Environmental factors affecting burrowing by brown shrimp *Farfantepenaeus aztecus* and white shrimp *Litopenaeus setiferus* and their susceptibility to capture in towed nets

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Abstract

Laboratory experiments were conducted under simulated daytime conditions to examine the effects of salinity, sediment texture, size, density, and hunger on burrowing behavior of juvenile brown shrimp *Farfantepenaeus aztecus* and white shrimp *Litopenaeus setiferus*. Over all experimental conditions (20,929 observations of 2411 individual shrimp), 77.5% of brown shrimp and 21.4% of white shrimp were observed burrowed with more than half of their body beneath the substrate. The tendency of burrowed shrimp to emerge from burrows when disturbed also was tested. When burrowing rates were examined in combination with this tendency to emerge upon disturbance, only 46.7% of brown shrimp would be susceptible to capture in towed nets, while almost all (97%) white shrimp would be susceptible. All environmental factors examined in this study, except salinity for white shrimp, significantly affected burrowing of these species. When these environmental effects on burrowing were combined with the likelihood of emergence, however, the effects of salinity and substrate type on brown shrimp

behavior appeared most likely to affect capture by towed nets. Estuarine abundance indices from resource surveys using towed nets could be adjusted using such vulnerability estimates.

Key Words: burrowing, penaeid shrimp, catch efficiency, trawls

1.0 Introduction

Burrowing in the substrate by penaeid shrimps is a common behavior that can affect availability to sampling and fishing gear and also appears to increase survival rates by protecting shrimp from fish predators (Fuss and Ogren 1966, Minello et al. 1987). Shrimp generally burrow during daylight hours and emerge during the night, but the intensity of this behavior varies among species and with environmental factors. The two most common and commercially important penaeids in the northern Gulf of Mexico, brown shrimp *Farfantepenaeus aztecus* and white shrimp *Litopenaeus setiferus*, display different burrowing behaviors (Wickham and Minkler 1975). Adult brown shrimp burrow through most of the day with the trawl fishery for this species mainly occurring at night. White shrimp burrow less than brown shrimp, and the main fishery for this species is during the day.

Little effort has been made to understand how environmental factors interact with shrimp behavior to affect catchability despite the known variability in burrowing behavior, the potential effect of this behavior on catchability, and the recognition that catch efficiency for shrimp can be low in trawls and seines (Zimmerman et. al. 1986, Rozas and Minello 1997). Most resource surveys in estuaries of the northern Gulf of Mexico are conducted during daylight hours (Brown et al. 2013), and these estimates of juvenile shrimp abundance are key inputs into ecosystem models and stock assessments. With a better understanding of burrowing behavior, estimates of shrimp abundance based on Catch per Unit Effort (CPUE) in trawls could be adjusted for catchability based on environmental covariates found to significantly affect burrowing. This approach would reduce bias in nominal CPUE and result in more accurate abundance indices.

Most experimental studies examining environmental effects on burrowing of shrimp species have been conducted on adults and subadults. Juveniles have not been considered to be strong burrowers, but relatively few studies have examined burrowing during this life stage. Adult brown shrimp and white shrimp occur in offshore waters, but juveniles of both species use estuaries as nursery grounds. Here, they grow from postlarvae to subadults (from approximately 10 – 90 mm total length) in several months and are often sampled using towed nets. Burrowing by brown shrimp has been shown to be affected by light intensity and water turbidity (Wickham and Minkler 1975, Minello et al. 1987, Martinez 1991), temperature (Aldrich et al. 1968), salinity (Lakshmi et al. 1976), and substrate texture (Williams 1958). White shrimp burrow less than brown shrimp, and few environmental factors have been shown to affect their burrowing except for light intensity.

The laboratory experiments described here were conducted to examine environmental and biological factors affecting burrowing by juvenile brown shrimp and white shrimp. The effects of size, density, salinity, substrate texture, and hunger were examined to test the null hypotheses that these factors would not affect burrowing behavior. The tendency of burrowed shrimp to emerge from burrows when disturbed also was tested to simulate vulnerability to capture in towed nets. A better understanding of these interactions should be useful in estimating shrimp abundance from CPUE using towed nets.

2.0 Methods and Materials

Juvenile shrimp were collected in the Galveston Bay system of Texas, U.S.A. and held before experiments in the laboratory under natural light conditions (skylights) in fiberglass tanks filled with a crushed shell substrate. Burrowing experiments were conducted in twelve rectangular tanks (58 cm x 149 cm; 0.86 m^2 area) located in a dark temperature controlled room equipped with fluorescent lighting and under a 12:12 h day:night light regime. Light was constant during the daylight period in these experimental tanks and was measured near the substrate using a LI-COR quantum meter (Model LI-185B). The mean light intensity during the simulated daylight hours was 10.6 (SE=0.18) μE (microEinsteins) $s^{-1}m^{-2}$ based on 10 observations in each tank. This light intensity is comparable to the light reaching the bay bottom during a sunny day when incident light at the water's surface is ~ 1000-2000 μE $s^{-1}m^{-2}$ and the following approximate conditions occur: water depth 2 m, nephelometric turbidity 20 FTUs, an attenuation coefficient (Kd) of 2.0, and a Secchi disk depth of 0.5-0.7 m (Carter and Rybicki 1990, Martinez 1991, Koenings and Edmundson 1991). Experimental tanks were filled to a depth of 25 cm with sand-filtered seawater pumped from the Gulf of Mexico off Galveston Island.

Treatments were randomly applied to tanks except for substrate experiments where the substrates remained in the same tanks throughout the experimental series. Shrimp from holding tanks, however, were randomly placed in tanks during all experiments. Shrimp were moved from holding tanks to experimental tanks in the afternoon on the day before observations were initiated. The next day, the lights came on at 0730 h, and observations on behavior were recorded hourly (starting at 0830 h) throughout the daylight period (generally 10 hourly observations during a day). Black plastic curtains surrounded each tank, and observations were made through small portals to avoid disturbance. During each hourly observation period, individual shrimp were categorized into one of eight behaviors (Table 1). Completely burrowed shrimp could often be identified by depressions in the sediment, the presence of a respiratory tube, or parts of their antennules above the substrate (see Dall et al. 1990), but some shrimp had to be categorized as completely burrowed through a process of elimination. The tanks were drained after the last daily observation, and shrimp were counted and measured from the tip of the rostrum to the tip of the telson (TL, total length). The mean size of shrimp for each experiment is reported in Supplemental Table 1. Shrimp species were tested separately, and each experiment was repeated on a second day; thus there were generally observations from 8-12 replicate tanks for each treatment combination.

The standard experimental conditions, unless the factor was being manipulated in the experiment, included: a) shrimp with a mean TL of 68 mm; b) ten shrimp per tank (11.6 m^{-2}); c) a salinity of 24-26; d) a fine washed beach sand substrate (very well sorted with a graphic mean grain size of 2.99 phi; Folk 1980); e) a mean temperature of 23.5 ^{0}C (SE=0.23); and f) shrimp fed daily (each evening) before experiments with a pelleted shrimp chow. The following levels of experimental factors were tested: salinity (5, 25, and 40), approximate mean shrimp size (50, 75, and 100 mm TL), substrate (fine sand, coarse sand, crushed shell), density (5.8, 11.6, and 23.1 shrimp m^{-2}), and hunger (fed, starved).

2.1 Salinity experiments

Shrimp were held in three separate tanks before these experiments at an initial salinity of 25. Shrimp were slowly acclimated in two of the holding tanks to the experimental salinities of 5 and 40 over approximately 8 days using dechlorinated tap water and sea salts. Experimental tanks (four replicates for each treatment) were randomly selected and filled with seawater at salinities of 5, 25, and 40 the day before observations were initiated.

2.2 Sediment experiments

Burrowing and activity were compared among three different sediment types. Sediments were thoroughly washed before each experiment to reduce suspended sediments that may have interfered with observations and between experiments to remove any accumulated organic matter from shrimp feces. Sediment grain size was determined by sieving and analyzed according to Folk (1980). In addition to the standard fine grained sand described above, sediments consisted of coarse blasting sand (moderately sorted with a graphic mean grain size of 0.16 phi) and finely crushed oyster shell. About half of this shell hash was retained on a -1 phi sieve (2-mm), and overall this sediment was moderately well-sorted with a graphic mean grain size of -0.60 phi.

2.3 Size and Density experiments

Three different shrimp size groupings (Large, Medium, Small) were used in the Size experiments, but mean size varied because of limited availability (Supplemental Table 1). In brown shrimp experiments, overall mean size in mm TL (and SEs) for large, medium, and small shrimp was 95 (0.9), 68 (0.5), and 43 (0.8), respectively. In white shrimp experiments, this overall mean size (and SEs) for large, medium, and small shrimp was 101 (0.7), 74 (0.5), and 50 (0.6), respectively. In the density experiments, 5, 10, and 20 shrimp were placed in experimental tanks, and these densities were equivalent to 5.8, 11.6, and 23.1 shrimp m^{-2}, respectively.

2.4 Hunger experiments

Shrimp were separated into two holding tanks before these experiments. Shrimp in one tank were fed daily with pelleted shrimp chow, and the shrimp in the second tank were not fed for 5 days before the experiment. There was no food in any experimental tanks for the first five hourly observations (as in all other experiments throughout the day). At 1400 hrs during this experiment only, however, 2 g of pelleted shrimp chow was scattered throughout each experimental tank. Hourly observations in the presence of food continued in the tanks throughout the remainder of the day.

2.5 Emergence tests

Following the last observations during some experiments, the likelihood of burrowed shrimp to emerge from their burrows was tested by attempting to simulate effects of a trawl or seine on this behavior. A lead weight (3-mm wide, 28 g) from a seine net was attached to a string and dragged slowly over partially burrowed (Eyes and Head) shrimp from anterior to posterior. This test was conducted on 357 brown shrimp and 73 white shrimp.

2.6 Data Analysis

The primary objective was to examine the effects of experimental factors on burrowing, defined by whether the shrimp in a tank were at least half beneath the substrate (Table 1). The observation used in these analyses was the percentage of burrowed shrimp in each tank for each hourly observation. These percentages were arcsin transformed to reduce the skewed distribution common to percentage data (Sokal and Rolf, 2012). The transformed data were then analyzed using a linear mixed model in a repeated measures design using JMP software (Version 11.1.1, SAS Institute Inc.). In the Analysis of Variance model, Treatment was a fixed effect, Day was a fixed effect blocking variable, and the Time of observation was a random variable. If more than two levels of a treatment were present, then Tukey's HSD was used to compare means. While all statistical tests were conducted on transformed data, the untransformed means and SEs are presented in figures.

The distributions of shrimp among the different behavioral categories also were compared among treatments using Kolmogorov-Smirnov tests ($p < 0.05$ was considered significant). In these analyses the relative percentages of shrimp among the eight behavioral categories listed in Table 1 were compared between treatment levels using two-sample tests (Sokal and Rolf, 2012).

The emergence data were analyzed in 2 x 2 contingency tables for each species separately. The number of shrimp emerging after disturbance and those remaining burrowed was compared for the different burrowing behaviors (i.e., Eyes vs Head) in a test of independence. Fisher's exact test (2-tailed) was used to test for homogeneity between the number of shrimp emerging and those remaining burrowed, with the null hypothesis being that emergence was independent of the burrowing category.

3.0 Results

The difference between the two shrimp species in burrowing and activity was apparent from a summary of data over all experiments combined (Figure 1). There were 20,929 observations on 2411 shrimp, and the distributions among the eight behaviors were significantly different for the species (Kolmogorov-Smirnov two-sample test). Using the criteria for burrowed shrimp in Table 1, 77.5% of brown shrimp were burrowed during the study compared with 21.4% of white shrimp. No white shrimp were ever recorded as completely burrowed in the experiments, and the most frequently observed behavior for this species was "stationary on the substrate". The most frequently observed behavior for brown shrimp in experiments was "burrowed with their eyes emerging from the substrate". For the subset of the data under standard experimental conditions (i.e., medium shrimp size, fine sand, salinity 25, 11.6 shrimp m^{-2}, fed) present in each trial, 89.2% of brown shrimp were burrowed compared with 27.1% for white shrimp.

3.1 The effect of Size

There was a significant effect of size on burrowing of both shrimp species (Table 2, Figure 2). Large brown shrimp (mean TL 95 mm; SE = 0.9) burrowed significantly more than both medium sized (mean TL 68 mm; SE = 0.5) and small shrimp (mean TL 43 mm; SE = 0.8), but there was no significant difference between burrowing of medium and small shrimp (Tukey's HSD). Large white shrimp (mean TL 101 mm; SE = 0.7) burrowed more than small white shrimp (mean TL 50 mm; SE = 0.6), but there was no significant difference between medium sized shrimp and either large or small shrimp (Table 2).

Although the percentage of burrowed shrimp was affected by size, there was no significant size effect on the distribution of different behavior criteria for either species (Kolmogorov-Smirnov two-sample tests). Few small or medium brown shrimp were observed crawling or swimming; the highest frequency of occurrence for all brown shrimp was burrowed with only eyes emerged (E) from the substrate (Figure 3). Relative frequencies of white shrimp among the behavioral categories appeared similar for the different sizes examined, with the highest frequency of occurrence for stationary shrimp on the substrate.

3.2 The effect of Density

Despite the relatively small differences in mean burrowing rates of brown shrimp among the three densities tested (Figure 4), the ANOVA on arcsin transformed data indicated a significant effect of density. Burrowing was highest at low brown shrimp densities, with no significant difference between burrowing at the two highest densities tested (Table 2). Density also significantly affected burrowing of white shrimp, and burrowing was lowest in the high-density tanks (11%) compared with the medium (45%) and low (38%) density tanks.

The distributions among behavior criteria were not significantly different among treatments for brown shrimp (Kolmogorov-Smirnov two-sample tests), and as in the other experiments most brown shrimp fell into the behavior category of only eyes emerged (E) from the substrate (Figure 5). The distributions of white shrimp, however, were significantly different among the treatments. The high density treatment distribution was significantly different from both the medium and low density treatments. Fewer shrimp burrowed and more white shrimp were in the stationary behavior at high densities (Figure 5). White shrimp distributions among behavior criteria were not significantly different between the medium and low density treatments.

3.3 The effect of Salinity

Brown shrimp burrowing was significantly affected by salinity (Table 2) with the lowest burrowing rate at 5 and no significant difference in burrowing between 25 and 40 (Figure 6). White shrimp burrowing was not significantly affected by salinity.

There also was a significant difference in the distribution of brown shrimp between the 5 and 25 salinity treatments, with most of the shrimp completely burrowed or with just eyes emerged at 25, and more brown shrimp in the unburrowed categories at a salinity of 5 (Figure 7). There were no significant differences in brown shrimp distributions between salinities of 5 and 40 or between 25 and 40, and no differences in any comparisons for white shrimp (Kolmogorov-Smirnov two-sample tests).

3.4 The effect of Substrate type

Burrowing rates decreased for both species as the substrate became coarser (Table 2); the mean percentage of brown shrimp burrowed in fine sand, coarse sand, and crushed shell was 89%, 22%, and 8%, respectively (Figure 8). White shrimp only burrowed in fine sand (12%) and never in coarse sand or shell.

The distributions of brown shrimp among behavioral categories differed between fine sand and both coarse sand and shell; in fine sand most shrimp were classified as burrowed with their eyes emerged, while in the other substrate types most shrimp were stationary on the substrate (Figure 9). No differences in these distributions were apparent for white shrimp (Kolmogorov-Smirnov two-sample tests).

3.5 The effect of Hunger

Hunger level significantly affected burrowing for both species (Table 2, Figure 10). In these experiments, half of the shrimp were starved for 5 days before the experiment was initiated. No food was present in experimental tanks until 1400 h when food was added. For brown shrimp, there was no difference in burrowing behavior between fed and starved animals until food was added to the experimental tanks; burrowing rates of starved shrimp (62%) were then significantly lower than for fed shrimp (90%). Starved and fed white shrimp had similar burrowing rates during the first two observations of the day (Figure 10), but based on the ANOVA that integrated all observations before and after food was introduced, starved white shrimp had significantly lower burrowing rates (11%) compared with fed shrimp (32%) regardless of whether food was present or absent.

The distributions among behavior categories were examined using Kolmogorov-Smirnov two-sample tests. For brown shrimp there was no difference between fed and starved shrimp as long as no food was present, and no difference between fed shrimp whether food was present or not. The distribution of starved shrimp with food present, however, was different from both fed and starved shrimp with no food present. Starved brown shrimp emerged from the substrate to forage, and a large percentage were stationary on the substrate (Figure 11). No significant differences in these distributions were apparent for white shrimp, with the most shrimp in all treatments categorized as stationary on the substrate.

3.6 Emergence

Testing whether shrimp would emerge from the substrate after being disturbed with a lead weight passing over them was opportunistic. It was difficult to test emergence for completely burrowed shrimp, but the few brown shrimp tested did not emerge from burrows, supporting the assumption that completely burrowed shrimp would remain burrowed following disturbance. A total of 309 brown shrimp with just their eyes showing above the substrate (E) was tested, and 42.1% of these emerged; 48 brown shrimp with only their head showing (H) were tested and 29.2% emerged completely (Table 3). The contingency analysis indicated that emergence was independent of the different behavior categories (Fisher's Exact test, $p = 0.113$), and overall 40.3% of the shrimp tested emerged after disturbance. The percentage of brown shrimp that would be susceptible to capture in a trawl during the day was estimated under the assumptions that: 1) none of the completely burrowed shrimp would emerge when disturbed, 2) 40.3% of those with their head or eyes exposed would emerge, 3) all brown shrimp in the other burrowed category (i.e., > ½ burrowed) would emerge, and 4) all emerged shrimp would be captured. If 77.5% of brown shrimp are burrowed as in Figure 1, then less than half (46.7%) of the population would be captured under the above conditions. Under the standard experimental conditions used as a treatment level in each experiment (i.e., medium size, fine sand, salinity 25, 11.6 shrimp m^{-2}, fed), 89.2% of brown shrimp were burrowed, and 38.8% would be available for capture in a towed net. This same approach was used to calculate the availability of brown shrimp for the different treatment combinations examined in the laboratory experiments (Table 4); sediment texture appeared to have the largest effect on availability.

Relatively few white shrimp burrowed, providing fewer opportunities to test emergence. Only 20 white shrimp with just their eyes showing above the substrate (E) were tested, and 65.0% of these emerged; 53 white shrimp with only their head showing (H) were tested and all of these emerged completely after disturbance (Table 3). There was a significant difference in emergence related to these different behavior categories (Fisher's Exact test, $p < 0.0001$). Following the approach outlined above for brown shrimp, and based on the estimate that 25.3% of white shrimp would be burrowed as in Figure 1 and 27.1% would be burrowed under the standard experimental conditions, then almost all (~97%) white shrimp would be emerged and susceptible to capture in towed nets during the day. This percentage was also high (>94%) throughout all experimental conditions (Table 4).

4.0 Discussion

The burrowing behavior of penaeid shrimp is of interest because it varies among species, varies with environmental factors (see reviews by Fuss and Ogren 1966 and Dall et al. 1990), and provides shrimp with protection from predators and from capture in towed nets. Brown shrimp and white shrimp are the most common commercial shrimp species in the northern Gulf of Mexico, and both of these species use coastal estuaries as nurseries. The abundance of juveniles in these systems is estimated by various resource agencies using trawls and seines, and information on burrowing and susceptibility to capture in towed nets may help improve these abundance estimates.

Light is generally recognized as the primary driver of burrowing behavior, with most species burrowing during the day and emerging at night (Wickham and Minkler 1975, Wassenberg and Hill 1994). Brown shrimp are typical in this regard, and Martinez (1991) modeled the effect of light on burrowing of juvenile brown shrimp in Galveston Bay, Texas. His model and an experiment by Minello et al. (1987) indicated that increased water depth and turbidity could reduce burrowing during the day by reducing light levels near the substrate. The experimental results presented here indicate that, under light conditions typically found during the day in the open bay, other environmental and biological factors can significantly affect burrowing of brown shrimp as well.

Burrowing of juvenile brown shrimp was significantly affected by size, density, salinity, substrate type, and hunger. Larger (subadult) brown shrimp burrowed significantly more than smaller juveniles, but the difference may not be important in relation to susceptibility to towed nets; subadults were estimated to be 44% susceptible compared to 49-50% for smaller juveniles. Similarly, while there was a significant decrease in burrowing of brown shrimp at high densities, this density effect was not large and not likely to affect susceptibility to capture in nets. The experimental densities used were within the range of mean shrimp densities measured in shallow estuarine habitats (Minello 1999, Minello et al. 2008), but they were orders of magnitude greater than mean abundance values estimated in open bays with trawls (Brown et al. 2013).

The effect of salinity and substrate type on burrowing appeared to have the greatest potential for affecting capture efficiency of brown shrimp. Burrowing of juvenile brown shrimp was reduced at low salinities, and 37% of the population was estimated to be emerged and susceptible to capture at a salinity of 5 compared with 24-29% of the population at higher salinities. These values suggest that samples using towed nets in low salinity water may be overestimating abundance compared with samples from higher salinity locations. These results, however, differ from those reported by Lakshmi et al. (1976), although their experimental conditions also differed. They found that 40-mm TL brown shrimp in low salinity water (8.5) burrowed more than in high salinity water (34) when exposed to a light source for 30 min. The short duration of their experimental exposure and the intensity of their light source may have affected these results. The effect of substrate type on burrowing was large for both shrimp species. Eighty-nine percent of brown shrimp were burrowed in fine sand compared with 22% in coarse sand and 8% in crushed shell. When these values were adjusted for the likelihood of emergence from shallow burrows, only 45% of brown shrimp would be susceptible to capture on fine sand versus 84-97% on coarser substrates. In substrate selection tests, Williams (1958) and Yip-Hoi (2003) observed a similar relationship between juvenile brown shrimp burrowing and substrate type.

While not examined in this study, and in addition to light and turbidity, temperature and dissolved oxygen are other covariates that may affect burrowing of brown shrimp and catchability in towed nets. Aldrich et al. (1968) showed that 94% of postlarval brown shrimp (8.5-13 mm TL) burrowed when water temperatures dropped to 12-16.5 ^{o}C, and all emerged as temperatures were increased to 18-24.5 ^{o}C. Yip-Hoi (2003) reported that juvenile brown shrimp emerged from burrows under hypoxic conditions (<1.5 ppm dissolved oxygen). Environmental factors that also may be of importance and have been shown to affect burrowing of other penaeids include water depth or pressure (Hughes 1966, Wickham 1967, Vance 1992), water ammonia concentrations (Allan and Maguire 1995), and the type of seagrass (Kenyon et al. 1995).

Juvenile white shrimp appeared to be highly susceptible to capture in towed nets compared to brown shrimp. White shrimp burrowed much less than brown shrimp in the laboratory experiments, and they also were more likely to emerge from their shallow burrows upon disturbance. Despite significant effects of size, density, and hunger on burrowing of this species, almost all appear to be available to capture in towed nets during the day. There are of course many additional caveats here, because a wide variety of variables in addition to burrowing can affect the capture efficiency of nekton in towed nets (Watson et al. 1984, Dickson 1993, Rozas and Minello 1997, Brown et al. 2013).

The experimental results on shrimp hunger and its effect on burrowing may not be helpful in determining susceptibility to capture, but they are of interest from the standpoint of risk-sensitive foraging because burrowing offers shrimp some protection from fish predators (Fuss and Ogren 1966, Minello and Zimmerman 1984, Minello et al. 1987). Both species showed a significant effect of hunger, burrowing less when they had been starved. These data also support the conclusion that shrimp need to emerge from burrows to feed, and that there may be a relationship between burrowing, foraging, and growth. Faster growth and higher energy requirements of small juvenile *Litopenaeus vannamei* were related to reduced burrowing by Moctezuma and Blake (1981). In contrast, Lakshmi et al. (1976) and Venkataramiah et al. (1975) suggested that burrowing allowed brown shrimp to conserve energy and promoted faster growth. If foraging time and growth are related, however, shrimp that burrow less should have faster growth rates. While somewhat speculative as to cause and effect, there appears to be a general negative correlation between shrimp burrowing and growth. The shrimp species that are primarily used in mariculture are largely chosen because of their rapid growth (e.g., *Litopenaeus vannamei, L. stylirostris, Penaeus monodon, Fenneropenaeus indicus;* Boyd et al. 2006), and these species seldom burrow (Hughes 1966, Moller and Jones 1975, Moctezuma and Blake 1981, Primavera and Lebata 1995).

These results on burrowing in laboratory experiments support what fishers have long known regarding differences between brown shrimp and white shrimp. Despite this understanding of species-specific catchability in fishing gear, measures of abundance derived from CPUE have seldom been corrected for this difference. Based on the general emergence and burrowing data for these two species, I conclude that almost all juvenile white shrimp are likely available to be caught in estuarine trawls during the day, while less than half of brown shrimp are susceptible to capture. Attempts to measure catch efficiency of trawls for juvenile brown shrimp are consistent with this estimate and suggest that efficiency is between 17-50% (Loesch et al. 1976, Zimmerman et al. 1986, Rozas and Minello 1997). Various modifications to shrimp trawls and towed nets have been made to improve catch efficiency (Watson et al. 1984) including modifications to encourage emergence of burrowed penaeid shrimps using water jets (Penn and Stalker 1975), electric pulse generators (Seidel 1969, Watson 1976), and tickler chains (Stokesbury et al. 1999). An alternative approach to improving estimates of abundance is to model the probability of emergence as attempted by Hill (1985) for adult *Penaeus esculentus* at night in Australia. A better understanding of the environmental and biological factors that affect the burrowing behavior and catchability of juvenile shrimp is needed to develop such models and ultimately to reduce bias in abundance estimates based on the CPUE from towed nets.

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List of Figures

Figure 1. The difference between brown shrimp and white shrimp in burrowing and activity based on all experiments (2411 shrimp and 20,929 observations). Behavioral categories are completely burrowed (CB), eyes emerged (E), head emerged (H), more than half below sediment (>1/2), less than half below sediment (<1/2), stationary (S), crawling (CR), swimming (SW). More detailed descriptions of these categories are in Table 1. Shrimp exhibiting behaviors to the left of the dashed line were considered burrowed.

Figure 2. The effect of size on the percent of shrimp burrowed (as defined in Table 1). Mean values are based on replicate tank means (n = 8 for each bar) from hourly records of behavior during each day of experiments (error bars are +/- 1 SE). The overall mean TLs of Small, Medium, and Large were 43, 68, and 95 mm for brown shrimp and 50, 74, and 101 mm for white shrimp, respectively.

Figure 3. The effect of shrimp size on burrowing behavior and activity. Relative frequencies are based on all observations during experiments. Shrimp exhibiting behaviors (defined in Table 1) to the left of the dashed line were considered burrowed.

Figure 4. The effect of density on the percent of shrimp burrowed (as defined in Table 1). Observations are replicate tank means (n = 8 for each bar) from hourly records of behavior during each day of experiments (error bars are +/- 1 SE). Densities are based on 5, 10, and 20 shrimp per tank.

Figure 5. The effect of shrimp density on burrowing behavior and activity. Shrimp exhibiting behaviors (defined in Table1) to the left of the dashed line are considered burrowed.

Figure 6. The effect of salinity on the percent of shrimp burrowed (as defined in Table 1). Observations

are replicate tank means (n = 8 for each bar) from hourly records of behavior during each day of experiments (error bars are +/- 1 SE).

Figure 7. The effect of salinity on burrowing behavior and activity of shrimp. Shrimp exhibiting behaviors (defined in Table1) to the left of the dashed line are considered burrowed.

Figure 8. The effect of substrate type on the percent of shrimp burrowed (as defined in Table 1). Observations are replicate tank means (n = 8 for each bar) from hourly records of behavior during each day of experiments (error bars are +/- 1 SE).

Figure 9. The effect of substrate type on burrowing behavior and activity of shrimp. Shrimp exhibiting behaviors (defined in Table1) to the left of the dashed line are considered burrowed.

Figure 10. The effect of hunger and the presence of food on the percent of shrimp burrowed (as defined in Table 1). Observations are means from replicate tank means (n = 11-12 for each point) from each hour during the experiments (error bars are +/- 1 SE).

Figure 11. The effect of hunger and the presence of food on the burrowing and activity of shrimp. Shrimp exhibiting behaviors (defined in Table1) to the left of the dashed line are considered burrowed.

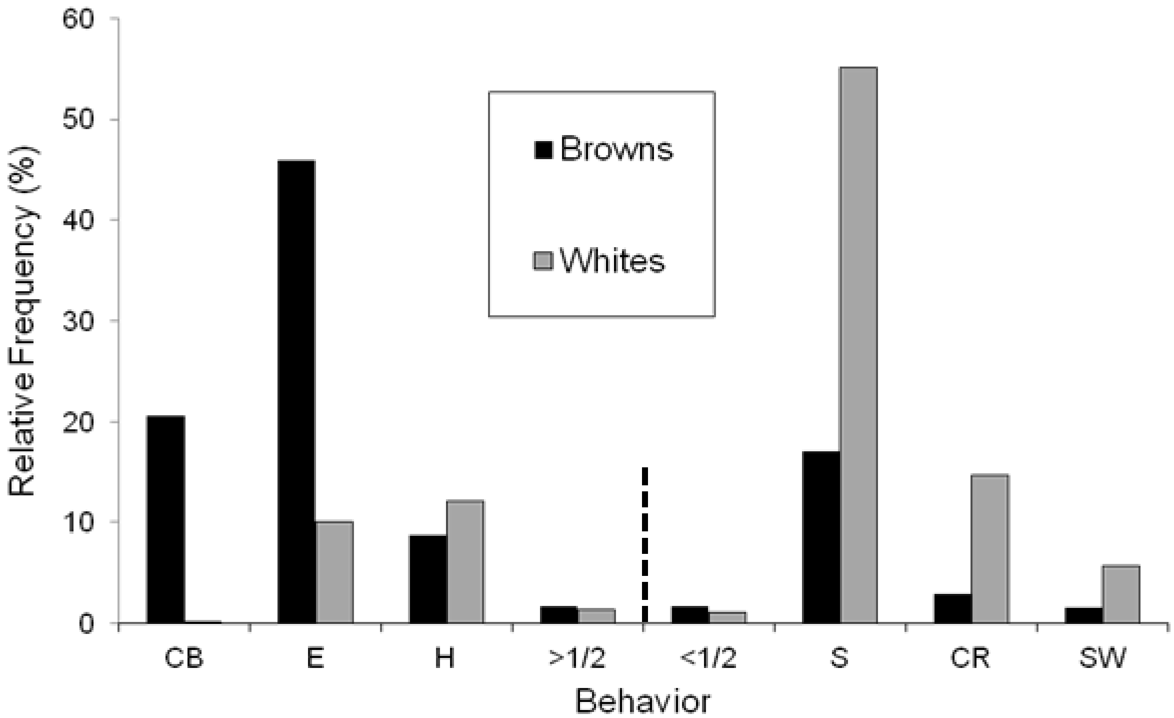

60
50
40
30
20
10
0
Relative Frequency (%)
Browns
Whites
CB
E
H
>1/2
<1/2
S
CR
SW
Behavior

Fig. 1

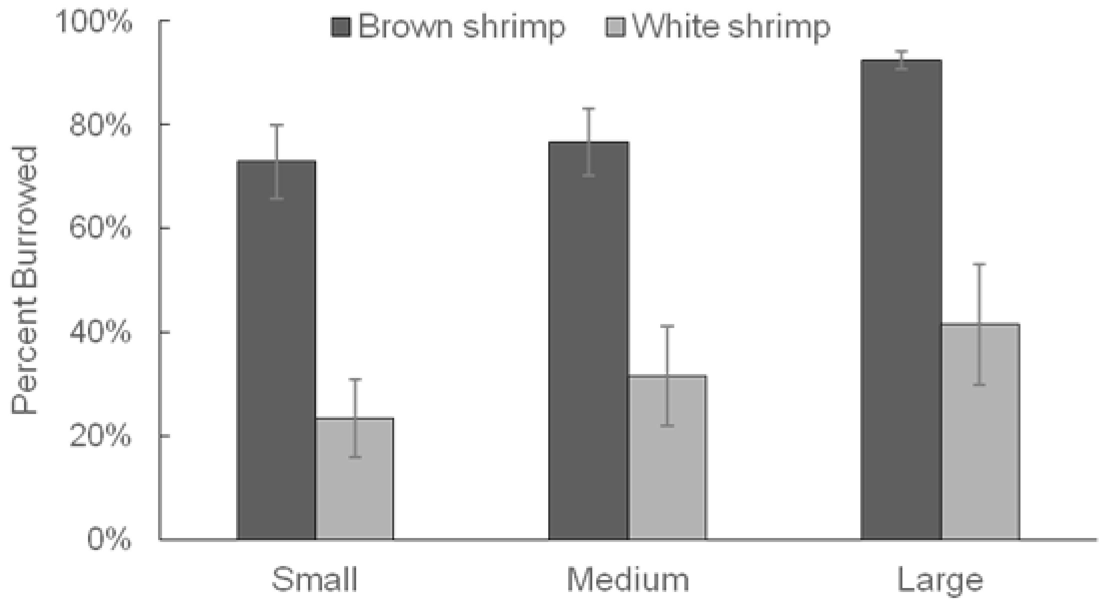

Brown shrimp
White shrimp
100%
80%
60%
40%
20%
0%
Percent Burrowed
Small
Medium
Large

Fig. 2

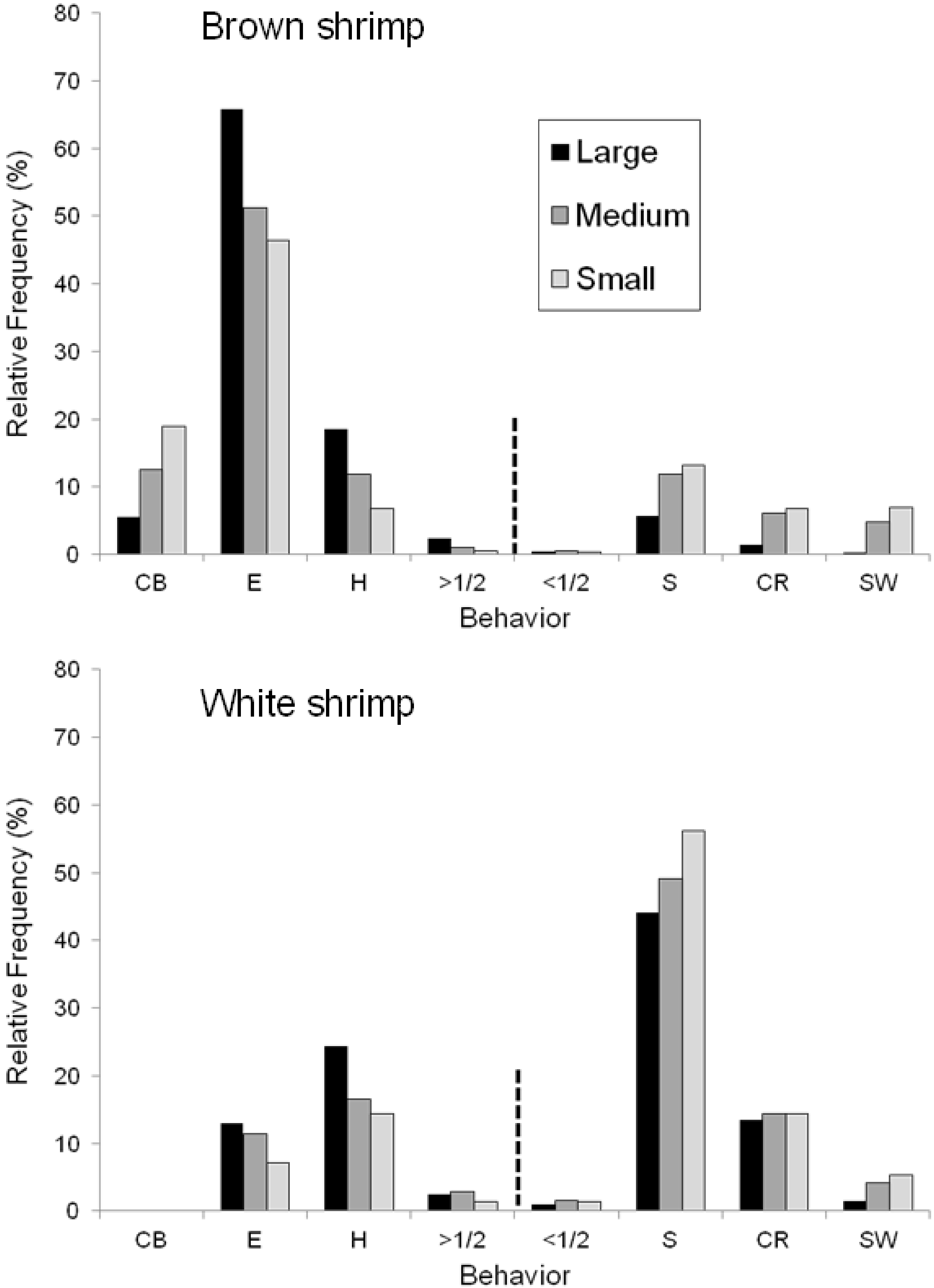

Brown shrimp
Large
Medium
Small
Relative Frequency (%)
80
70
60
50
40
30
20
10
0
CB
E
H
>1/2
<1/2
S
CR
SW
Behavior
White shrimp
Relative Frequency (%)
80
70
60
50
40
30
20
10
0
CB
E
H
>1/2
<1/2
S
CR
SW
Behavior

Fig. 3

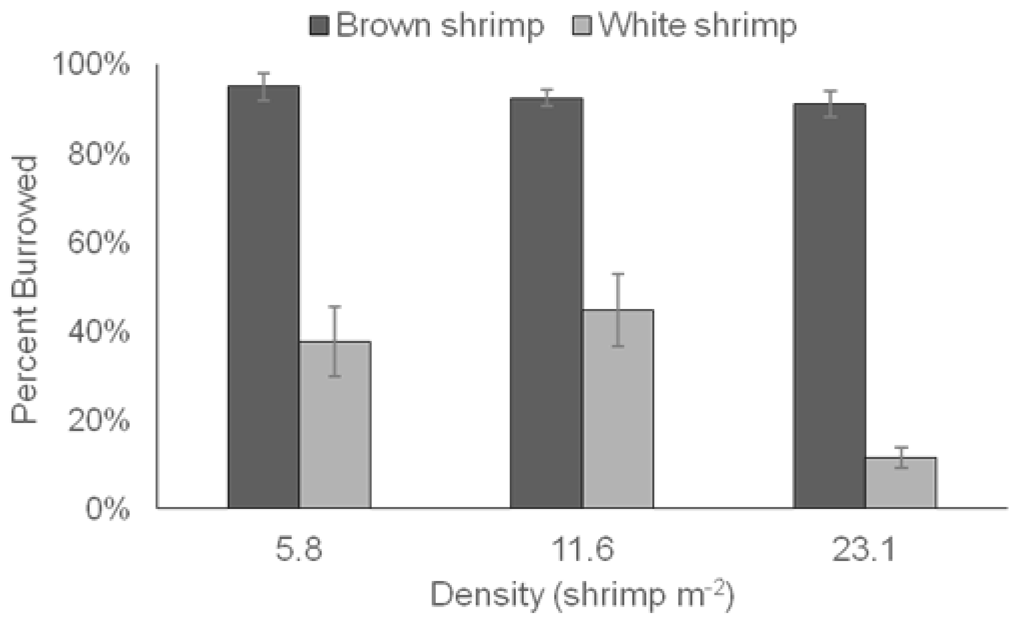
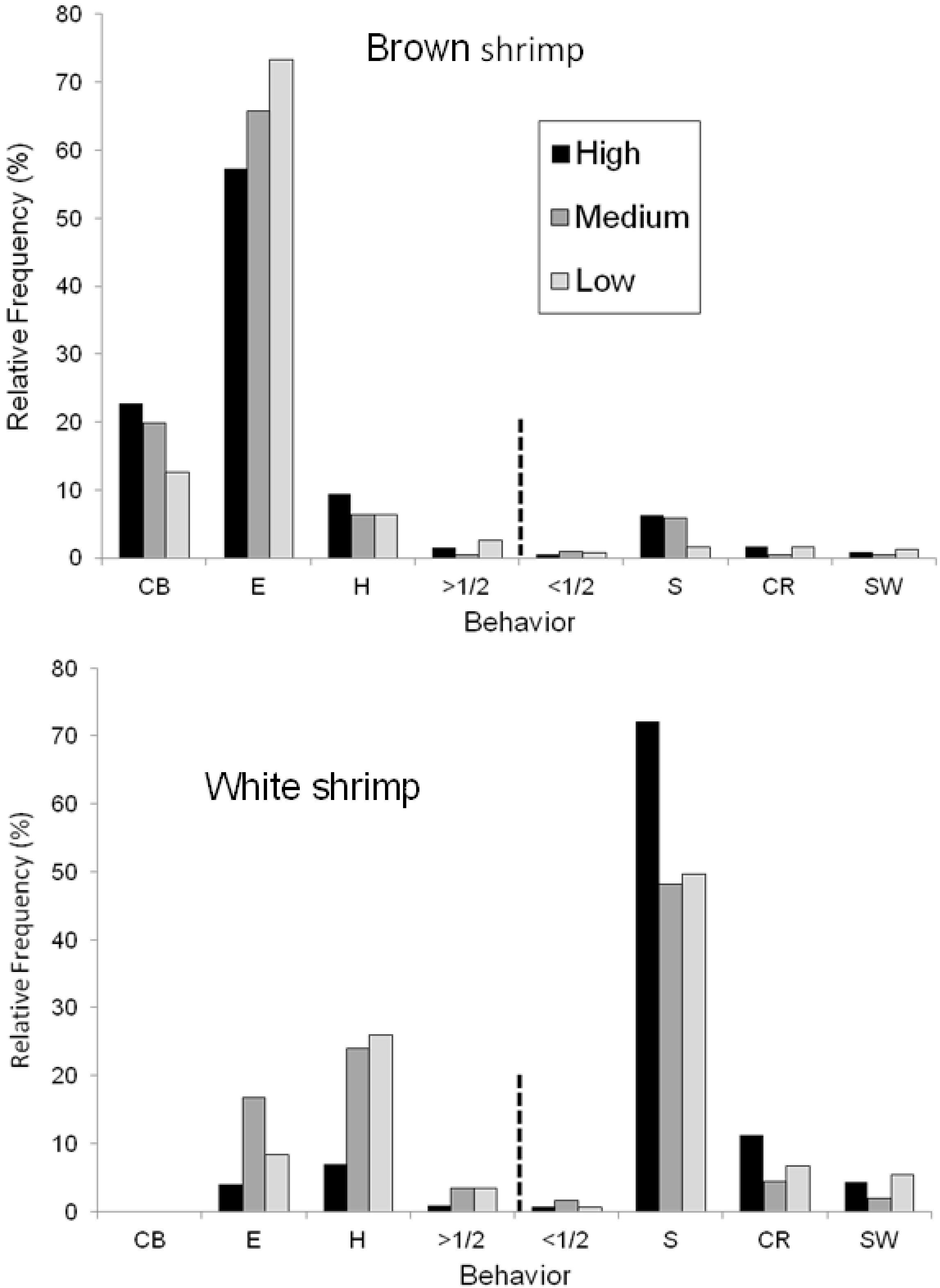
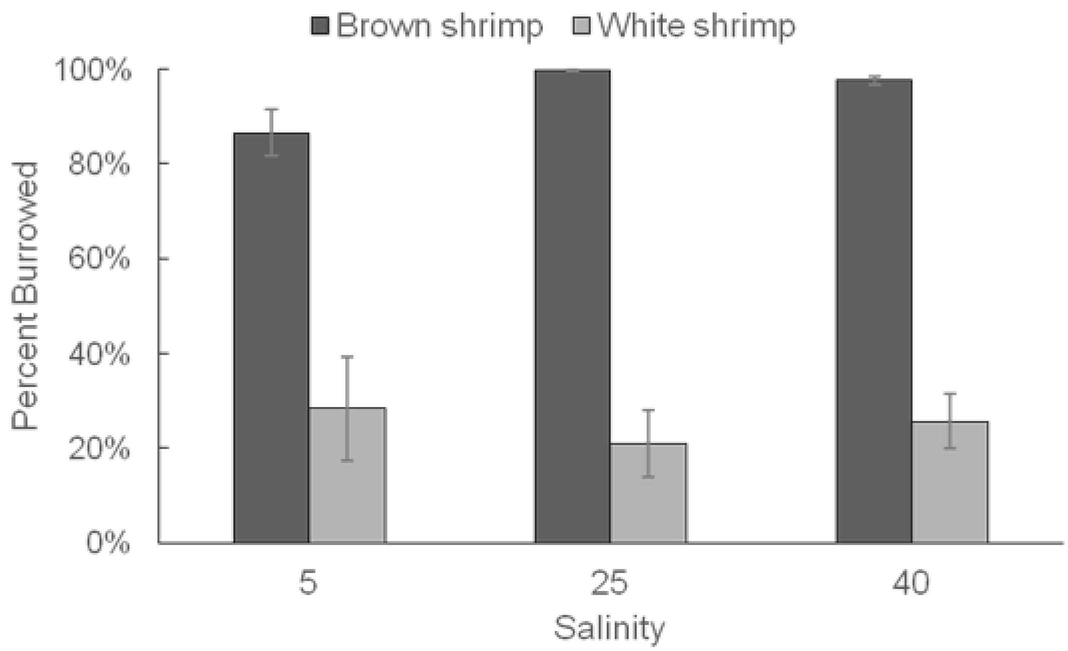

Brown shrimp
White shrimp
100%
80%
60%
40%
20%
0%
Percent Burrowed
5.8
11.6
23.1
Density (shrimp m-2)

Fig. 4



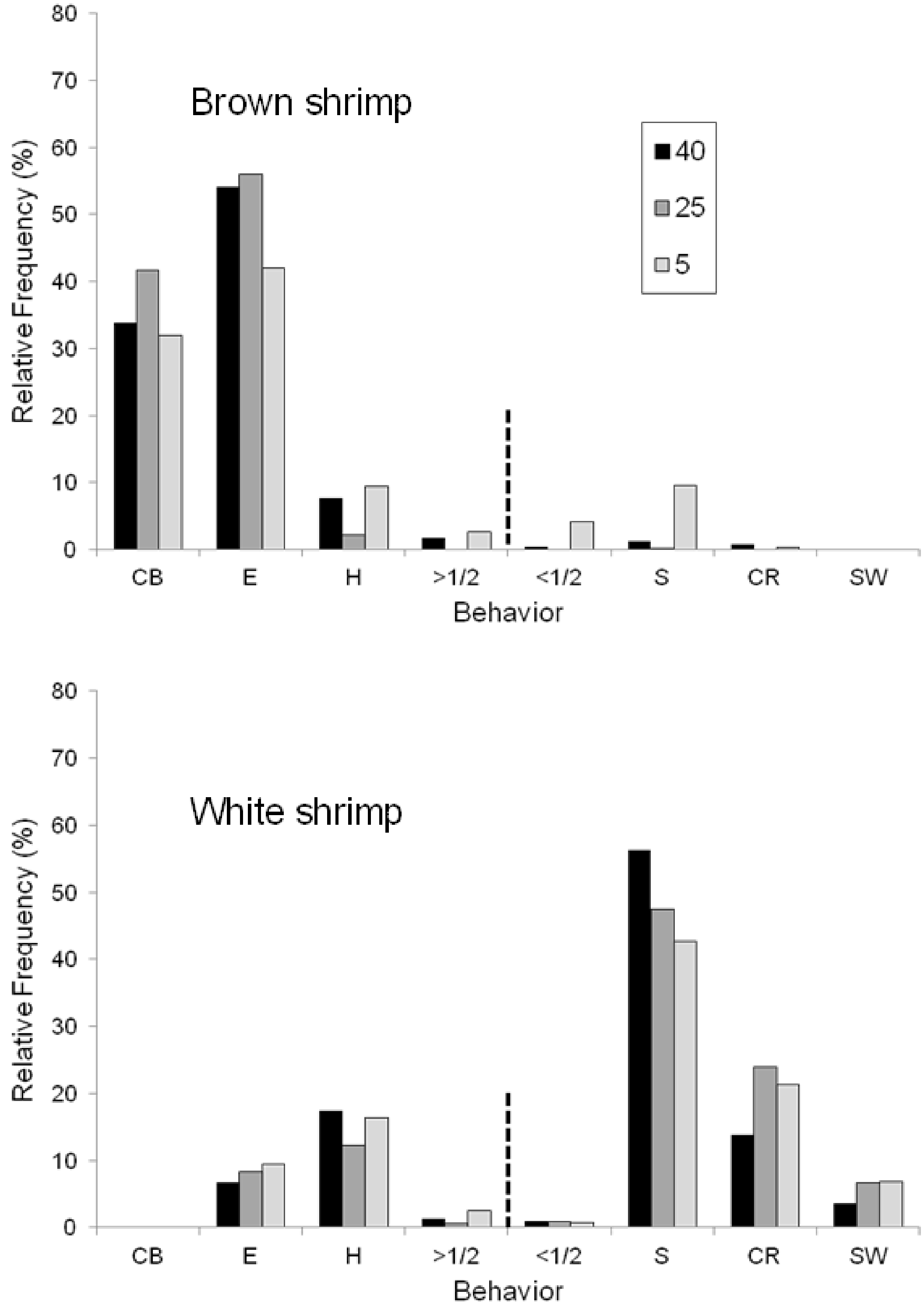
Brown shrimp
High
Medium
Low
Relative Frequency (%)
0
10
20
30
40
50
60
70
80
CB
E
H
>1/2
<1/2
S
CR
SW
Behavior
White shrimp
Relative Frequency (%)
0
10
20
30
40
50
60
70
80
CB
E
H
>1/2
<1/2
S
CR
SW
Behavior

Fig. 5



Brown shrimp
White shrimp
100%
80%
60%
40%
20%
0%
Percent Burrowed
5
25
40
Salinity

Fig. 6



Brown shrimp
40
25
5
Relative Frequency (%)
80
70
60
50
40
30
20
10
0
CB
E
H
>1/2
<1/2
S
CR
SW
Behavior
White shrimp
Relative Frequency (%)
80
70
60
50
40
30
20
10
0
CB
E
H
>1/2
<1/2
S
CR
SW
Behavior

Fig. 7

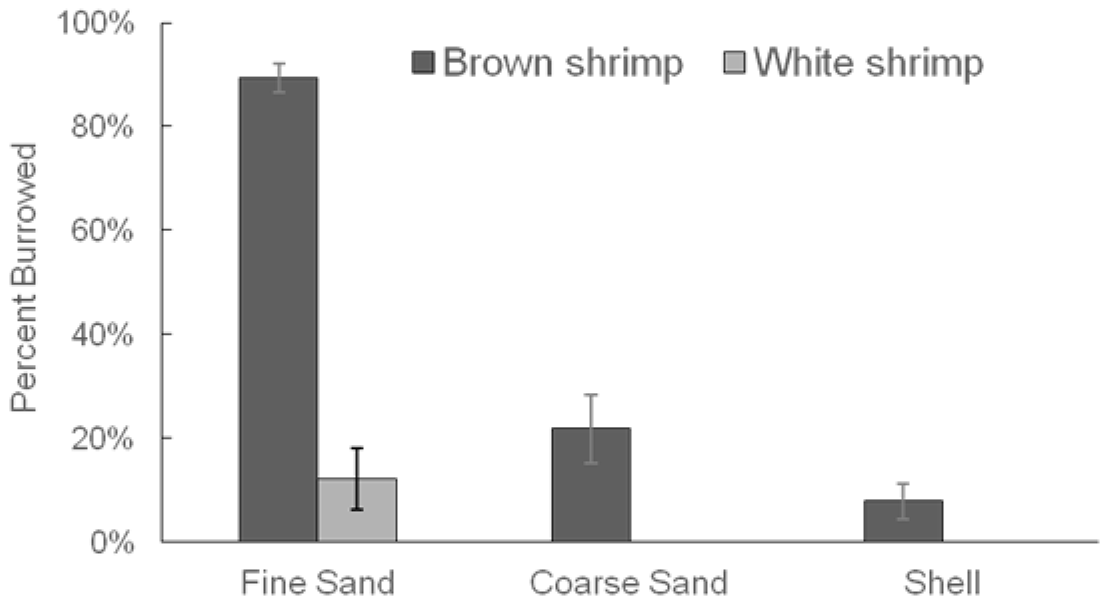

100%
80%
60%
40%
20%
0%
Percent Burrowed
Brown shrimp
White shrimp
Fine Sand
Coarse Sand
Shell

Fig. 8

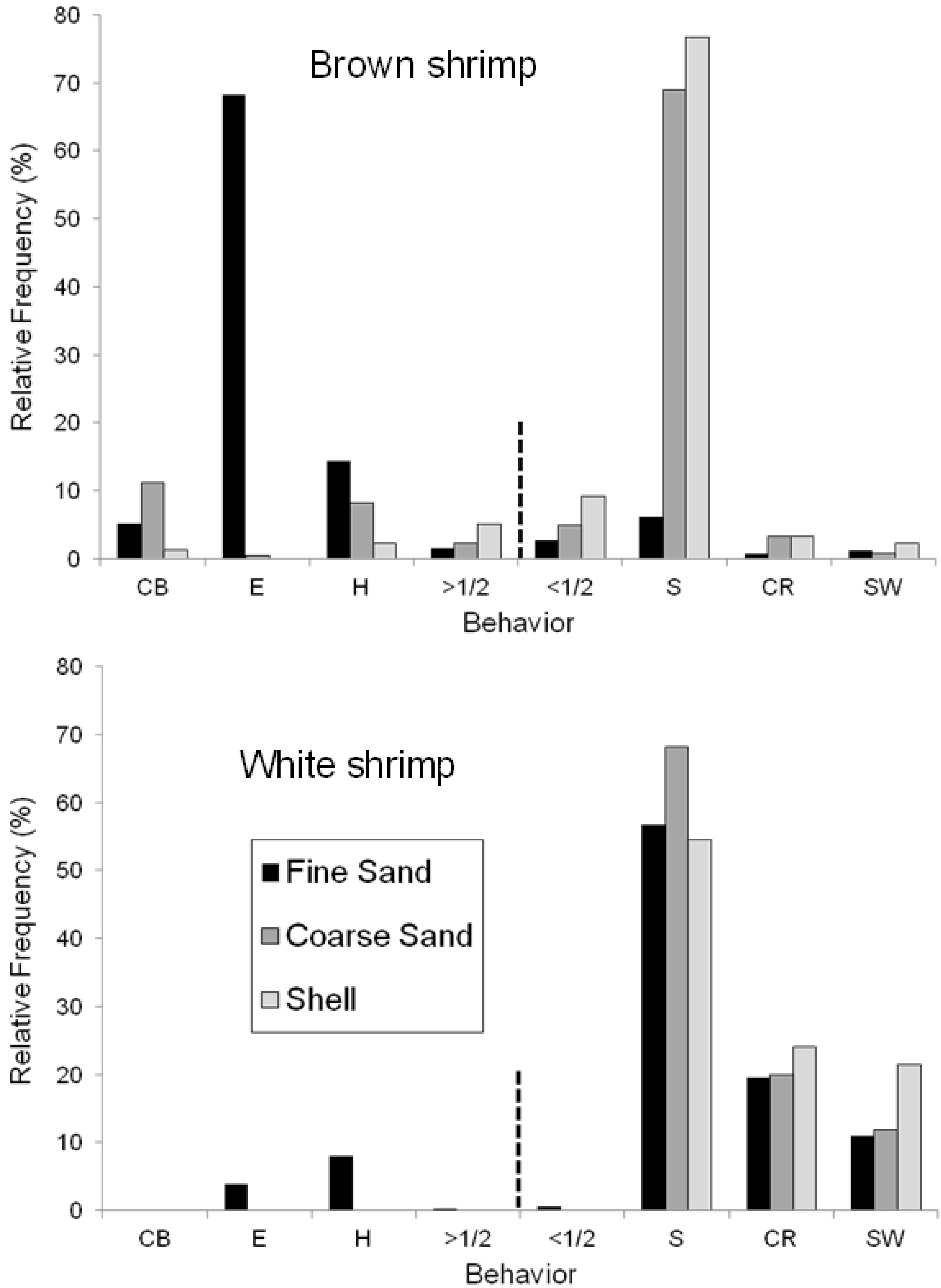

Brown shrimp
White shrimp
Relative Frequency (%)
Behavior
CB
E
H
>1/2
<1/2
S
CR
SW
0
10
20
30
40
50
60
70
80
Fine Sand
Coarse Sand
Shell

Fig. 9

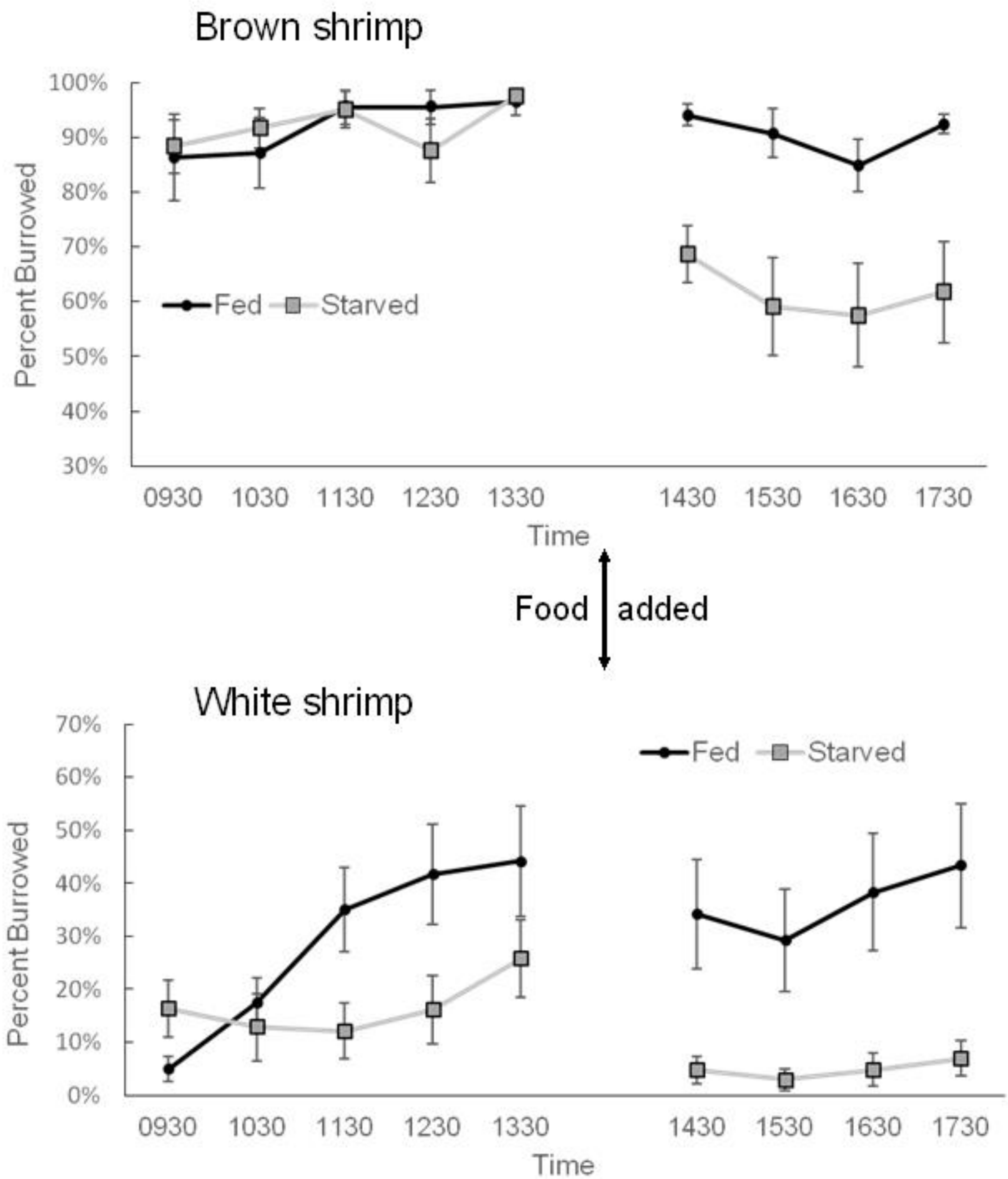
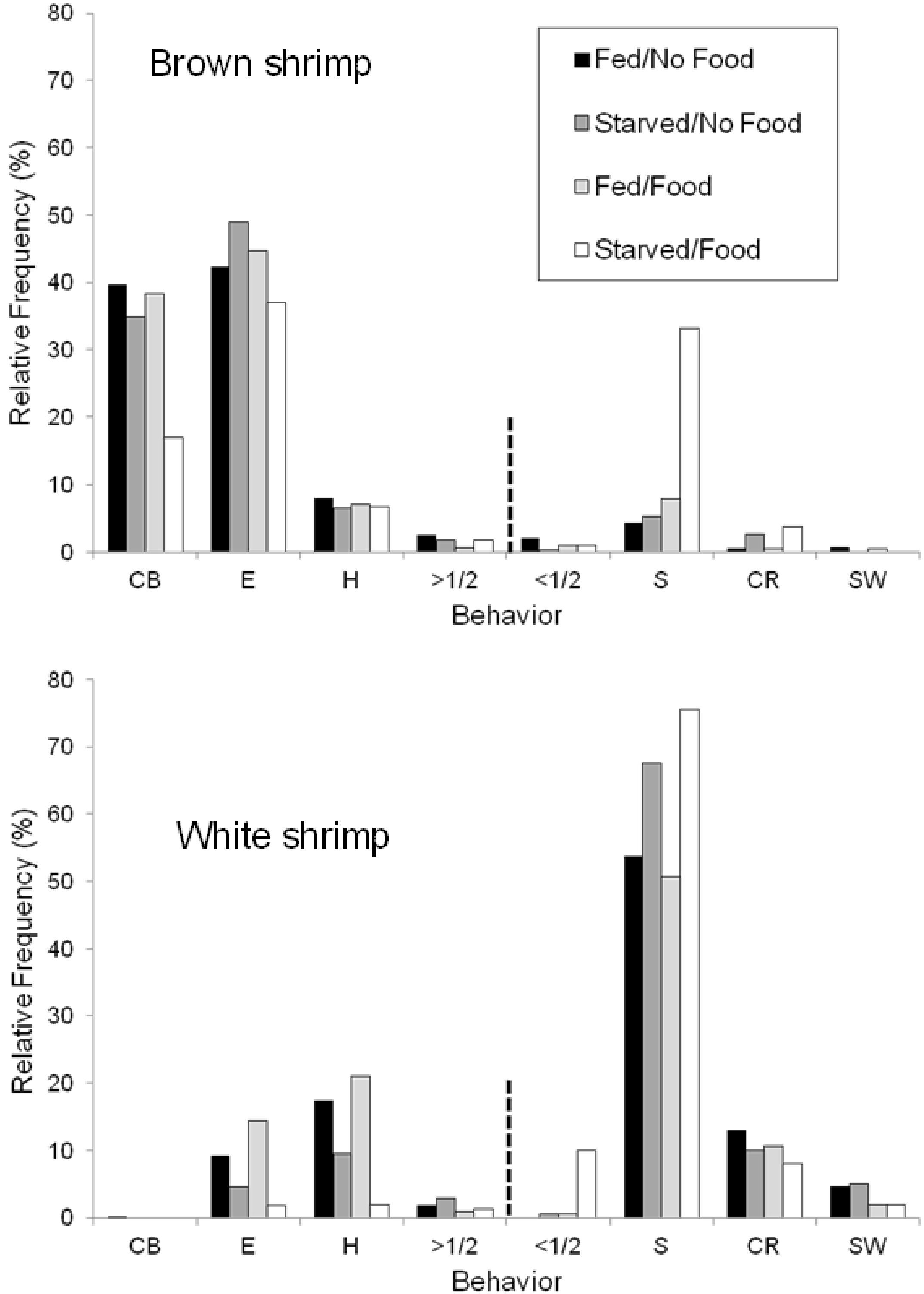

Brown shrimp
100%
90%
80%
70%
60%
50%
40%
30%
Percent Burrowed
Fed
Starved
0930
1030
1130
1230
1330
1430
1530
1630
1730
Time
Food
added
White shrimp
70%
60%
50%
40%
30%
20%
10%
0%
Percent Burrowed
Fed
Starved
0930
1030
1130
1230
1330
1430
1530
1630
1730
Time

Fig. 10



Brown shrimp
Fed/No Food
Starved/No Food
Fed/Food
Starved/Food
Relative Frequency (%)
0
10
20
30
40
50
60
70
80
CB
E
H
>1/2
<1/2
S
CR
SW
Behavior
White shrimp
Relative Frequency (%)
0
10
20
30
40
50
60
70
80
CB
E
H
>1/2
<1/2
S
CR
SW
Behavior

Fig. 11

Table 1. List of behaviors recorded in experiments. Shrimp exhibiting behaviors below the dashed line were considered burrowed.

Abbreviation	Description
SW	Swimming in water column
CR	Crawling or walking on substrate
S	Stationary (generally on substrate)
<1/2	Less than half of body beneath substrate
>1/2	More than half of body beneath substrate
H	Only the head present above the substrate
E	Only the eyes present above the substrate
CB	Completely burrowed under the substrate

Table 2. Results from linear mixed model repeated measures analysis of variance on arcsin transformed percent of burrowed shrimp. Day was a fixed block effect in the model, and only results for the fixed Treatment effect are shown. Tukey's HSD test of least square means was used (alpha = 0.05) for comparisons when there was more than two levels of a Treatment.

Species	Treatment	F	P	Tukey's test
Brown shrimp	Size	12.1	< 0.0001	Large > (Medium = Small)
White Shrimp	Size	5.36	0.0055	(Large > Small) = Medium
Brown shrimp	Density	8.08	0.0004	5 > (10 = 20)
White Shrimp	Density	21.1	< 0.0001	(5 = 10) > 20
Brown shrimp	Salinity	40.1	< 0.0001	(25 = 40) > 5
White Shrimp	Salinity	1.16	0.316	
Brown shrimp	Substrate	1059.7	< 0.0001	Fine sand > Coarse sand > Shell
White Shrimp	Substrate	no test		Only burrowed in fine sand
Brown shrimp	Hunger no Food	0.19	0.659	
White Shrimp	Hunger no Food	7.92	0.0058	Fed > Starved
Brown shrimp	Hunger with Food	50.3	< 0.0001	Fed > Starved
White Shrimp	Hunger with Food	30.9	< 0.0001	Fed > Starved

Table 3. Contingency tables for a test of emergence when disturbed. The p value from Fisher's Exact test of independence is shown for each species.

	Behavior	Emerged	Remained Burrowed	Sum	% Emerged
Brown shrimp	Eyes	130	179	309	42.1%
($p = 0.113$)	Head	14	34	48	29.2%
	Sum	144	213	357	40.3%
				Sum	
White shrimp	Eyes	13	7	20	65.0%
($p = 0.0001$)	Head	53	0	53	100.0%
	Sum	66	7	73	90.4%

Highlights for "Environmental factors affecting burrowing by brown shrimp F*arfantepenaeus aztecus* and white shrimp *Litopenaeus setiferus* and their susceptibility to capture in towed nets"

Daytime burrowing behavior of penaeid shrimp was examined in a laboratory study.

Over all experiments, 77.5% of brown shrimp and 21.4% of white shrimp burrowed.

Less than half of brown shrimp population is likely susceptible to capture in trawls.

Salinity and substrate type likely affect net catch efficiency for brown shrimp.

Most (97%) white shrimp emerged from burrows after disturbance and were susceptible.