogeneity of variance could not be met, a Kruskal Wallis ANOVA was used as an alternative to ANOVA and Mann-Whitney U-tests were used as alternatives to T-tests (MINITAB Release 14). When Kruskal-Wallis ANOVA was used, post-hoc comparisons were made by comparing the intervals between the 5th and 95th percentiles of each distribution. Only

three values for intermolt period, one from each site within the SMMAP, could be calculated for each habitat/sampling period with the method employed in this study. To increase statistical power, the molting frequency of P. intermedius (molts day⁻¹) was used as a proportional variable and analyzed via X² tests (MINITAB Release 14) with the distribution of the molting shrimp assumed to be independent of habitat or time period.

X² tests were also used to compare the other proportional variables (sex ratio and proportion of gravid females), between habitat types, time periods, and estuaries (MINITAB Release 14). When there were only two categories being compared, i.e., marsh edge vs. seagrass, overall test significance at $\alpha < 0.05$ was sufficient to infer significant differences between mean values. When there were more than two categories being compared, such as time periods or estuaries, and the X² test was significant at $\alpha < 0.05$, then statistically significant differences were inferred by comparing 95% confidence intervals. In all cases, the variables were assumed to be independent of habitat, time period, or estuary. Sampling periods were only compared within the SMMAP, and among estuary comparisons were only made with data from August 2003.

RESULTS

P. intermedius were not collected from oyster bar habitats during the course of this investigation. As a consequence, subsequent analyses focus only on grass shrimp in marsh edge habitats and seagrass beds.

Temporal Variability

Within Habitat Variability

As expected, because of the close proximity of sampling sites within the SMMAP, there were no statistically significant differences in salinity, dissolved oxygen concentrations, or water temperature between habitat types within any given sampling period. Thus, data from all habitats were pooled for all statistical comparisons. Dissolved oxygen concentrations and salinity were always well within the ranges reported for Palaemonetes (Vernberg and Piyatitivorakul 1998, Stickle et al. 1989, Bass et al. 2001, Table 1). Statistically significant temporal changes in water temperature were consistent with expected seasonal patterns (Frazer et al. 1998 and 2003, Table 1), but were within the range reported for grass shrimp (Knowlton and Schoen 1984). Water temperature was significantly lower during February 2003 (12.69°C) than in any other time period (Table 1). Although water temperature was higher in November 2002 (18.80°C) than in February 2003, the mean value was lower than in either July/August (29.57°C) or May 2003 (29.73°C) sampling periods, which were similar to one another (Table 1).

Within seagrass beds, there were significant temporal differences in the relative abundance of P. intermedius, and several ISF variables, specifically total length, sex

ratio, the proportion of gravid females, and IMP. Surprisingly, there were no significant differences observed for the percent cover of any individual seagrass species or cover of seagrass in general. The median abundance of P. intermedius was significantly lower in February 2003 (1.5 shrimp/sweep) than in any other sampling period (Figure 1a, Table 2), coinciding with the period when mean water temperatures were lowest (Table 1). Gravid females were not collected from seagrass beds in February. (Figures 1d, Table 2). In May 2003, shrimp were more abundant than in February (14.5 vs. 1.5 shrimp/sweep), although smaller on average (Figures 1a,b, 2b,c, Table 2). Nineteen percent of females were gravid in May (Table 2). In the July/August sampling periods, the median abundance of shrimp was similar to that in May 2003 (18.0 shrimp/sweep), but shrimp were significantly larger (Figures 1a,b, 2a,d, Table 2). In May 2003, 77.8% of the shrimp were ≤ 15 mm total length and probably not sexually mature (Figure 2d). In comparison, 70.1% of captured shrimp during the July/August sampling periods were > 15 mm total length, indicating that the majority of the sampled population was sexually mature (Figure 2a). Changes in ISF variables were consistent with previously documented life history information for P. intermedius. The proportion of gravid females in July/August was 47%, indicative of a peak reproductive period (Figure 1d, Table 2). Shrimp abundance was higher in November 2002 than in summer (46.5 vs. 18.0 shrimp/sweep), though size distribution was skewed towards smaller size classes (Figure 2b), reflecting a late summer/early fall recruitment period. In November 2002, 87.1% of the shrimp were ≤ 15 mm total length (Figure 2b), and only 23% of the larger shrimp were gravid (Figure 1d, Table 2). In addition, the IMP for the sampled population

was 8.4 d in November, which was significantly longer than in either July/August (5.5 days) or May (4.4 days) (Figure 1e, Table 2).

Marsh edge habitats exhibited less temporal variability than seagrass beds. There were no statistically significant differences in the relative abundance of P. intermedius within the marsh edge habitats sampled during the different time periods in SMMAP (Table 3). In fact, no variables exhibited significant or large temporal differences other than size and the proportion of gravid females (Table 3). Shrimp occupying marsh edges were significantly larger in July/August (median TL = 22.929 mm) than in May (median TL = 12.714 mm). In November and February, shrimp were intermediate in size (15.710 mm and 16.429 mm, respectively), but did not differ significantly from the summer sampling period (Figure 3, Table 3). A majority (94.4%) of P. intermedius sampled in marsh edges during summer were > 15 mm and 27% of the females caught were gravid (Table 3, Figure 4). In fact, gravid females were only captured from marsh edges in summer. During the other sampling periods, there was a much greater proportion of individuals in the < 15 mm size classes (Figure 4).

In summary, while the highest shrimp abundances in seagrass beds occurred in November 2002, the ISF variables measured indicated that conditions during July/August were the most appropriate for the cross-habitat comparisons central to this study.

SMMAP Cross-Habitat Comparisons (Seagrass vs. Marsh Edges)

Shrimp were significantly more abundant in seagrass than in marsh edges during every sampling period (Tables 4-7). Seagrasses yielded somewhere between twice as many shrimp in February and sixty times as many shrimp in November 2002 (Tables 4-7). During the July/August sampling period, the proportion of gravid females was also higher in seagrass (48%) than in marsh edge habitats (27%). Average shrimp

size in July/August, however, was less in seagrass beds (19.143 mm) than in marsh edges (22.929 mm) (Table 4) as was clutch size (42.5 eggs/gravid female in seagrass beds and 89.0 eggs/gravid female in marsh edge habitats). Differences in shrimp size confounded a rigorous comparison of growth parameters (Table 4, Figures 2a, 4a) during the summer sampling periods. Estimates of fecundity at the population level were made by multiplying shrimp abundance by % females in the sample population (averaged between marsh edge and seagrass values due to lack of significant differences), by % gravid females, and by clutch size. These estimates showed that the average number of eggs/sweep was 209.3 in seagrass, and 0.7 in marsh edges, which strongly suggests that seagrass provides a higher quality habitat for P. intermedius.

Although the July/August sampling period was determined to be the most appropriate time to compare measures of relative abundance with other ISF variables, the estimates of abundance and ISF variables during other sampling periods provided an opportunity to make additional seagrass/marsh edge comparisons. In November 2002, for example, gravid females were only encountered in seagrass (23% gravid and 28.0 eggs/gravid female), but shrimp from marsh edges were larger (9.714 mm in seagrass and 15.710 mm in marsh edges) (Table 5). When fecundity was compared at the population level, the average number of eggs/sweep was 143.2 in seagrass and 0.0 in marsh edges.

In May 2003, shrimp abundances and ISF variables both indicated that seagrass provided higher habitat quality than marsh edges. IMP was shorter in seagrass beds than in marsh edge habitats (4.4 d in seagrass and 8.1 d in marsh edge), while mean shrimp size and size distributions were similar, implying faster growth in seagrass beds than marsh edges for individual shrimp (Table 6).

Interestingly, in February 2003, there was a higher proportion of females in marsh edge habitats than in seagrass beds (47% females in seagrass and 78% in marsh edges) (Table 7). However, the difference in abundance between seagrass and marsh edges was of lesser magnitude than during other sampling periods (1.5 shrimp/sweep in seagrass and 0.7 shrimp/sweep in marsh edges) (Table 7). When female abundance was estimated by multiplying relative abundance by sex ratio, the average number of females/sweep was 0.70 in seagrass and 0.55 in marsh edges, suggesting that these two habitats were capable of providing resources for similar numbers of female shrimp.

Among Estuaries Comparisons

Cross-habitat comparisons in the Weeki Wachee and Steinhatchee estuaries produced conflicting results. In the Weeki Wachee estuary, abundance was significantly greater in seagrass than marsh edges (11.5 shrimp/sweep in seagrass and 0.6 shrimp/sweep in marsh edges), although there were no significant differences between habitat types for any other ISF variables (Table 8). Within the Steinhatchee estuarine area, there were no significant differences between seagrass and marsh edge habitats in either abundance or any of the ISF variables measured.

Among the three estuaries in this study, Steinhatchee had the lowest abundance of P. intermedius in seagrass, and highest abundance of P. intermedius in marsh edges (Table 9). There were only two ISF variables which showed significant differences among estuaries. i.e., proportion of gravid females in seagrass beds and size in marsh edge habitats. In Weeki Wachee seagrass beds, the proportion of gravid females (35%) was higher than in seagrass beds in the Steinhatchee (18%) or SMMAP (26%). Median total lengths were significantly less for shrimp occupying marsh edges in Steinhatchee

(17.429 mm) than in the other two estuaries (22.857 mm in Weeki Wachee and 26.000 mm in SMMAP) (Table 9).

There were also several differences detected in the species composition and biomass of the seagrass beds among estuaries (post-hoc comparisons made by comparison of intervals between the 5th and 95th percentiles), which may have significance for the shrimp. The percent areal cover and shoot density of Thalassia testudinum was different in each estuary, lowest in Weeki Wachee (0.0% cover, 9.6 shoots/m²), higher in SMMAP (0.7% cover, 11.6 shoots/m², and highest in Steinhatchee (80.0% cover, 14.4 shoots/m²) (Table 10). Percent areal cover of Halodule wrightii was different in each estuary, and followed the reverse spatial pattern, increasing from Steinhatchee (1.9% cover) to SMMAP (80.0% cover) to Weeki Wachee (100.0% cover) (Table 10). Above-ground biomass of H. wrightii, however, was higher in SMMAP (624.0 g/m²) than in Weeki Wachee (280.0 g/m²) (Table 10). While there were statistically significant differences in salinity and dissolved oxygen concentrations among the estuaries, these were well within the ranges reported for P. intermedius. There was not a significant difference in water temperature between the estuaries (Table 11).

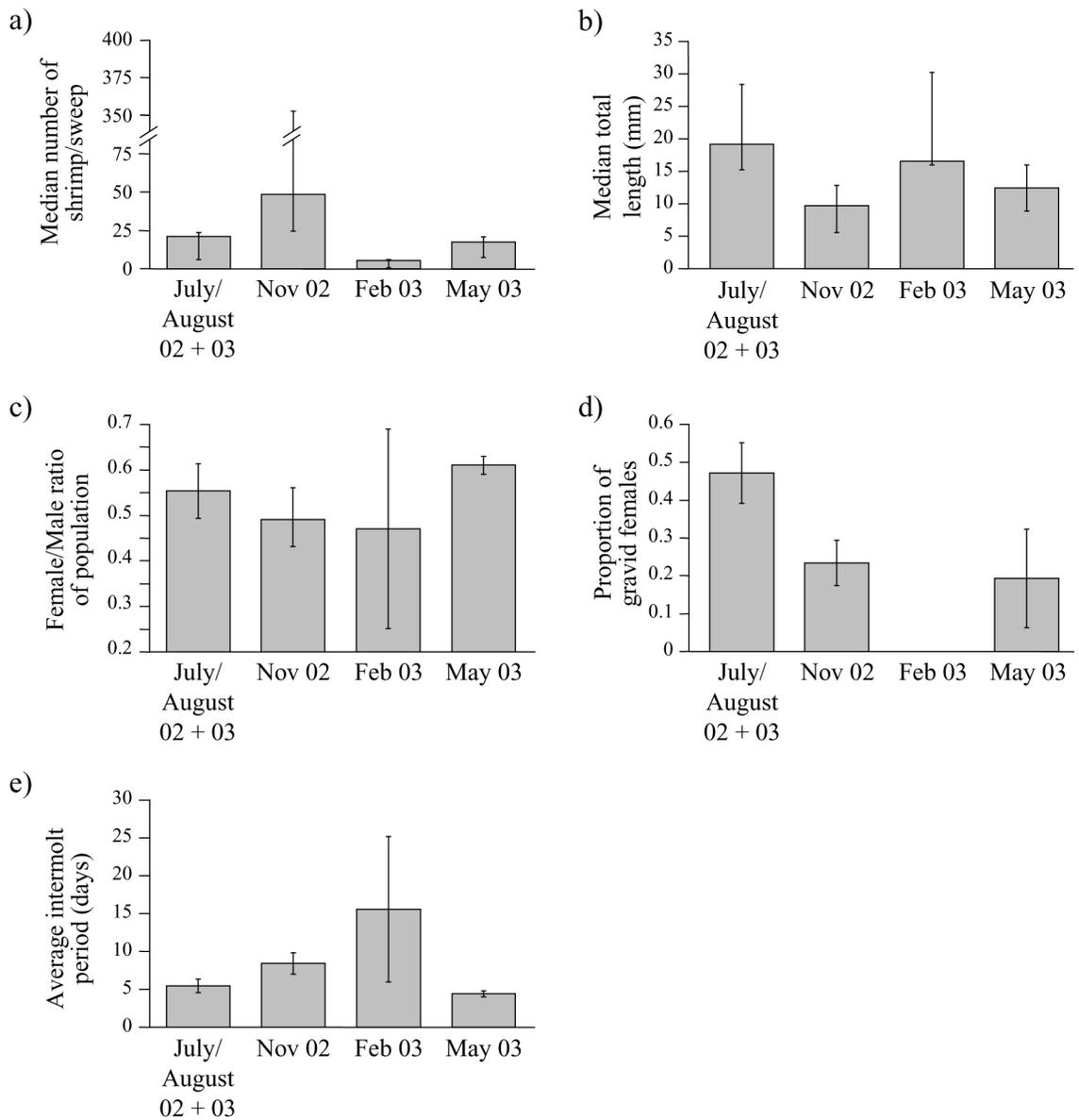


Fig 1a-e. Significant temporal changes in abundance and ISF variables in seagrass at SMMAP (error bars represent 5th and 95th percentiles in a and b and 95% confidence intervals in c, d, and e). a) abundance. b) total length. c) sex ratio. d) Proportion of gravid females e) IMP.

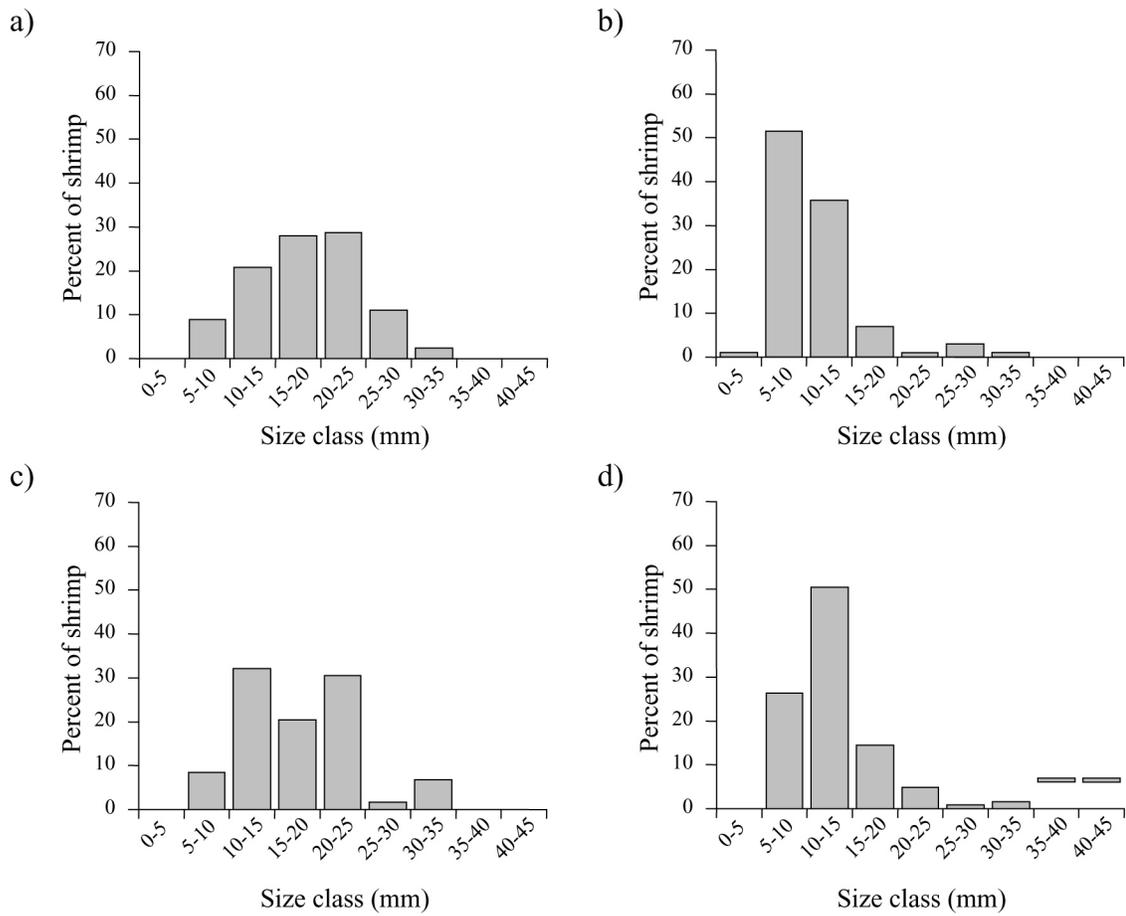


Fig. 2a-d. Size distribution of shrimp populations in seagrass beds in different sampling periods. a) July/August 2002 and 2003. b) November 2002. c) February 2003. d) May 2003.

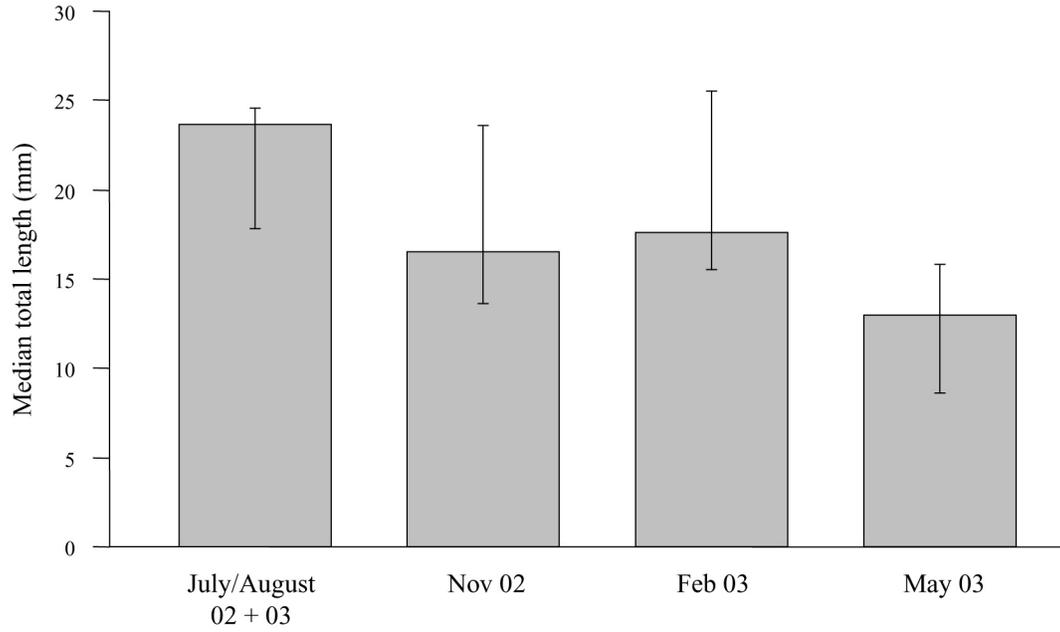


Fig. 3. Temporal differences in median size of shrimp from marsh edges at SMMAP (error bars represent 5th and 95th percentiles).

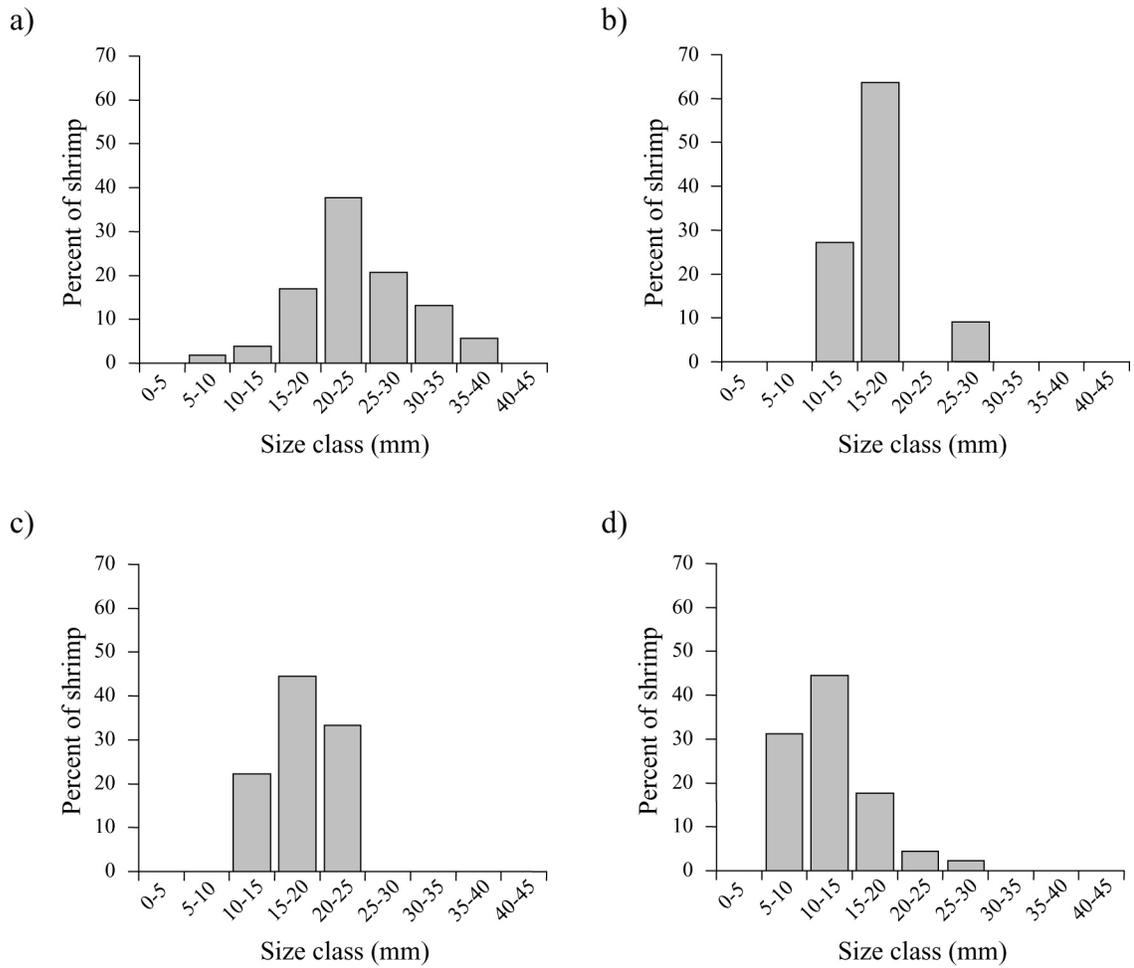


Fig. 4a-d. Size distribution of shrimp populations in marsh edges in different sampling periods. a) July/August 2002 and 2003. b) November 2002. c) February 2003. d) May 2003.

Table 1. Water chemistry at SMMAP by sampling period.

Variable	Test Used	p value	Mean (95% Confidence Interval)			
			July/August	November 2002	February 2003	May 2003
Dissolved oxygen (mg/l)	ANOVA	< 0.001	8.80 (7.96-9.64)	13.36 (11.44-15.28)	10.07 (9.53-10.61)	5.41 (5.08-5.74)
Salinity (ppt)	ANOVA	0.476	16.33 (13.49-19.17)	19.54 (18.27-20.81)	14.06 (13.25-14.87)	15.11 (13.71-16.51)
Water temperature (°C)	ANOVA	< 0.001	29.57 (28.79-30.35)	18.80 (18.37-19.23)	12.69 (12.28-13.10)	29.73 (29.18-30.28)

Table 2. Temporal changes in variables characterizing samples of *P. intermedius* taken from seagrass at SM MAP.

Variable	Test Used	p value	Central Tendency* (95% confidence interval)**			
			July/August	November 2002	February 2003	May 2003
Abundance (shrimp/sweep)	Kruskal-Wallis ANOVA	< 0.0001	18.0 (3.0-21.1)	46.5 (22.0-352.8)	1.5 (0.2-2.6)	14.5 (4.0-18.2)
Total length (mm)	Kruskal-Wallis ANOVA	< 0.0001	19.143 (15.233-21.371)	9.714 (5.571-12.824)	16.571 (15.979-30.214)	12.429 (8.877-15.979)
Sex ratio (female/male)	X ²	0.006	0.55 (0.49-0.61)	0.49 (0.43-0.56)	0.47 (0.25-0.69)	0.61 (0.59-0.68)
Proportion gravid females	X ²	< 0.0001	0.47 (0.39-0.62)	0.23 (0.17-0.30)	0.00 (0.00-0.00)	0.19 (0.06-0.32)
Clutch size	Kruskal-Wallis ANOVA	0.181	42.5 (16.6-102.5)	28.0 (18.0-47.0)	*** ***	29.0 (11.8-71.2)
Intermolt period	X ²	0.018	5.5 (4.6-6.5)	8.4 (7.0-16.4)	15.6 (6.0-25.2)	4.4 (3.8-5.2)
Growth increment	Kruskal-Wallis ANOVA	0.547	0.043 (-0.098-0.230)	0.079 (-0.139-0.127)	0.030 (-0.079-0.180)	0.049 (-0.089-0.243)
Growth rate mm/day	Kruskal-Wallis ANOVA	0.168	0.0009 (0.0003-0.0020)	0.001 (0.0006-0.0014)	0.0002 (0.0000-0.0007)	0.0017 (0.0010-0.0018)

* Mean when test is X², median when test is Kruskal-Wallis ANOVA

** 5th and 95th percentiles when test is Kruskal-Wallis ANOVA

*** Sample size is 0 or 1, therefore data were not included in statistical tests and confidence intervals were not calculated.

Table 3. Temporal changes in variables characterizing samples of *P. intermedius* taken from marsh edges at SMMAP.

Variable	Test Used	p value	Central Tendency* (95% confidence interval)**			
			July/August	November 2002	February 2003	May 2003
Abundance (shrimp/ sweep)	Kruskal-Wallis ANOVA	0.331	0.6 (0.2-4.5)	0.8 (0.1-7.9)	0.7 (0.1-3.0)	0.6 (0.1-15.8)
Total length (mm)	Kruskal-Wallis ANOVA	<0.001	22.929 (17.080-23.845)	15.710 (12.786-22.786)	16.429 (14.343-21.286)	12.714 (8.286-15.514)
Sex ratio (female/male)	X ²	0.468	0.06 (0.00-0.33)	0.46 (0.00-1.00)	0.78 ***	0.53 (0.00-0.92)
Proportion gravid females	***	***	0.27 (0.11-0.43)	0.00 ***	0.00 ***	0.00 (0.00-0.00)
Clutch size	***	***	89.0 (16.0-116.6)	*** ***	*** ***	*** ***
Intermolt period	X ²	0.326	6.1 ***	4.8 (4.4-14.3)	*** ***	8.1 (6.8-10.3)
Growth increment	Kruskal-Wallis ANOVA	0.233	0.006 (0.001-0.013)	0.010 (-0.070- 0.184)	0.008 (-0.056-0.182)	0.000 (-0.079-0.117)
Growth rate mm/day	Kruskal-Wallis ANOVA	0.194	0.0008 ***	0.0015 ***	*** ***	0.0000 (-0.0001-0.0001)

* Mean when test is X², median when test is Kruskal-Wallis ANOVA

** 5th and 95th percentiles when test is Kruskal-Wallis ANOVA

*** Sample size is 0 or 1, therefore data were not included in statistical tests and confidence intervals were not calculated.

Table 4. Differences in variables characterizing samples of *P. intermedius* taken in different habitats at SM MAP in the July/August 2002 and 2003 sampling periods.

Variable	Test Used	p value	Central Tendency* (95% Confidence Interval)**	
			Seagrass	Marsh Edge
Abundance (shrimp/sweep)	Mann-Whitney U Test	< 0.001	18.0 (3.0-30.3)	0.6 (0.2-4.5)
Total Length (mm)	Mann-Whitney U Test	< 0.001	19.143 (15.233-28.371)	22.929 (17.080-23.845)
Sex ratio (female/male)	X ²	0.773	0.55 (0.49-0.61)	0.06 (0.00-0.33)
Proportion of females gravid	X ²	0.015	0.47 (0.39-0.62)	0.27 (0.11-0.43)
Clutch Size	Mann-Whitney U Test	0.0428	42.5 (16.6-102.5)	89.0 (16.0-116.6)
Intermolt period	***	0.679	5.5 (4.6-6.5)	6.1 ***
Growth increment	Mann-Whitney U Test	0.9213	0.006 (-0.098-0.230)	0.006 (0.0012-0.0129)
Growth rate	***	***	0.0009 (-0.0001-0.0020)	0.0008 ***

* Mean when test is X², median when test is Mann Whitney U Test

** 5th and 95th percentiles when test is Mann-Whitney U Test

*** Sample size is 0 or 1, therefore data were not included in statistical tests and confidence intervals were not calculated.

Table 5. Differences in variables characterizing samples of *P. intermedius* taken in different habitats at SM MAP in the November 2002 sampling period.

Variable	Test Used	p value	Central Tendency* (95% Confidence Interval)**	
			Seagrass	Marsh Edge
Abundance (shrimp/sweep)	Mann-Whitney U Test	0.0002	46.5 (22.0-352.8)	0.8 (0.1-7.9)
Total length (mm)	Mann-Whitney U Test	< 0.0001	9.714 (5.571-12.824)	15.710 (12.786-22.786)
Sex ratio (female/male)	X ²	0.798	0.49 (0.43-0.56)	0.46 (0.00-1.00)
Proportion of females gravid	X ²	< 0.0001	0.23 (0.17-0.30)	0.00 ***
Clutch size	***	***	28.0 (18.0-47.0)	*** ***
Intermolt period	X ²	0.259	8.4 (7.0-16.4)	4.8 (4.4-14.3)
Growth increment	Mann-Whitney U Test	0.259	0.011 (-0.139-0.127)	0.010 (-0.070-0.184)
Growth rate	Mann-Whitney U Test	0.083	0.0007 (0.0004-0.0010)	0.0015 ***

* Mean when test is X², median when test is Mann Whitney U Test

** 5th and 95th percentiles when test is Mann-Whitney U Test

*** Sample size is 0 or 1, therefore data were not included in statistical tests and confidence intervals were not calculated.

Table 6. Differences in variables characterizing samples of *P. intermedius* taken in different habitats at SM MAP in the May 2003 sampling period.

Variable	Test Used	p value	Central Tendency* (95% Confidence Interval)**	
			Seagrass	Marsh Edge
Abundance (shrimp/sweep)	Mann-Whitney U Test	< 0.0001	14.5 (4.9-27.7)	0.6 (0.1-15.8)
Total Length (mm)	Mann-Whitney U Test	0.91	12.429 (8.877-15.979)	12.714 (8.286-15.514)
Sex ratio (female/male)	X ²	0.337	0.61 (0.59-0.68)	0.53 (0.00-0.92)
Proportion of females gravid	X ²	< 0.0001	0.19 (0.06-0.32)	0.00 (0.00-0.00)
Clutch Size	***	***	29.0 (11.8-71.2)	*** ***
Intermolt period	X ²	0.009	4.4 (3.8-5.2)	8.1 (6.8-10.3)
Growth increment	Mann-Whitney U Test	0.7388	0.007 (-0.089-0.243)	0.000 (-0.079-0.117)
Growth rate	Mann-Whitney U Test	0.083	0.0017 (0.0010-0.0018)	0.0000 (-0.0001-0.0001)

* Mean when test is X², median when test is Mann Whitney U Test

** 5th and 95th percentiles when test is Mann-Whitney U Test

*** Sample size is 0 or 1, therefore data were not included in statistical tests and confidence intervals were not calculated.

Table 7. Differences in variables characterizing samples of *P. intermedius* taken in different habitats at SM MAP in the February 2003 sampling period.

Variable	Test Used	p value	Central Tendency* (95% Confidence Interval)**	
			Seagrass	Marsh Edge
Abundance (shrimp/sweep)	Mann-Whitney U Test	0.0023	1.5 (0.2-2.6)	0.7 (0.1-3.0)
Total Length (mm)	Mann-Whitney U Test	0.8777	16.571 (15.979-30.214)	16.429 (14.343-21.286)
Sex ratio (female/male)	X ²	0.027	0.47 (0.36-0.62)	0.78 ***
Proportion of females gravid	***	***	0.00 (0.00-0.00)	0.00 ***
Clutch Size	***	***	*** ***	*** ***
Intermolt period	X ²	0.246	15.600 (6.0-25.2)	*** ***
Growth increment	Mann-Whitney U Test	0.1622	0.004 (-0.079-0.180)	0.008 (-0.056-0.182)
Growth rate	***	***	0.0017 (0.0012-0.0021)	*** ***

* Mean when test is X², median when test is Mann Whitney U Test

** 5th and 95th percentiles when test is Mann-Whitney U Test

*** Sample size is 0 or 1, therefore data were not included in statistical tests and confidence intervals were not calculated.

Table 8. Differences in variables characterizing samples of *P. intermedius* collected from different habitats in the Weeki Wachee estuary in August 2003.

Variable	Test Used	p value	Central Tendency* (95% confidence intervals)**	
			Seagrass	Marsh Edge
Abundance (shrimp/sweep)	Mann-Whitney U Test	< 0.0001	11.5 (4.4-27.0)	0.6 (0.1-0.7)
Total Length (mm)	Mann-Whitney U Test	0.635	20.571 (16.686- 23.536)	22.857 (20.500- 27.929)
Sex ratio (female/male)	X ²	0.534	0.54 (0.34-0.93)	0.64 (0.34-0.93)
Proportion of females gravid	X ²	0.718	0.35 (0.28-0.64)	0.29 (0.00-0.65)
Clutch Size	Mann-Whitney U Test	0.101	32.5 (22.0-58.1)	50.5 (42.0-59.1)

* Mean when test is X², median when test is Mann Whitney U Test

** 5th and 95th percentiles when test is Mann-Whitney U Test

Table 9. Differences in variables characterizing samples of *P. intermedius* in different habitats in different estuaries during August 2003.

Variable	Test Used	p value	Central tendency* (95% Confidence Interval**)		
			SMMAP	Weeki Wachee	Steinhatchee
Seagrass					
Abundance	Kruskal-Wallis ANOVA	0.002	11.5 (7.4-26.2)	11.5 (4.4-27.0)	0.7 (0.1-3.2)
Shrimp Total Length	Kruskal-Wallis ANOVA	0.133	21.000 (14.600-29.764)	20.571 (16.686-23.536)	18.288 (10.571-26.943)
Sex Ratio	X ²	0.911	0.55 (0.04-0.58)	0.54 (0.34-0.93)	0.53 (0.22-0.84)
Proportion of Females Gravid	X ²	0.012	0.26 (0.08-0.28)	0.35 (0.28-0.64)	0.18 (0.03-0.23)
Clutch Size	Kruskal-Wallis ANOVA	0.354	27.0 (16.4-89.8)	32.5 (22.0-58.1)	39.0 (22.4-54.0)
Marsh Edge					
Abundance	Kruskal-Wallis ANOVA	0.023	0.6 (0.1-0.7)	0.6 (0.1-0.7)	0.8 (0.7-1.5)
Shrimp Total Length	Kruskal-Wallis ANOVA	0.004	26.000 (20.300-34.250)	22.857 (20.500-27.929)	17.429 (13.400-19.929)
Sex Ratio	X ²	0.978	0.60 (0.36-0.84)	0.64 (0.34-0.93)	0.62 (0.36-1.60)
Proportion of Females Gravid	X ²	0.763	0.25 (0.00-0.51)	0.29 (0.00-0.65)	0.17 (0.06-0.93)
Clutch Size	Kruskal-Wallis ANOVA	0.165	89.0 (11.8-116.6)	50.5 (42.0-59.1)	32.5 (20.3-34.8)

* Mean when test is X², median when test is Kruskal-Wallis ANOVA

** 5th and 95th percentiles when test is Kruskal-Wallis ANOVA

Table 10. Characteristics of seagrass vegetation in different estuaries in August 2003.

Variable	Test Used	p value	Median (5th, 95th percentile)		
			SMMAP	Weeki Wachee	Steinhatchee
<u>Halodule</u> % Areal Cover	Kruskal- Wallis ANOVA	< 0.001	80.0 (20.0-90.0)	100.0 (90.0-100.0)	1.9 (0.2-3.6)
<u>Halophila</u> % Areal Cover	Kruskal- Wallis ANOVA	1	0.0 (0.0-0.0)	5.5 (1.0-10.0)	0.0 (0.0-0.0)
<u>Syringodium</u> % Areal Cover	Kruskal- Wallis ANOVA	0.55	0.0 (0.0-0.0)	0.0 (0.0-0.0)	0.6 (0.1-12.8)
<u>Ruppia</u> % Areal Cover	Kruskal- Wallis ANOVA	1	0.0 (0.0-0.0)	0.0 (0.0-0.0)	0.0 (0.0-0.0)
<u>Thalassia</u> % Areal Cover	Kruskal- Wallis ANOVA	< 0.001	0.7 (0.3-1.3)	0.0 (0.0-0.0)	80.0 (10.0-100.0)
<u>Halodule</u> shoot density (shoots/m ²)	Kruskal- Wallis ANOVA	< 0.001	792.0 (36.8-1651.2)	544.0 (80-1152.0)	14.4 (1.6-544.0)
<u>Halophila</u> shoot density (shoots/m ²)	Kruskal- Wallis ANOVA	0.609	0.0 (0.0-0.0)	0.0 (0.0-0.0)	0.0 (0.0-0.0)
<u>Thalassia</u> shoot density (shoots/m ²)	Kruskal- Wallis ANOVA	< 0.001	11.6 (1.6-17.6)	9.6 (1.6-41.6)	14.4 (1.6-225.6)
<u>Syringodium</u> shoot density (shoots/m ²)	Kruskal- Wallis ANOVA	0.114	0.0 (0.0-0.0)	0.0 (0.0-0.0)	11.2 (1.6-625.6)
<u>Halodule</u> aboveground biomass (g/m ²)	Kruskal- Wallis ANOVA	< 0.001	624.0 (36.8-1368.0)	280.0 (80.0-640.0)	14.4 (1.6-449.6)
<u>Halophila</u> aboveground biomass (g/m ²)	Kruskal- Wallis ANOVA	0.976	0.0 (0.0-0.0)	0.0 (0.0-0.0)	0.0 (0.0-0.0)
<u>Thalassia</u> aboveground biomass (g/m ²)	Kruskal- Wallis ANOVA	0.002	9.6 (1.6-614.4)	8.0 (1.6-43.2)	14.4 (1.6-142.7)
<u>Syringodium</u> aboveground biomass (g/m ²)	Kruskal- Wallis ANOVA	0.114	0.0 (0.0-0.0)	0.0 (0.0-0.0)	11.2 (1.6-481.6)

Table 11. Water chemistry in the SMMAP, Weeki Wachee and Steinhatchee estuaries in August 2003.

Variable	Test Used	p value	Mean (95% Confidence Interval)		
			SMMAP	Weeki Wachee	Steinhatchee
Dissolved oxygen (mg/l)	ANOVA	0.013	7.60 (6.30-8.90)	11.86 (11.43-12.28)	4.78 (1.61-7.96)
Salinity (ppt)	ANOVA	0.007	9.99 (9.39-10.59)	17.68 (16.40-18.95)	10.52 (6.85-14.19)
Water temperature (°C)	ANOVA	0.299	29.34 (28.76-29.91)	27.61 (26.66-28.56)	31.26 (29.91-32.61)

DISCUSSION

Determination of the Relative Quality of Habitat Types

A habitat type was considered to provide higher habitat quality than another for P. intermedius if one of the following three conditions were met: (1) if shrimp abundance and ISF variables both indicated higher habitat quality in the same habitat or estuary, (2) if shrimp abundance was similar between the two and the ISF variables indicated greater fitness in one over the other, (3) if the ISF variables were similar, but abundance was higher in one over the other. In the situations where abundance and ISF variables proved to be contradictory, then fitness related measures and abundances were used to estimate fecundity at the population level in an effort to provide additional insights into the relative qualities of the habitats.

Temporal Variability within the SMMAP

SMMAP Within Habitat Sampling

Observed temporal changes in the demographics and physiology of grass shrimp within the seagrass and marsh edge habitats suggest seasonal changes consistent with those found in other studies (Kneib 1987, Knowlton et al. 1994, Grabe 2003). These temporal changes provide important background information that should be considered when comparing the relative habitat quality of seagrass beds and marsh edges for P. intermedius. The results suggest that summer months are the most appropriate time to compare and contrast estimates of abundance and fitness to infer relative habitat quality.

This can best be illustrated through discussion of results from each of the sampling periods.

In February 2003, the relative abundance of P. intermedius was at its minimum in SMMAP, similar to reduced winter abundances documented by Knowlton et al. (1994) in North Carolina. The shift in sex ratio towards a more male-dominated population from November 2002 to February 2003 in this study suggested that females may have begun to suffer the effects of reduced habitat quality before males, which is consistent with Reinsel et al. (2001), who showed that limited food availability caused increased mortality of females relative to males. This increased susceptibility of females may be due to the large amount of energy invested in reproduction (Vernberg and Piyatitivorakul 1998). This large reproductive investment could, however, also support the alternative conclusion that female shrimp are simply succumbing to the metabolic demands of repeated reproduction during summer and late fall irrespective of changes in the quality of the habitat in which they are found.

However, changes in other ISF variables in February 2003 also suggest declining habitat quality in winter. Apparently spawning did not occur in February 2002, because gravid females were not collected, a pattern observed in other decapods during winter months (e.g. Grabe 2003). In February 2002, P. intermedius size was at its maximum, suggesting that only the largest individuals were capable of surviving an autumn-winter mortality event. This result is consistent with that of Chockley and St. Mary (2003), who found that mortality of Stenopus hispidus decreased with increasing shrimp size. In addition, the long IMP during this sampling period suggested that conditions in the

seagrass beds, or the estuarine waters in general, were negatively influencing growth rates in addition to precluding spawning.

In May 2003, an increase in shrimp abundance, proportion of gravid females, and shorter IMPs suggested that conditions in the seagrass beds were improved relative to winter. In the July/August sampling periods, conditions within seagrass beds were most favorable for reproduction, as indicated by the high proportion of gravid females in the sample population. This result suggests that summer months are the primary breeding period for grass shrimp along the Gulf of Mexico coast, which is what would be expected for a decapod in a temperate or subtropical climate.

Although the total number of shrimp increased in November 2002, the median size was reduced as a consequence of an influx of newly recruited shrimp. The increase in abundance is consistent with autumnal increases documented in other studies (Knowlton et al. 1994). Spawning continued during this time, but at a reduced rate compared to either spring or summer, as indicated by the lower proportion of gravid females. Along with decreased spawning, an increase in the intermolt period and a reduced proportion of females in the population suggested a decline in the quality of seagrass habitats or the environment as a whole during November and a critical period in the life history of P. intermedius. Shrimp abundance had declined markedly by February, indicating increased mortality during late fall and winter. Alternatively, shrimp may have emigrated to other areas. However, due to their small size, presumed lack of long distance mobility, apparent absence from offshore habitats and lack of increased abundance in any other habitats sampled in this study, emigration is an unlikely explanation for the decline in numbers between November and February.

So what were the primary habitat characteristics or environmental factors driving these changes in shrimp demography? The lack of significant changes in the percent areal cover of seagrass as a whole, or of species composition of seagrasses, implies that seasonal changes in vegetation were not driving the changes observed in shrimp demographics. The most likely explanation for the changing demographics within the shrimp population is water temperature, which is an environmental, rather than a habitat, characteristic. Fall/winter mortalities of shrimp similar to those observed in this study have been documented in other locations (Knowlton et al. 1994), and Lemaire et al. (2002) suggested that reduced water temperatures could compromise the osmoregulatory abilities of juvenile and subadult Pennaeus stylirostris. Vernberg and Piyatitivorakul (1998) demonstrated that temperature had significant effects on many grass shrimp metabolic processes. Changes in temperature and salinity have been shown to affect changes in caridean shrimp abundances in other locations as well (Walsh and Mitchell 1998). However, temperature and food production are also often correlated in marine environments, and productivity of seagrass beds is known to vary seasonally (e.g. Peterson and Fourquean 2001). Brockington and Clarke (2001), in an attempt to determine the relative influence of temperature and food availability for the sea urchin Sterechinus neumayeri, found that food availability may indeed be the key factor driving metabolic rates, as opposed to temperature. Further study is necessary to determine which factor is more important for grass shrimp, and P. intermedius in particular.

In the marsh edges, temporal variability was less pronounced than in the seagrass beds. There were no significant changes in abundance or any ISF variable other than total length. However, the quality of marsh edges seemed higher in the July/August sampling

period than other sampling periods. Grass shrimp were significantly larger within marsh edge habitats in July/August, and this was the only period in which gravid females were encountered. Since the percent areal cover of plant species did not change significantly, and the DO, salinity, and water temperature values were similar to those encountered in seagrass, water temperature is the most likely cause of temporal changes in shrimp demographics in marsh edges as well.

SMMAP Cross-Habitat Comparisons (Seagrass vs. Marsh Edge)

In all sampling periods, greater abundances of shrimp and higher proportions of gravid females were found in seagrass beds than along marsh edges. Although this appears to contradict the findings of Rozas and Minello (1998), who documented higher abundances of grass shrimp in salt marshes than seagrass beds in a Texas estuary, it may simply reflect a difference in occupancy patterns between marsh edges and salt marshes that were not captured by either study. In May 2003, shrimp from seagrass had shorter IMPs, and gravid females were only caught in seagrass beds during this time period. Thus, it is concluded (based on criterion 1 above) that seagrass beds provided higher quality habitat than marsh edges in May. During the July/August sampling periods, shrimp size and clutch size indicated higher habitat quality in marsh edges. These variables were expected to covary, however, as a relationship between crustacean size and clutch size has been previously documented, notably by Chockley and St. Mary (2003), who documented this relationship for banded coral shrimp. Despite the differences in total length and clutch size, the much greater abundances and the higher proportion of gravid females in the seagrass beds were far more important in determining the net number of eggs produced per area of habitat than the larger clutch sizes in marsh edges, as indicated by the estimated number of eggs/sweep. The larger size of shrimp in

marsh edges may suggest that only large shrimp are capable of surviving in this habitat, or that dominant individuals are monopolizing the habitat at low densities, implying that there is some degree of habitat segregation by size in these shrimp, as has been shown for the daggerblade grass shrimp (P. pugio) when subjected to mummichog (Fundulus heteroclitus) predation (Davis et al. 2003), and also for tiger prawns (Pennaeus esculentus and P. semisulcatus) in Australian seagrass beds (Loneragan et al. 1998). Based on the greater potential reproductive output of shrimp in seagrass beds, it was concluded that marsh edges provided an inferior habitat for P. intermedius during summer time periods.

In February 2003, the pattern was apparently somewhat different. Although shrimp abundance remained higher in seagrass beds than marsh edges, the difference was not as pronounced. However, the sex ratio of shrimp in the marsh was skewed towards females, in comparison with the nearly even sex ratio of the sampled shrimp population in seagrass beds. When the abundance values were multiplied by the sex ratios in each of the habitats, it was clear that there were approximately the same number of females per unit area in each of the habitats. The higher proportion of females in marsh edges may imply that habitat quality there was higher, and the higher abundance in seagrass may imply some degree of overcrowding of subdominant individuals into suboptimal habitat during this time period. This possibility is further supported by the observation that female grass shrimp tend to be larger than males, and so would presumably be dominant in intraspecific agonistic competition. This possibility merits further investigation. Since no other variables were significantly different between the habitats, and the sex ratio and abundance do not both point to the same habitat as having higher quality, it can not be

conclusively stated that either of these habitats was higher quality than the other during February 2003.

Among Estuaries Comparisons

Weeki Wachee and SMMAP showed similar patterns in August 2003. Seagrass beds provided a higher quality habitat than the marsh edges for P. intermedius during July and August, and the same was true in the Weeki Wachee estuary. Seagrass beds in the Weeki Wachee estuary were determined to provide higher quality habitat than adjacent marsh edges because shrimp were more abundant in seagrass beds than marsh edges and there were no significant differences in measured ISF variables (criterion 3 above).

These results contrast with those from the Steinhatchee estuary, where shrimp abundances were similar between the two habitat types and no differences in ISF variables were observed. As a consequence it was not possible to designate either seagrass beds or marsh edges as the superior habitat in that estuary. Interestingly, the abundance of P. intermedius in Steinhatchee seagrass beds was less than the abundances found in seagrass in SMMAP or Weeki Wachee. In fact, it was the marked reduction in numbers of P. intermedius in seagrass that accounted for similarities in abundance between the two primary habitat types rather than an increase in marsh edge occupancy. Although shrimp abundance in the Steinhatchee marsh sites was greater than the other two estuaries, the cross-estuary differences in this habitat type were relatively small.

The lower abundance of shrimp in seagrass beds in Steinhatchee relative to either SMMAP or Weeki Wachee coupled with the fact that the proportion of gravid females was also less suggests that seagrass habitat in Steinhatchee was of lower quality for P. intermedius. Many reasons may explain these findings, but data reported here indicate

that the vegetative characteristics of the seagrass beds may be important. The percent areal cover of H. wrightii was lowest in Steinhatchee and greatest in Weeki Wachee. The percent areal cover and shoot density of T. testudinum, on the other hand, was greater in the Steinhatchee estuary than in either SMMAP or Weeki Wachee. These patterns suggest that seagrass beds dominated by Halodule may provide a higher quality habitat for P. intermedius than those dominated by Thalassia. Although preference for a species of seagrass has not been demonstrated for P. intermedius, preference for specific seagrass communities has been documented for other shrimp species (Loneragan et al. 1998).

The relative quality of the seagrass beds in these different estuaries may change temporally as they did in SMMAP. Broad generalizations based on these findings warrant caution.

Shrimp abundance and ISF variables were more uniform within marsh edges across estuaries. However, marsh edge habitats in the Steinhatchee estuary had greater abundances of shrimp than marsh edges in the other two estuarine areas, which may indicate an increased use of otherwise suboptimal marsh habitats, perhaps due to the reduced quality of seagrass habitats in Steinhatchee.

Overall Conclusions

The lack of any shrimp near oyster bars in SMMAP contrasts with Eggleston et al. (1998), who documented grass shrimp using these habitats. Throughout all estuaries and sampling periods, marsh edges appeared to maintain consistent, fairly low-quality habitat for P. intermedius. This contrasts with seagrass beds, where habitat quality was generally much higher and more variable. The similarity in habitat quality between seagrass beds and marsh edges in February 2003 was likely due to a decrease in the quality of seagrass habitat. If seagrass beds in North Carolina show similarly variable

habitat quality relative to alternative habitats such as marsh edge or oyster bars, this may provide an explanation for the findings of Eggleston et al. (1998), who found higher abundances in seagrasses than along oyster bars in spring but similar abundances between habitats in late fall. Temporal differences in the relative quality of seagrass and marsh edge habitats to grass shrimp in summer and winter sampling periods at SMMAP likely reflect broad-scale environmental shifts in temperature, that, in turn, may affect also food availability for this organism.

The variation in quality among seagrass beds may also explain why the quality of marsh in Steinhatchee, equaled or surpassed that of seagrass. Seagrass in Steinhatchee was poorer quality habitat compared to seagrass in these other estuaries. Where seagrass quality was determined to be poor for grass shrimp, such as at Steinhatchee in August 2003, or SMMAP in February 2003, marsh edges were determined of equal or greater value to the shrimp. Poor quality seagrass habitat for P. intermedius during summer was dominated by T. testudinum, and high quality habitat was dominated by H. wrightii.

Relative abundance was a good indicator of habitat quality both between habitats and between estuaries during most time periods, which fails to support Van Horne (1983). Perhaps, Van Horne's (1983) ideas do not apply to estuarine invertebrates as well as they do to terrestrial quadrupeds. However, relative abundance and the ISF variables did appear to be decoupled at certain times of the year, such as when small shrimp appeared in November 2002.

Perhaps the import of these findings can best be understood from a management perspective, if we consider P. intermedius to be a model organism for others (such as penaeid shrimp or Macrobrachium spp.) that are commercially important and therefore

more likely to require intensive management. If a manager wanted to set up a marine protected area for *P. intermedius*, abundance would likely be an acceptable measure for selecting the location with the best habitat quality and to protect. However, if a manager was attempting to use closed and open seasons as a management tool to generate productivity, then measures of fecundity, mortality, and growth rates would be necessary to determine the best time to restrict harvest. For example, during May, July, and August, when growth rates and fecundity were greatest, exploitation should be restricted to maximize productivity. Relative abundance (and likely biomass) was highest in November, when the period of mass mortality was beginning, and this would be the best time to utilize these shrimp as a resource. On this temporal scale, therefore, Van Horne's theory was supported because the greatest abundances did not always occur when ISF variables pointed to the highest quality of the habitat or environment.

Future study of grass shrimp habitat ecology would be most informative if it focused on five key issues: (1) better resolution of the temporal variability within populations so as to determine if the seasonal patterns suggested by this study do, in fact exist; (2) better determination of what factors (i.e., food availability, water temperature or others) most influence the temporal variability in grass shrimp populations; (3) better determination of what factors (i.e., dominant grass type or spatial distribution of habitats) most influence variability in grass shrimp populations within seagrass; (4) better determination of what characteristics make marsh edges a less high-quality habitat relative to seagrass; and (5) why Van Horne's predictions apparently fail to hold in the context of this estuarine invertebrate.

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BIOGRAPHICAL SKETCH

Daniel Scott Goodfriend was born on March 15, 1976, in Suffern, New York. He lived in the suburbs of New York City until his graduation from Rockland Country Day School in May of 1994, where he spent a lot of time enjoying the outdoors in and around New York's Harriman State Park. After graduating high school, he spent two semesters as a philosophy of religion major at Grinnell College in Iowa, but found this subject matter too abstract. He left school in an attempt to find a path that was more personally fulfilling and spent the next three years traveling around the United States, living briefly in New Orleans, Louisiana and Lake Worth, Florida. In January 1996 he moved to Encinitas, California, and began attending classes at MiraCosta College in the nearby town of Oceanside. Drawing on his experiences in the woods of New York and his travels to various National Parks, he decided on a major in wildlife. To pursue this goal, he transferred to Humboldt State University in Arcata, California, in August 1997. After three and a half very enjoyable years, he graduated with a Bachelor of Science in wildlife in December of 2001. He then spent a year in the Americorps program monitoring a population of threatened Blanding's turtles (*Emydoidea blandingii*) for the nonprofit group Hudsonia, based in Dutchess County, NY.

After his year at Hudsonia, Daniel decided that his goals required him to continue his education, and in January 2002 he enrolled at the University of Florida in Gainesville. There he spent two and a half rewarding years studying coastal ecology with Dr. Thomas Frazer, and will receive a Master of Science degree in May 2000.