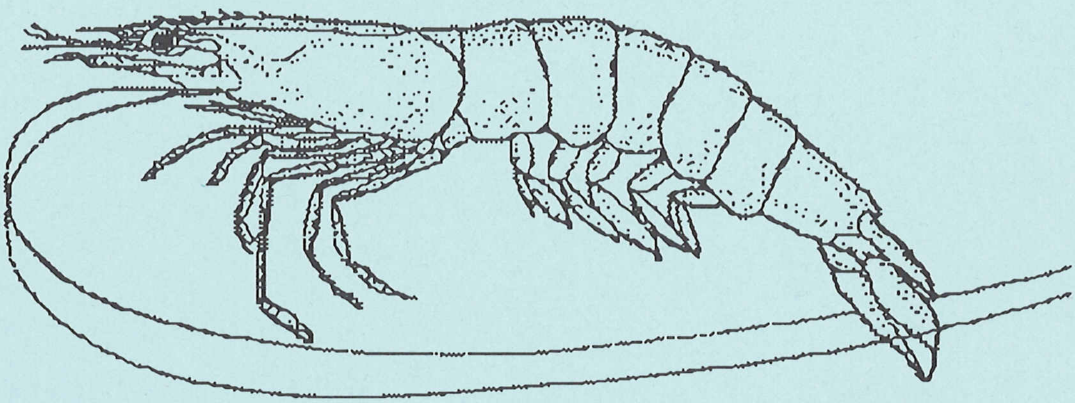
NOAA Technical Memorandum
NMFS - SEFC - 237

EXPERIMENTAL STUDIES ON SELECTION FOR VEGETATIVE STRUCTURE BY PENAEID SHRIMP



GALVESTON LABORATORY

SOUTHEAST FISHERIES CENTER

NATIONAL MARINE FISHERIES SERVICE

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION

DEPARTMENT OF COMMERCE

MARCH 1990

ACKNOWLEDGEMENTS

This project is the result of cooperative research between NOAA's National Marine Fisheies Service Galveston Laboratory in the Southeast Fisheries Center and the Texas Water Development Board and The Texas Parks and Wildlife Department. Both state agencies have been mandated to study the effects and needs of freshwater inflow to the State's estuaries by House Bill 2 (1985) and Senate Bill 683 (1987) enacted by the Texas Legislature. As part of this program, a portion of this research was funded through the Texas Water Development Board's Water Research and Planning Fund, authorized under Texas Water Code Sections 15.402 and 16.058 (e), and administered by the Texas Parks and Wildlife Department under interagency cooperative contract No. IAC(86-87) 1590, IAC(88-89) 0821 and IAC(88-89) 1457. Additional acknowledgements are due T. Delaney, T. Czapla, E. Martinez and V. Perez for their assistance during all phases of this study.

This study should be cited as follows:

Minello, T.J, R.J. Zimmerman and P.A. Barrick. 1990. Experimental studies on selection for vegetative structure by penaeid shrimp. NOAA Technical Memorandum NMFS-SEFC-237, 30 p.

Copies may be obtained by writing: National Technical Information Service
5258 Port Royal Road
Springville, VA 22161

or

National Marine Fisheries Service
SEFC Galveston Laboratory
4700 Avenue U
Galveston, Texas 77550-5997

NOAA TECHNICAL MEMORANDUM
NMFS-SEFC-237

Experimental Studies on Selection for Vegetative Structure by Penaeid Shrimp

BY

Thomas J. Minello, Roger J. Zimmerman and Pamela A. Barrick

U.S. DEPARTMENT OF COMMERCE
Robert Mosbacher, Secretary

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
John A. Knauss, Administrator

NATIONAL MARINE FISHERIES SERVICE
William W. Fox, Jr., Assistant Administrator for Fisheries

MARCH 1990

TABLE OF CONTENTS

EXECUTIVE SUMMARY

Variability in selection for vegetated habitats by juvenile brown shrimp, *Penaeus aztecus*, and white shrimp, *P. setiferus*, as evidenced by distributions in estuaries, suggests that the value of these habitats is not constant. Previous laboratory work indicates that selection for structure itself is one component of habitat selection, but environmental conditions and other habitat characteristics undoubtedly affect the utilization of vegetated estuarine habitats. This study was designed to examine the effect of environmental variables on selection for structure in the laboratory in an effort to increase our understanding of the way habitats are utilized by penaeid shrimp.

Brown shrimp are generally found in association with estuarine vegetation, and they selected for vegetative structure in the laboratory. An average of 81% of brown shrimp were distributed in the vegetated half of control tanks. Reductions in salinity to oligohaline levels, used to simulate flood events in estuaries, significantly reduced selection for structure. The reduction of light, either through the manipulation of lighting or through turbidity, had a similar effect on brown shrimp distributions. Neither reduced salinity or light, however, reduced the mean percentage of shrimp in the grass below 50%. The overall presence or absence of food or of an appropriate substrate for burrowing, did not alter selection for structure, but the distribution of these habitat characteristics had a dramatic effect on shrimp distributions. Attraction to food or to a substrate for burrowing can override the inherent selection for structure normally exhibited by brown shrimp. Other variables examined including day length and shrimp size did not significantly affect selection.

White shrimp distributions in relation to estuarine vegetation are more variable. In our experiments, white shrimp also showed an inherent selection for the vegetated half of the control tanks (75% of shrimp in the vegetation), but none of our experimental variables appeared to influence this selection to any great extent. There was a strong correlation between white shrimp activity and selection for structure, and this relationship may have contributed to the relatively large variability in selection by this species.

INTRODUCTION

Distributions of juvenile brown shrimp, *Penaeus aztecus*, and white shrimp, *P. setiferus* in estuaries, suggest that habitat selection and perhaps habitat value vary with environmental conditions. Young brown shrimp are often found in association with estuarine vegetation (Loesch 1965, Stokes 1974), and in Galveston Bay, Texas, they are generally concentrated in available salt marsh habitats (Zimmerman et al. 1984). During early spring, however, juvenile brown shrimp are more abundant on nonvegetated bottom (Zimmerman and Minello 1984), suggesting that the relative value of salt marshes for this species may not be constant. In contrast, white shrimp select for salt marsh vegetation sporadically, and exhibit an overall inconsistent distribution pattern in relation to vegetated habitats (Loesch 1965, Stokes 1974, Zimmerman and Minello 1984, Minello and Zimmerman 1985). Exploitation of the salt marsh surface appears to be beneficial to brown shrimp, providing increased food for growth (Zimmerman et al. in press) and protection from fish predators (Minello and Zimmerman 1983, Minello et al. 1989). Although relatively little is known of estuarine habitat value for white shrimp, this species does not appear to obtain the same benefits from vegetated habitats as brown shrimp. Assuming that distributional patterns are related to habitat value, environmental characteristics affecting habitat selection may be related to habitat functions.

An understanding of the factors controlling selection for vegetative structure, should be useful in determining how habitats are utilized. Therefore, we examined the effect of environmental variables on selection for structure by brown shrimp and white shrimp in a series of laboratory experiments. These variables included salinity, a simulated freshwater event (rapid salinity reduction), turbidity, food availability, substrate type, day length, light, and the presence of predators. The effects of shrimp size and density were also examined.

METHODS

General

Experimental animals were collected with trawls in West Galveston Bay, held in a laboratory with an artificial day/night light cycle of 12 hr, and fed each evening with pelleted food. Salinities were slowly altered (over several hours) from collection levels to 20 ‰ in holding tanks, and this salinity was used in all experiments except those where salinity was an experimental factor. Water temperatures in holding and experimental tanks were maintained near 25 to 27 °C.

The 16 rectangular experimental tanks (1.5 m x 0.6 m) had light brown fiberglass walls, and were filled with seawater to a depth of 25 cm. Light was provided by daylight fluorescent bulbs, was measured just above the water's surface using a LI-COR integrating quantum meter (Model LI-188B), and ranged between 22 and 27 microeinsteins(μE) $s^{-1}m^{-2}$. To provide a substrate which prevented shrimp from burrowing and facilitated observations, we placed black plastic mesh (6.4 mm) over washed beach sand and then added enough additional sand to cover the mesh. Green plastic drinking straws were used to simulate vegetation and were placed over one half the bottom of each tank in evenly spaced clumps of four straws each. Clumps were spaced 5.5 cm apart, resulting in a density of 670 straws/m^2 in the vegetated half of the tank (0.75 m x 0.6 m area). Curtains were hung around each tank to reduce disturbances.

Tanks were randomly assigned to experimental treatments, and ten juvenile shrimp (45-60 mm, total length) were placed in each tank the evening before an experiment. Lights came on at 0700 hrs, and observations were made through small openings in the curtains every 2 hrs throughout the day beginning at 0900 hrs and ending at 1700 hrs. The number of shrimp in the vegetated and nonvegetated halves of each tank was recorded, and the activity level of the shrimp was classified as sedentary or active (crawling and swimming).

The percentage of shrimp in the vegetated half of each tank was used as the observation in an ANOVA after an arcsin transformation. The multiple observations taken in each tank throughout the day (generally 5) were treated as subsamples which provided a within tank error term in the analysis. All main effects were tested over the among tank error. The percentage of active shrimp in each tank was analyzed in a similar manner. If the experiment was repeated on a second day, day was treated as a blocking variable in the analysis.

Salinity and a Simulated Freshwater Event

Before each experiment, shrimp were placed in acclimation tanks, and salinities were adjusted to experimental levels of 3 ‰, 20 ‰, and 38 ‰ over a 5-day period using dechlorinated tap water or seawater mixed with artificial sea salts. Initial daily changes were 5 ‰ followed by changes of 2-3 ‰ per day as experimental salinities were approached. Shrimp were then held at these salinities for at least 2 days before an experiment was initiated.

The two treatments with initial salinities of 38 ‰ and 20 ‰ were both assigned six experimental tanks and the 3 ‰ treatment contained four tanks. The effect of salinity itself was determined from observations made during the first day that shrimp were subjected to these experimental conditions. That evening, shrimp were fed with a small amount of pelleted food distributed evenly between vegetated and nonvegetated sides of each experimental tank. The following morning, half of the six tanks with 38 ‰ and 20 ‰ were subjected to a simulated freshwater event. Beginning at 0830 hrs, salinities were lowered in these tanks from 38 to 20 ‰ and from 20 to 3 ‰ over a 3-hr period at a rate of 3 ‰ every half hour. Salinities were reduced by lowering water levels with a small electric pump and incrementally replacing water with dechlorinated freshwater. Airstones provided vertical mixing. Water levels in all other tanks were also lowered and replaced with water of the original salinity to control for the disturbance effect of water removal and addition. Salinity reductions were completed by 1200 hrs, and observations on the distribution and activity level of shrimp in the tanks were recorded at 1300, 1500, and 1700 hrs.

To maintain a balanced design, data from four tanks per treatment level were used in the analysis of overall salinity effects, while three tanks per treatment level (five levels) were analyzed to determine the effect of a freshwater event. The entire experiment was repeated on a second day. In the ANOVAs on salinity reduction, combinations of the five treatment levels were examined through contrasts. In Contrast A, the three treatments with no salinity change were contrasted with the two treatments where salinity was lowered (38 to 20 ‰ and 20 to 3 ‰), and in Contrast B, the two treatments with a final salinity of 3 ‰ were contrasted with the remaining three treatments.

Turbidity

A slurry of bentonite and seawater was used to create turbid water, and selection for structure was measured at four turbidity levels (0, 10, 25, 50 FTUs). Clay was added to the tanks during the dark cycle on the morning of an experiment, and periodically throughout the morning to maintain treatment turbidity levels. Turbidities were measured with a nephelometric turbidimeter (H-F Instruments Model DRT-15) using a formazin standard and recorded as Formazin Turbidity Units (FTUs). Effects of disturbance due to adding the clay mixture were controlled by adding clear water to the 0 FTU treatment. Because direct observations on the distribution of shrimp could not be made in all treatments, the number of shrimp in each half of the tank was determined by draining the tanks (around 1200 hrs) after a mesh wall was placed at the edge of the vegetation dividing the tank in half. Before draining, but after the wall was in place, light intensity was measured at the water's surface and 13 cm off the bottom in the center of the nonvegetated half of each tank. Underwater light readings were taken with the sensor directed both towards the surface and horizontally towards the wall of the tank. The experiment was repeated on a second day.

Food

The effect of food distribution was examined using rings of squid (1.0-1.3 g each) attached to small lead weights. Observations on the distribution of shrimp with no food in the tanks were made at 0900 and 1100 hrs; food was then added at 1200 hrs. The four treatment levels were: no food present, food in both vegetated and nonvegetated halves of the tank, food only in the vegetated half, and food only in the nonvegetated half. Three squid rings were placed in each tank half, and lead weights without squid were placed in the non-food treatments. Shrimp distribution and activity and the number of shrimp feeding were recorded at 1300, 1500, and 1700 hrs. The effect of food on selection for structure was also examined at night following the brown shrimp experiment. Food was removed after the 1700 hr observations, and replaced at midnight. The distribution of the shrimp was recorded at 0100 hrs using a small red light.

Substrate

In experiments on the effect of substrate, approximately 5 cm of washed beach sand was compared with the sand/plastic mesh (no sand) used in all other experiments. Shrimp readily burrowed in the beach sand. The four treatment levels examined were: no sand throughout the tank, sand throughout the tank, sand only in the vegetated half, and sand only in the nonvegetated half. Observations on shrimp distribution and activity were made every 2 hrs throughout the day and at midnight following the experiment. Observations were also made on burrowing frequency; a shrimp was considered burrowed if more than 1/2 of its body was beneath the substrate surface.

Day Length

The effect of day length was experimentally examined with brown shrimp to determine whether seasonal changes in day length might alter selection for vegetation. The shrimp were collected on July 28 when the natural day length is approximately 13.5 hrs in Galveston, Tx. Shrimp were placed in holding tanks under two laboratory day/night cycles, our standard 12 hr day/night cycle (similar to early spring conditions in Texas) and a 14 hr day/10 hr night cycle. Lights in both treatments were synchronized to come on at 0700 hrs each morning. During the dark cycle on August 12, we transferred shrimp from holding tanks to seven experimental tanks per treatment. Observations on shrimp distribution and activity were recorded throughout the following day.

Light

We also examined whether the presence or absence of light affected selection for structure by brown shrimp. At 0900 hrs the distribution and activity of shrimp was recorded in 12 lighted tanks (standard illumination of 22-27 $\mu E\ s^{-1}\ m^{-2}$). We turned the lights off over 6 of the 12 tanks at 0930 hrs. Light in these dark tanks was below the sensitivity of our meter (0.001 $\mu E\ s^{-1}\ m^{-2}$). Observations on the distribution and activity of shrimp in both light and dark tanks were recorded at 1100 and 1300 hrs.

Predators

Southern flounder, *Paralichthys lethostigma*, were used to examine the effect of a predator on selection for structure by white shrimp. Fish ranged in size from 135 to 266 mm (TL), and they were starved for 24 hrs before the experiment. Initial shrimp density in this experiment was 12/tank, and the distribution and the number of shrimp in the experimental tanks was recorded throughout the day. We used five tanks without fish and five tanks containing one southern flounder, and repeated the entire experiment on a second day.

RESULTS

Salinity

The mean percentage of brown shrimp in the vegetated half of the tanks was lowest at a salinity of 3 ‰ (Table 1, Figure 1), and the effect of salinity on selection for structure was marginally significant (P=0.052). The overall difference, however, in the percentage of shrimp in the grass at 3 ‰ (86% in the grass) compared to 38 ‰ (94%) was only 8% and may be of little biological significance. Selection for structure by white shrimp was not significantly affected by salinity (Table 1, Figure 2).

Activity levels (shrimp swimming or crawling) of brown shrimp were low, and overall only 3% of the shrimp were active (Figure 1). In the white shrimp experiment, overall activity was around 33% (Figure 2). There was no significant effect of salinity on activity of either species (Table 1).

Simulated Freshwater Event

The overall treatment effect in the salinity-reduction experiment was highly significant for brown shrimp (Table 2), but a comparison of the two salinity reduction treatments with the three constant salinity treatments (3 ‰, 20 ‰, and 38 ‰) was not significant (Contrast A). The reduction in salinity from 38 to 20 ‰ had no significant effect on selection for structure, but the reduction from 20 to 3 ‰ was significantly different from all other treatment levels, reducing the percentage of brown shrimp in the grass to 62% (Table 3). In general, low salinity resulted in relatively low numbers of shrimp in the grass, and salinity reduction to a final low salinity had the greatest effect. The two treatments with final salinities of 3 ‰ were significantly different from the other treatment levels (Contrast B). The effect of reducing salinity from 20 ‰ to 3 ‰ appeared greatest just after the reduction (at 1300 hrs), and the percentage of brown shrimp in the grass in this treatment increased with time following the addition of fresh water (Figure 3). Salinity reduction to 3 ‰ also caused shrimp mortality (observations on distribution were made only on survivors), and mean survival (out of 10 shrimp) in these tanks was 9.6 shrimp at 1300 hrs, 7.6 shrimp at 1500 hrs, and 6.0 shrimp at 1700 hrs. No mortality was observed in other treatments.

Salinity reduction did not appear to have the same strong effect on white shrimp, and the main effect of salinity reduction in the ANOVA was only marginally significant (P=0.055, Table 4). However, the trend of reduced numbers in the grass at low salinity

Table 1. The effect of salinity on the percentage of shrimp in the grass and the percentage of active shrimp. The probability value (P) listed is from an ANOVA comparing all treatment means (8 replicate tanks/mean) using an arcsin transformation. Individual means cannot be statistically distinguished at the 0.05 level if they are connected by a line (LSD multiple range test).

	P	Salinity		
Percent in the Grass		**38 ppt**	**20 ppt**	**3 ppt**
Brown shrimp	**0.052**	94%	89%	86%
White shrimp	0.35	82%	76%	78%
Percent Active				
Brown shrimp	0.78	2%	4%	4%
White shrimp	0.90	33%	35%	30%

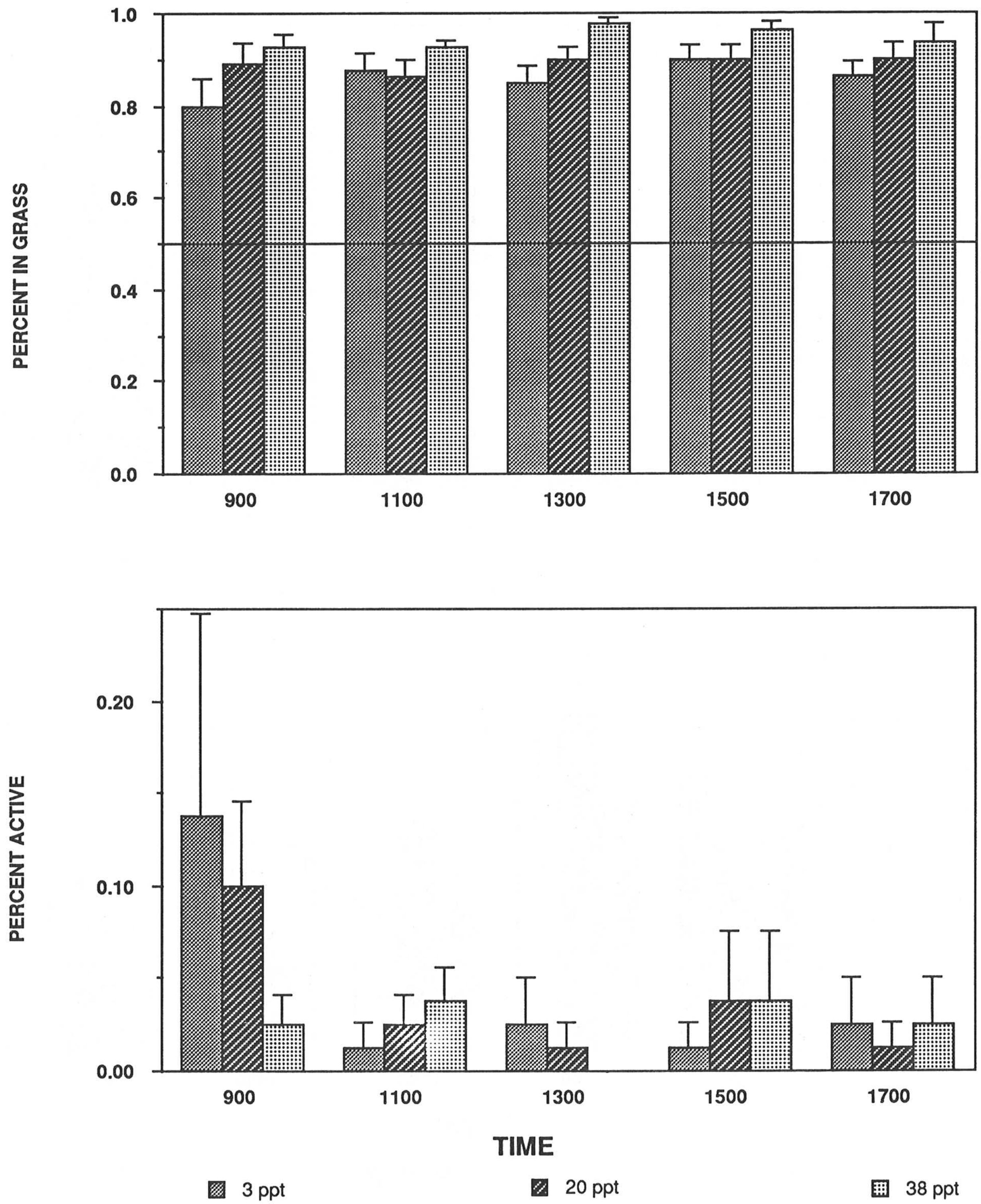


Figure 1. The effect of salinity on selection for structure and activity of brown shrimp. Each bar is a mean percentage from 8 replicate tanks; error bars represent 1 SE from untransformed data.

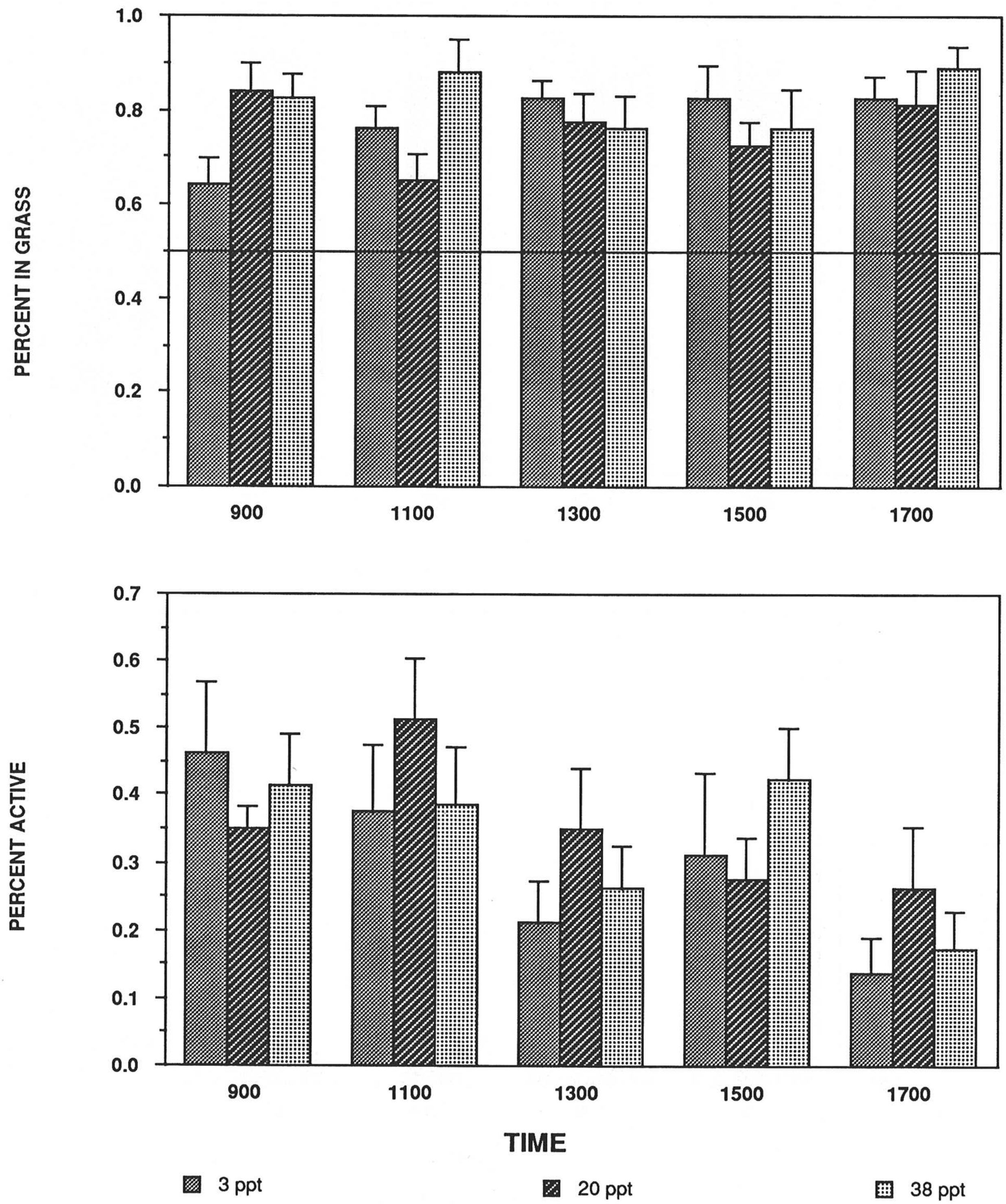


Figure 2. **The effect of salinity on selection for structure and activity of white shrimp. Each bar is a mean percentage from 8 replicate tanks; error bars represent 1 SE from untransformed data.**

Table 2. Analysis of variance results showing the effect of salinity reduction on the percentage of brown shrimp in the grass and the percentage of active shrimp. An arcsin transformation was used on the percentages. All main effects were tested using the Among Tank error term.

Percent in the Grass

Treatment	df	SS	F	P
Salinity Reduction	4	5.68	8.46	**< 0.001**
Contrasts				
A. No change vs Reduction	1	0.49	2.91	0.10
B. With 3 ppt vs Without 3 ppt	1	4.17	24.82	**< 0.001**
Day (Block)	1	0.50	2.99	0.10
Among Tank Error	19	3.19	2.78	**0.002**
Within Tank Error	50	3.02		

Percent Active

Treatment	df	SS	F	P
Salinity Reduction	4	1.00	1.35	0.29
Contrasts				
A. No change vs Reduction	1	0.00	0.00	0.98
B. With 3 ppt vs Without 3 ppt	1	0.82	4.37	0.050
Day (Block)	1	0.00	0.00	0.97
Among Tank Error	19	3.55	2.96	**0.001**
Within Tank Error	50	3.15		

Table 3. The effect of salinity reduction on the percent age of shrimp in the grass and the percentage of active shrimp. The probability (P) value listed is from an ANOVA comparing all treatment means (5-6 replicate tanks/mean) using an arcsin transformation (see Tables 2 and 4). Individual means cannot be statistically distinguished at the 0.05 level if they are connected by a line (LSD multiple range test).

	P	**Salinity Change (ppt)**				
Percent in the Grass		**38-38**	**38-20**	**20-20**	**3-3**	**20-3**
Brown shrimp	**< 0.001**	97%	97%	88%	83%	62%
White shrimp	**0.055**	86%	75%	70%	70%	64%
Percent Active						
Brown shrimp	0.29	3%	4%	13%	24%	28%
White shrimp	0.21	19%	25%	36%	36%	23%

for white shrimp was similar to that for brown shrimp (Table 3, Figure 4). The change from 20 ‰ to 3 ‰ also did not appear as stressful for white shrimp, and relatively few mortalities were observed for this species. The mean survival for white shrimp in this treatment was 10 shrimp (100%) at 1300 hrs, 9.5 shrimp at 1500 hrs, and 9.0 shrimp at 1700 hrs.

Activity levels of brown shrimp were again generally lower than those for white shrimp, and there was a trend of increased activity for brown shrimp with reduced salinity (Table 3). Brown shrimp in treatments with final salinities of 3 ‰ had significantly higher activity levels than shrimp in other treatments (Contrast B, Table 2). Salinity or salinity reduction did not significantly affect activity of white shrimp (Table 4). For both species, mean activity levels in the treatment with salinity reduced to 3 ‰ declined with time following the salinity change (Figures 3 and 4). Similar declines were also apparent in treatments without a salinity reduction, however, and these trends may be related to the disruption of removing and adding water to the experimental tanks.

Table 4. Analysis of variance results showing the effect of salinity reduction on the percentage of white shrimp in the grass and the percentage of active shrimp. An arcsin transformation was used on the percentages. All main effects were tested using the Among Tank error term.

Percent in the Grass

Treatment	df	SS	F	P
Salinity Reduction	4	1.67	2.70	**0.055**
Contrasts				
A. No change vs Reduction	1	0.31	1.99	0.17
B. With 3 ppt vs Without 3 ppt	1	0.53	3.45	0.076
Day (Block)	1	0.01	0.05	0.83
Among Tank Error	24	3.70	1.68	**0.054**
Within Tank Error	60	5.52		

Percent Active

Treatment	df	SS	F	P
Salinity Reduction	4	0.56	1.59	0.21
Contrasts				
A. No change vs Reduction	1	0.12	1.39	0.25
B. With 3 ppt vs Without 3 ppt	1	0.04	0.40	0.53
Day (Block)	1	1.05	11.84	**0.002**
Among Tank Error	24	2.13	2.32	**0.004**
Within Tank Error	60	2.30		

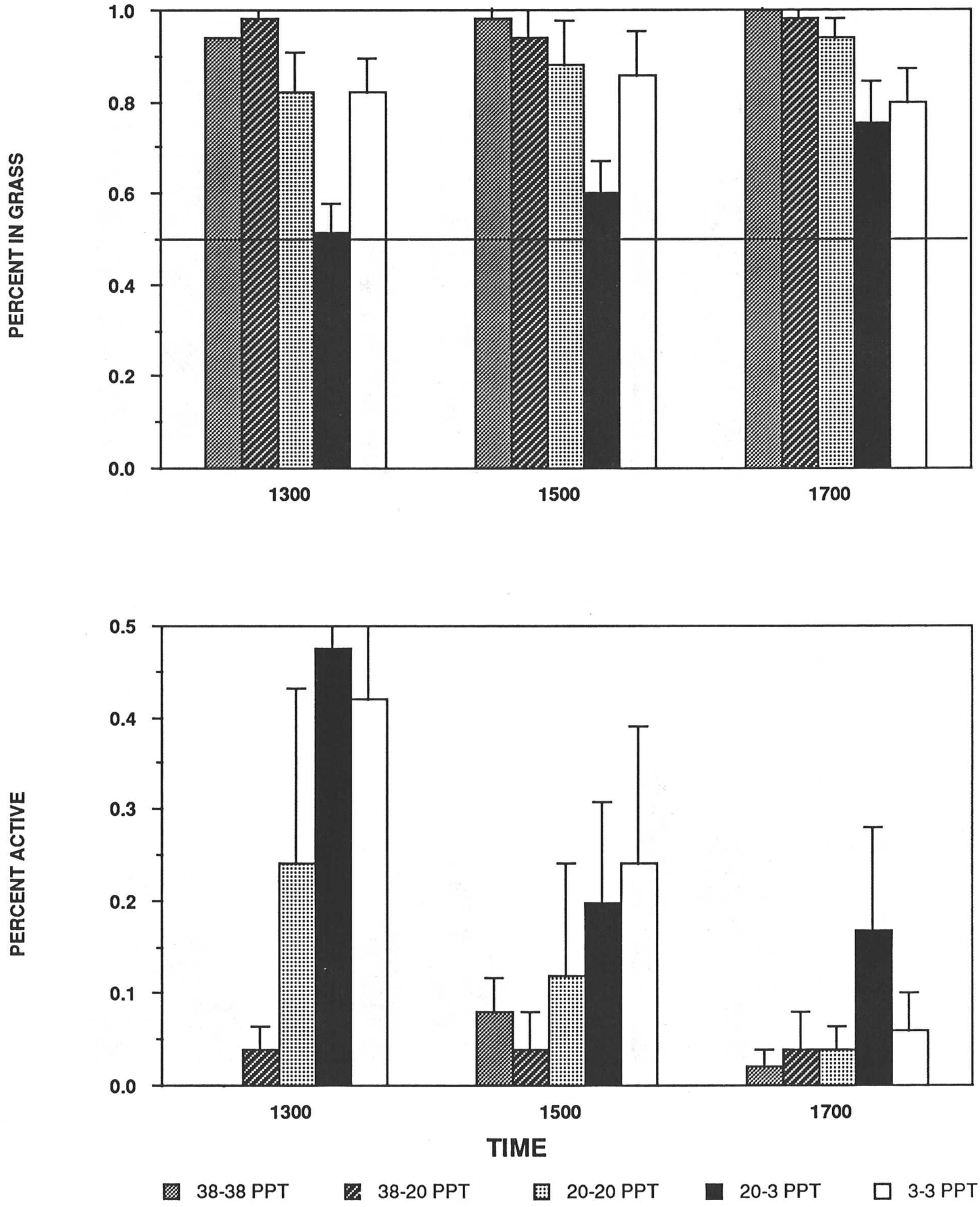


Figure 3. The effect of salinity reduction on selection for structure and activity of brown shrimp. Each bar is a mean percentage from 5 replicate tanks; error bars represent 1 SE from untransformed data.

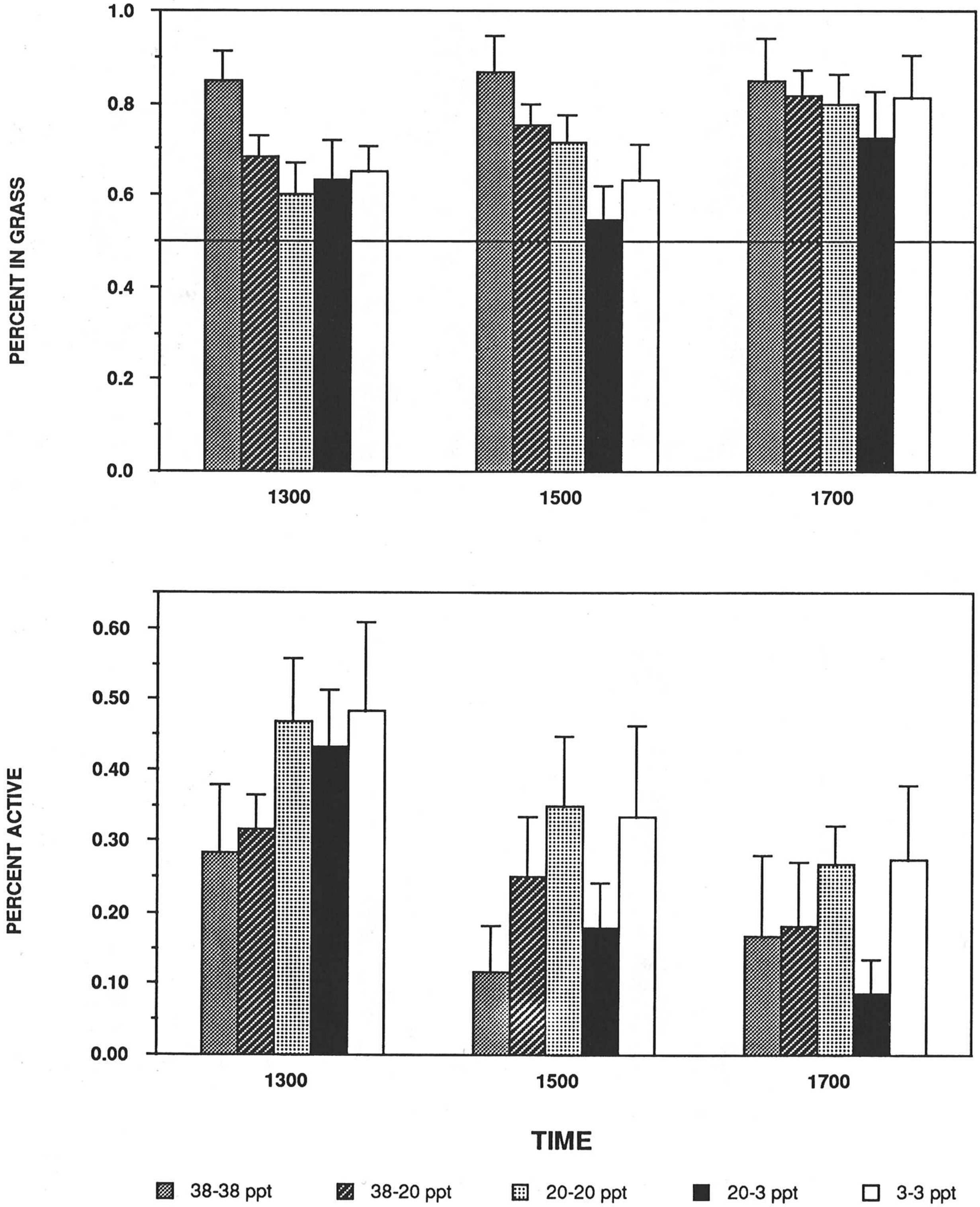


Figure 4. The effect of salinity reduction on selection for structure and activity of white shrimp. Each bar is a mean percentage from 6 replicate tanks; error bars represent 1 SE from untransformed data.

Turbidity

Water turbidity strongly affected selection for structure by brown shrimp, but did not affect selection by white shrimp (Table 5). The percentage of brown shrimp in the grass was highest at the intermediate turbidity of 10 FTUs, and the clear water treatment could not be statistically distinguished from the higher turbidity levels of 25 and 50 FTUs. This response was the same during both days of the experiment.

Sensor orientation had a dramatic effect on light attenuation readings in the experimental tanks. The sensor measures light in a 180° hemisphere, and when it was pointing towards the light source (vertically), light was not significantly reduced from 0 to 10 FTUs, but significant reductions occurred at higher turbidities (Table 5). When the sensor was pointed horizontally towards the wall of the tank, light significantly increased as turbidity increased. A comparison of light penetration between the 0 and 10 FTU treatments, therefore, indicated no significant difference in vertically penetrating light, but a significantly higher horizontal light reading at 10 FTUs.

Food

The distribution of food in the tanks strongly affected the distribution of brown shrimp in relation to structure (Table 6). The overall presence or absence of food did not significantly affect the percentage of shrimp in the grass ($\bar{x}$ = 67.5%), but the presence of food only in the vegetated half of the tanks increased the percentage of shrimp in the grass to 89% (a 32% increase in number), and the presence of food only in the nonvegetated half of the tanks decreased the percentage of shrimp in the grass to 45% (a 33% decrease in number). Separation among treatment effects was greatest just after food was added to the tanks (1300 hrs, Table 6, Figure 5). At night, the results for brown shrimp were similar, although statistically we could not distinguish any of the treatment levels except for food presence in the nonvegetated half of the tank which again had the lowest selection for structure (25% in the grass, Table 6). Night observations were taken only at one time, and the power of the ANOVA to detect significant differences at night was relatively low. In the white shrimp experiment, shrimp distribution

Table 5. The effect of turbidity on the percentage of shrimp in the grass and on light in the water column. Light was measured both with the sensor pointing towards the surface (Vertical) and pointing parallel to the tank substrate (Horizontal). The probability value (P) listed is from an ANOVA comparing all treatment means (8 replicate tanks/mean); an arcsin transformation was used on percentage data. Individual means cannot be statistically distinguished at the 0.05 level if they are connected by a line (LSD multiple range test).

	P	Turbidity			
Percent in the Grass		**10 FTU**	**0 FTU**	**25 FTU**	**50 FTU**
Brown shrimp	**< 0.001**	90%	76%	66%	58%
White shrimp	0.39	77%	80%	69%	68%
Light					
Vertical	**< 0.001**	20.9	21.8	18.6	16.6
Horizontal	**< 0.001**	6.3	4.0	7.5	8.6

was not significantly affected by the presence or distribution of food (Table 6, Figure 6). The percentage of shrimp in the vegetated half of the tanks was high in all experimental treatments, ranging between 80% and 94%.

Squid may have been inappropriate as food for the white shrimp in this experiment because differences in feeding rates were apparent between species. Brown shrimp were feeding during 43% of the observations compared with only 5% for white shrimp. Hunger levels should have been similar in the experiments, because both species were held in the lab for 3-5 days before an experiment and fed daily with the same pelleted shrimp food.

Activity levels for both species of shrimp were not significantly affected by the distribution or presence of food (Table 6). Brown shrimp in this experiment were relatively active compared with those in other experiments, and white shrimp were relatively inactive (Table 6). The unusually low activity levels for white shrimp combined with low feeding levels may indicate that this group of animals was dissimilar to animals used in other experiments.

Table 6. The effect of food on the percentage of shrimp in the grass and the percentage of active shrimp. The probability (P) value listed is from an ANOVA comparing all treatment means (4 replicate tanks/mean) using an arcsin transformation. Individual means cannot be statistically distinguished at the 0.05 level if they are connected by a line (LSD multiple range test).

	P	Food Distribution			
Percent in the Grass		**FOOD GRASS**	**NO FOOD**	**FOOD BOTH**	**FOOD NONVEG**
Brown shrimp 1300, 1500 and 1700 Hrs	**< 0.001**	89%	74%	61%	45%
1300 Hrs	**< 0.001**	90%	70%	68%	40%
NIGHT	**< 0.001**	70%	60%	58%	25%
White shrimp 1300, 1500 and 1700 Hrs	0.62	94%	90%	91%	80%
1300 Hrs	0.49	98%	90%	88%	78%
Percent Active					
Brown shrimp 1300, 1500 and 1700 Hrs	0.28	10%	39%	15%	22%
1300 Hrs	0.28	5%	32%	10%	22%
NIGHT	0.18	25%	35%	42%	38%
White shrimp 1300, 1500 and 1700 Hrs	0.90	1%	1%	1%	2%
1300 Hrs	0.43	0%	2%	0%	0%

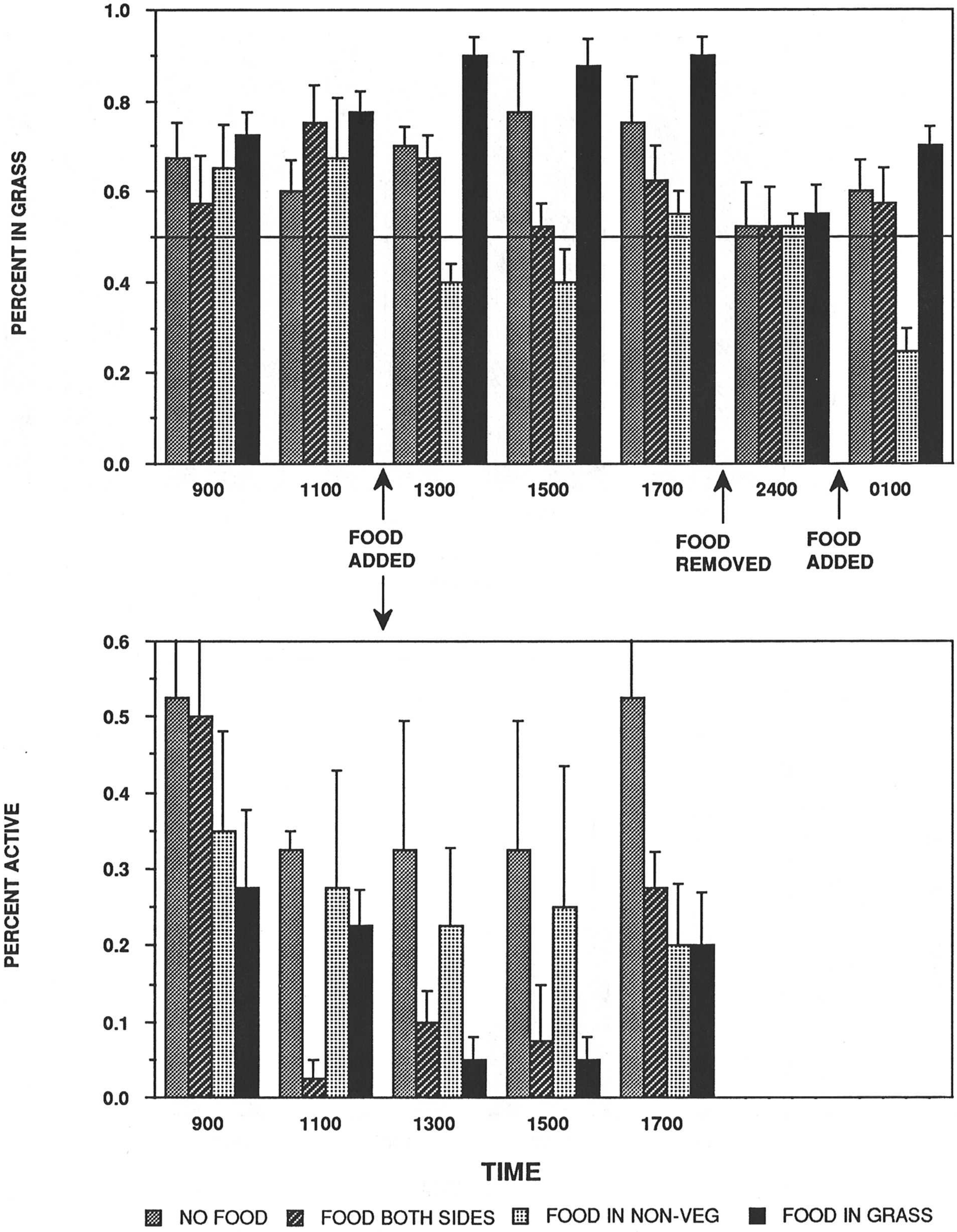


Figure 5. The effect of food on selection for structure and activity of brown shrimp. Each bar is a mean percentage from 4 replicate tanks; error bars represent 1 SE from untransformed data.

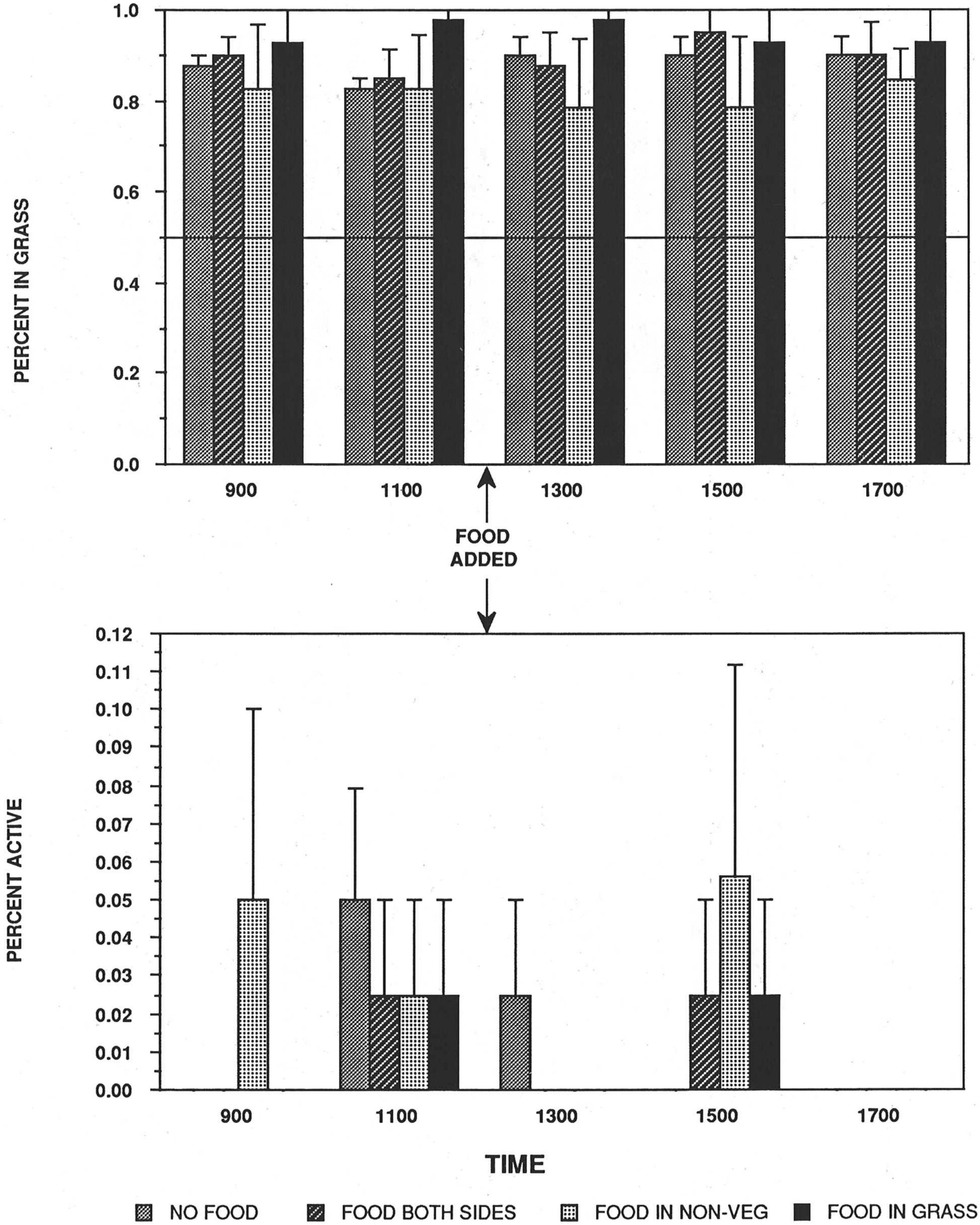


Figure 6. The effect of food on selection for structure and activity of white shrimp. Each bar is a mean percentage from 4 replicate tanks; error bars represent 1 SE from untransformed data.

Substrate

The effect of substrate on the distribution of brown shrimp during the day paralleled the effect of food (Table 7, Figure 7). The overall presence or absence of a substrate for burrowing did not affect selection for structure, but the distribution of the sand was important. When sand was present only in the vegetated half of the tank, 94% of the shrimp were in the grass. When sand was present only in the nonvegetated half of the tank, overall attraction for structure was eliminated, and 67% of the shrimp were on nonvegetated bottom. At night, there was no significant effect of substrate on the distribution of brown shrimp (Table 7), and the average percentage in the grass for all treatments was 61%. Brown shrimp frequently burrowed in the sand substrate during the day, and in treatments where some sand was present, 54% to 77% of brown shrimp were burrowed (Table 7). In tanks with sand only on nonvegetated bottom, 78% of the shrimp in the nonvegetated half of the tank were burrowed. At night, brown shrimp did not burrow in the substrate, coincident with the lack of a significant substrate effect on selection for structure.

White shrimp distribution in relation to structure was not affected by the presence or distribution of the substrate (Table 7, Figure 8). Burrowing activity by white shrimp was also low in comparison with brown shrimp (Table 7), and in treatments with some sand present, only 4% to 8% of white shrimp were burrowed. Overall activity levels were low (5-11%) for brown shrimp and relatively high for white shrimp (30-45%). The presence and distribution of the substrate, however, had no significant effect on activity for either species (Table 7).

Table 7. The effect of substrate on the percentage of shrimp in the grass, active, and burrowed. The probability (P) value listed is from an ANOVA comparing all treatment means (4 replicate tanks/mean) using an arcsin transformation. Individual means cannot be statistically distinguished at the 0.05 level if they are connected by a line (LSD multiple range test).

	P	Substrate Distribution			
Percent In the Grass		**SAND GRASS**	**NO SAND**	**SAND BOTH**	**SAND NONVEG**
Brown shrimp	**< 0.001**	94%	74%	68%	33%
(Night)	0.61	62%	62%	65%	52%
White shrimp	0.96	65%	68%	65%	64%
Percent Active					
Brown shrimp	0.34	5%	7%	11%	8%
White shrimp	0.84	30%	41%	43%	45%
Percent Burrowed					
Brown shrimp	**< 0.001**	77%		70%	54%
White shrimp	0.29	8%		6%	4%

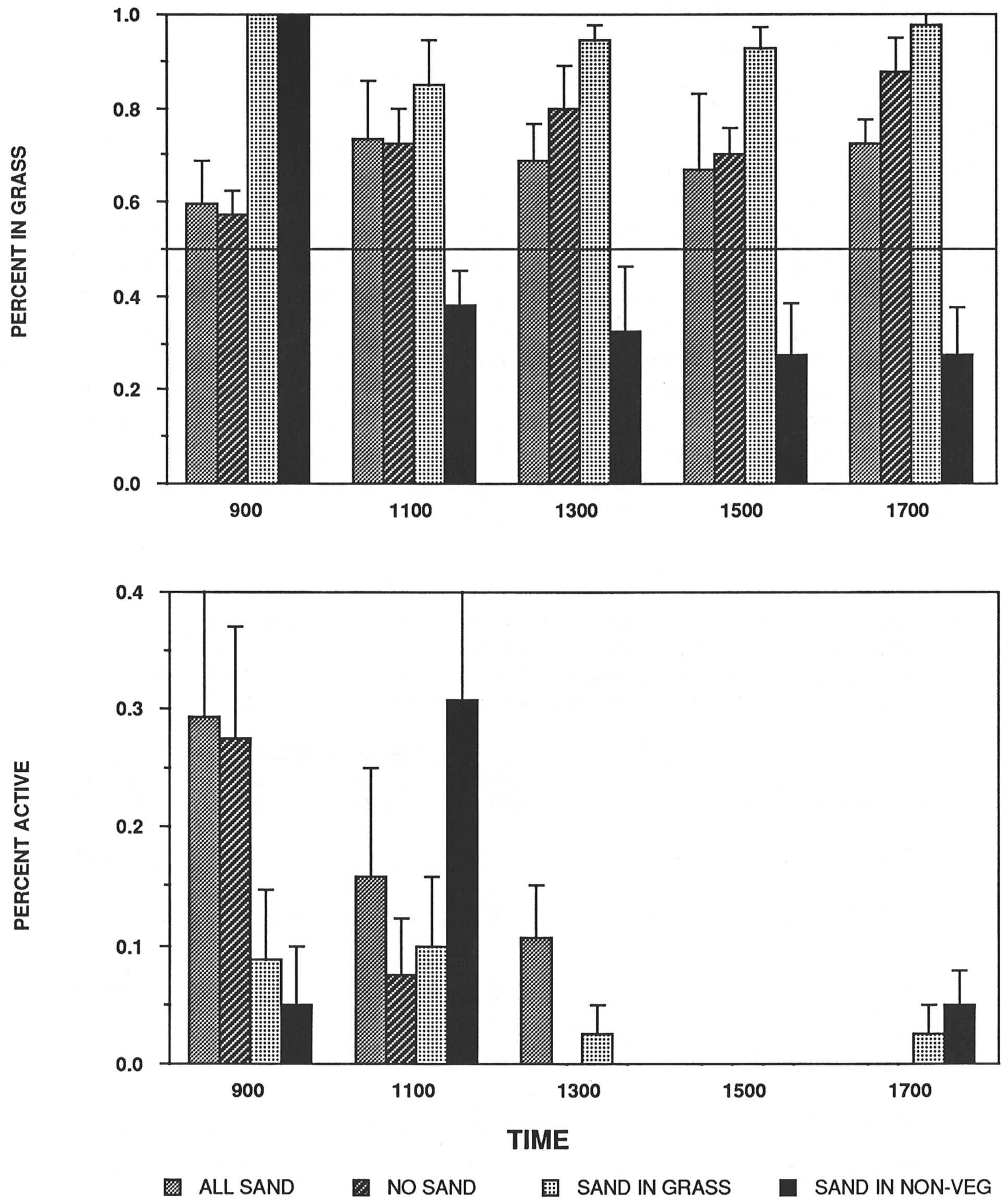


Figure 7. The effect of substrate on selection for structure and activity of brown shrimp. Each bar is a mean percentage from 4 replicate tanks; error bars represent 1 SE from untransformed data.

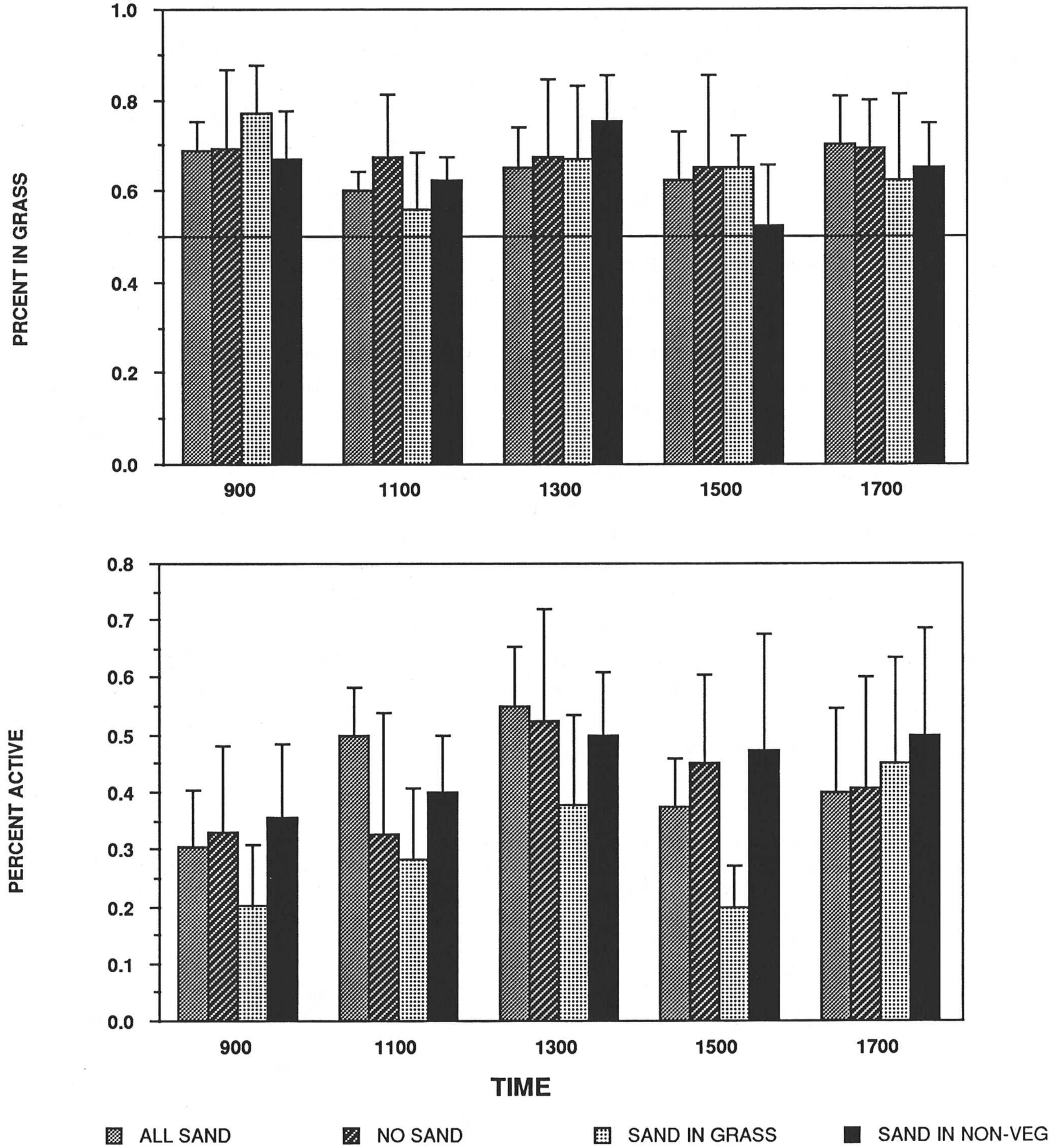


Figure 8. The effect of substrate on selection for structure and activity of white shrimp. Each bar is a mean percentage from 4 replicate tanks; error bars represent 1 SE from untransformed data.

Size

Within the size range of shrimp examined (35 to 84 mm, TL), size did not have a significant effect on selection for structure by either brown shrimp or white shrimp (Table 8, Figures 9 and 10). In addition, activity of the species did not appear to be affected by size.

Day Length and Light

Selection for structure by brown shrimp did not appear to be affected by day length (Figure 11). Shrimp had been held under the two day-length conditions (12-hr and 14-hr days) for approximately 2 weeks before the experiment, and ANOVA results indicated no significant differences in selection for structure (P=0.24, df= 1,12) or in activity (P=0.97, df= 1,12).

Light intensity during the day, however, did have an effect on selection for structure by brown shrimp (Figure 12). At 0900 hrs the lights were on in all 12 experimental tanks, and there was no significant difference in selection between the tanks randomly designated as "dark" and those designated as lighted. Lights in the dark tanks were turned off at 0930 hrs. At 1100 hrs the mean percentage of shrimp in the vegetated half of the tanks was lower in the dark tanks (Figure 12), but the difference was not significant in an ANOVA (P=0.11, df= 1,10). By 1300 hrs the percentage of shrimp in the grass in the dark tanks had dropped to 61%, significantly lower than the 89% in the lighted tanks (ANOVA, P=0.008, df= 1,10). There was a large decline in activity following the 0900 hr observations in this experiment, but this decline occurred in both lighted and dark tanks. Light did not significantly affect the activity of shrimp at either 1100 hrs or 1300 hrs (ANOVA, P>0.30, df= 1,10).

Shrimp Density

The white shrimp densities of 5, 10, and 20 shrimp per tank corresponded to densities of 5.4, 10.9, and 21.7 shrimp/m^2. The mean percentage of shrimp in the grass was highest in the low density treatment (82% in the grass) compared with percentages of 74 and 76% in the grass for densities of 10 and 20 shrimp per tank (Figure 13), but ANOVA results indicated no significant difference among the three density treatments (P=0.35, df= 2,12). Activity levels were highly variable, and no difference in activity could be attributed to shrimp density (ANOVA, P=0.92, df= 2,12).

Table 8. The effect of shrimp size on the percentage of shrimp in the grass and the percentage of active shrimp. The probability value (P) listed is from an ANOVA comparing all treatment means (5 replicate tanks/mean) using an arcsin transformation. Individual means cannot be statistically distinguished at the 0.05 level if they are connected by a line (LSD multiple range test).

	P	Total Length		
Percent in the Grass		**35-40 mm**	**50-60 mm**	**68-84 mm**
Brown shrimp	0.18	72%	68%	81%
White shrimp	0.16	72%	84%	88%
Percent Active				
Brown shrimp	0.78	4%	4%	6%
White shrimp	0.84	10%	12%	14%

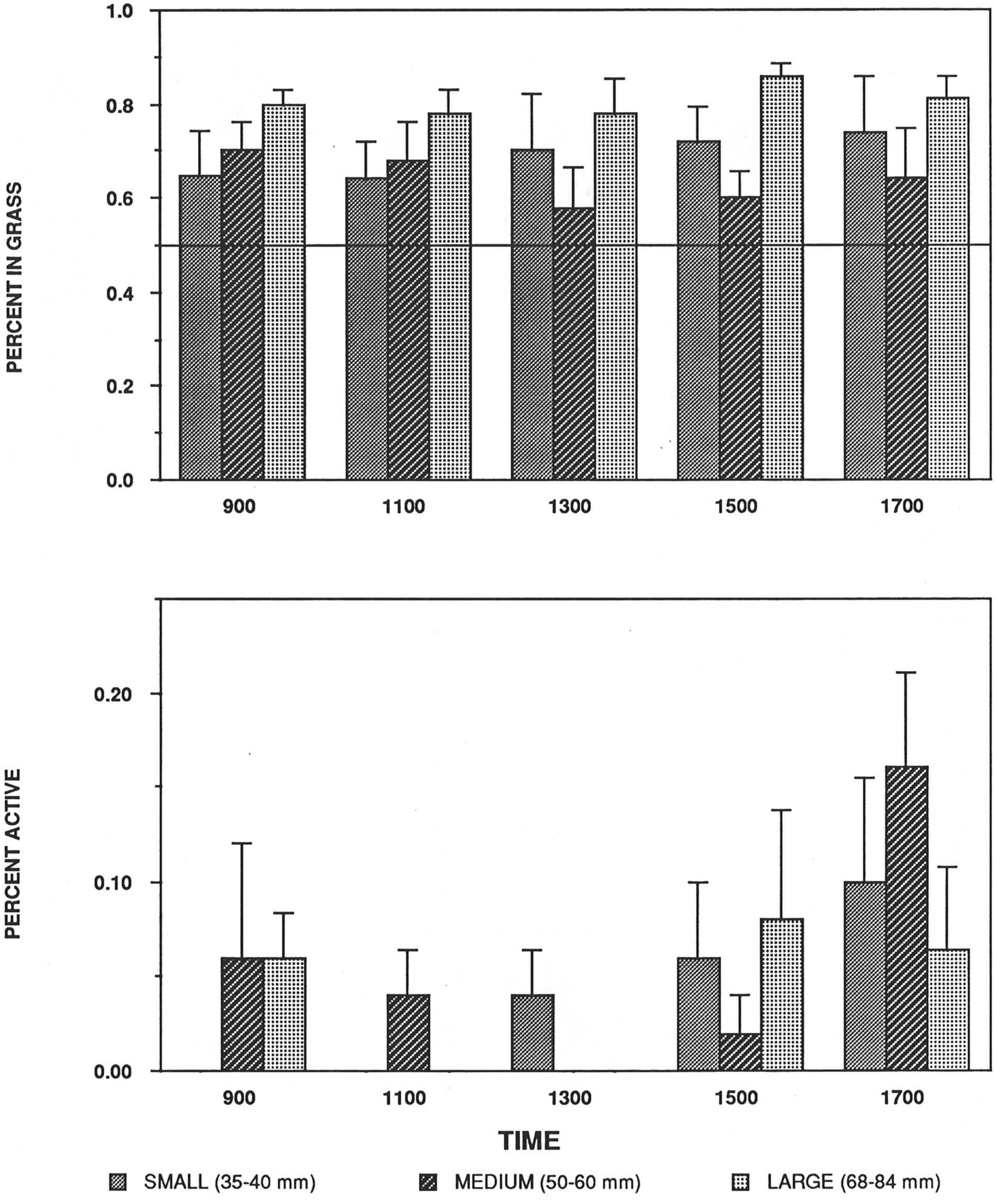


Figure 9. The effect of shrimp size on selection for structure and activity of brown shrimp. Each bar is a mean percentage from 5 replicate tanks; error bars represent 1 SE from untransformed data.

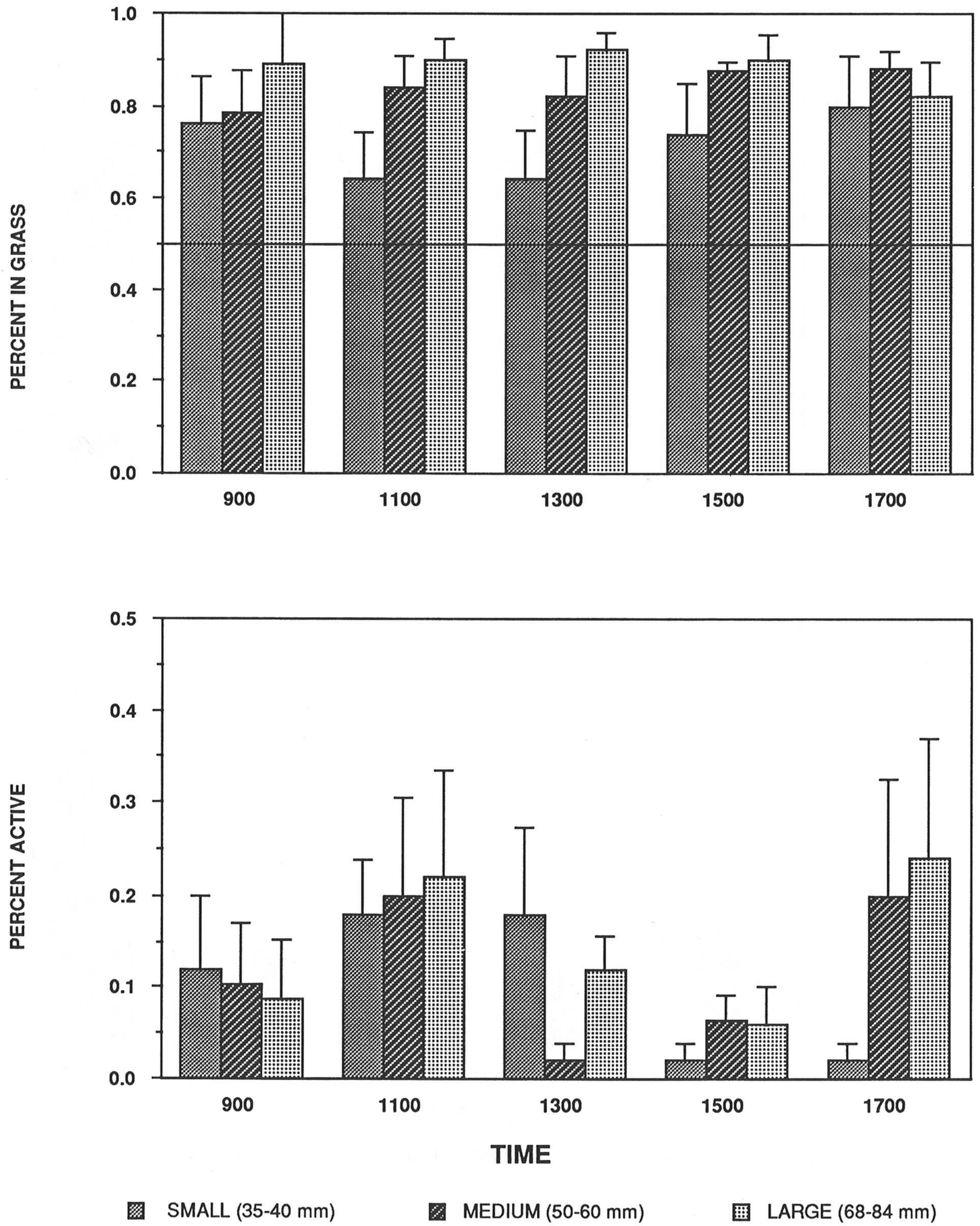


Figure 10. The effect of shrimp size on selection for structure and activity of white shrimp. Each bar is a mean percentage from 5 replicate tanks; error bars represent 1 SE from untransformed data.

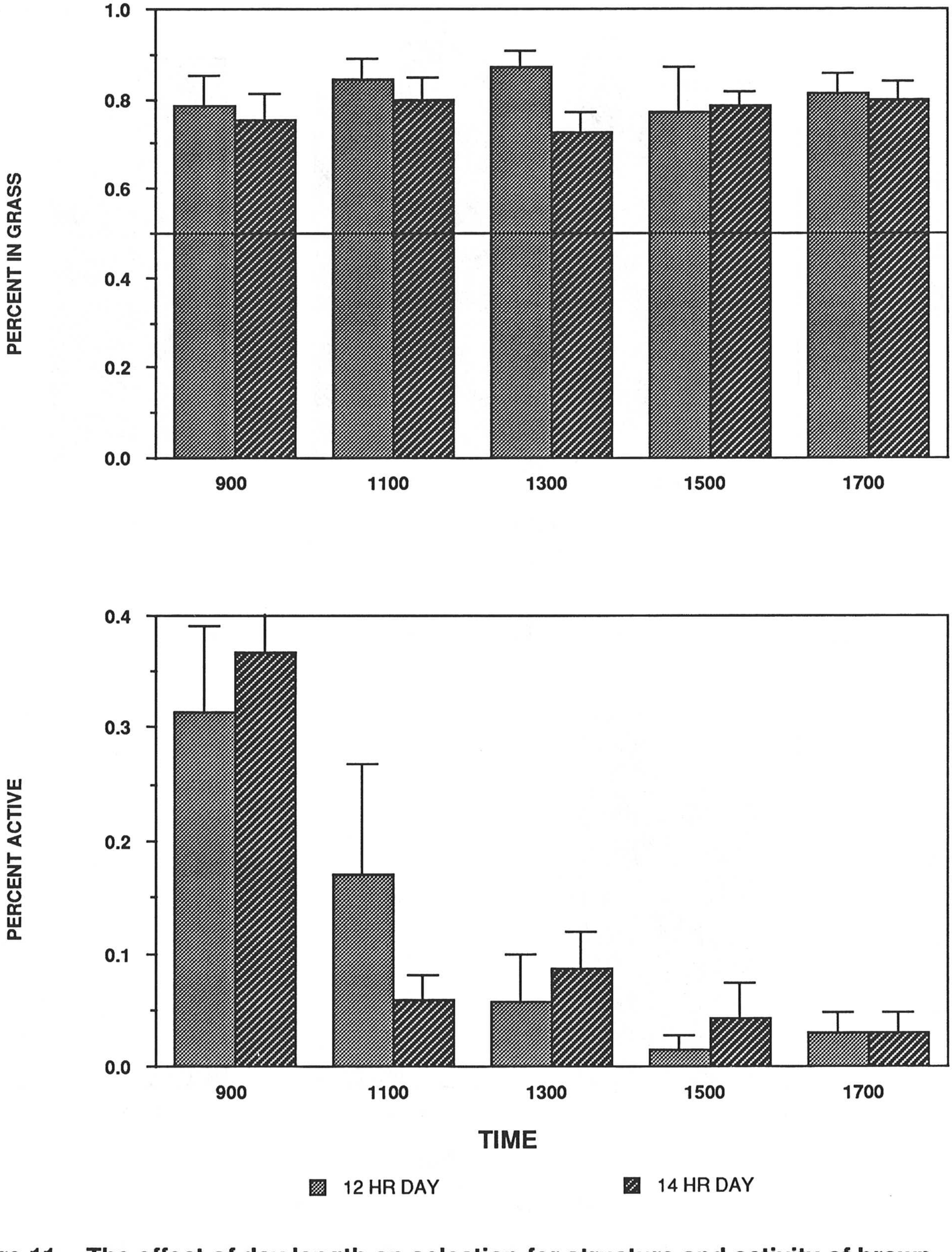


Figure 11. The effect of day length on selection for structure and activity of brown shrimp. Each bar is a mean percentage from 7 replicate tanks; error bars represent 1 SE from untransformed data.

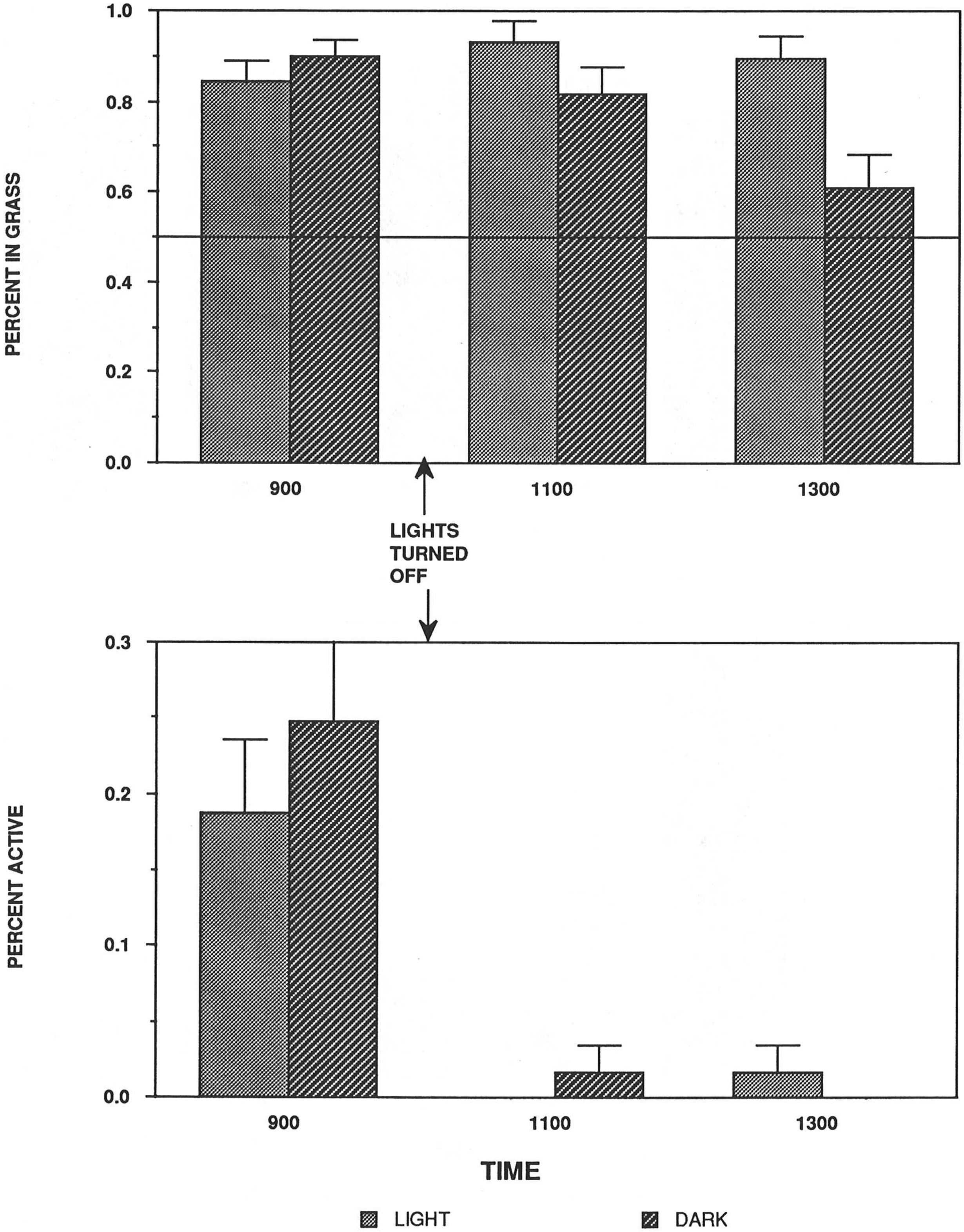


Figure 12. The effect of light on selection for structure and activity of brown shrimp. Each bar is a mean percentage from 6 replicate tanks; error bars represent 1 SE from untransformed data.

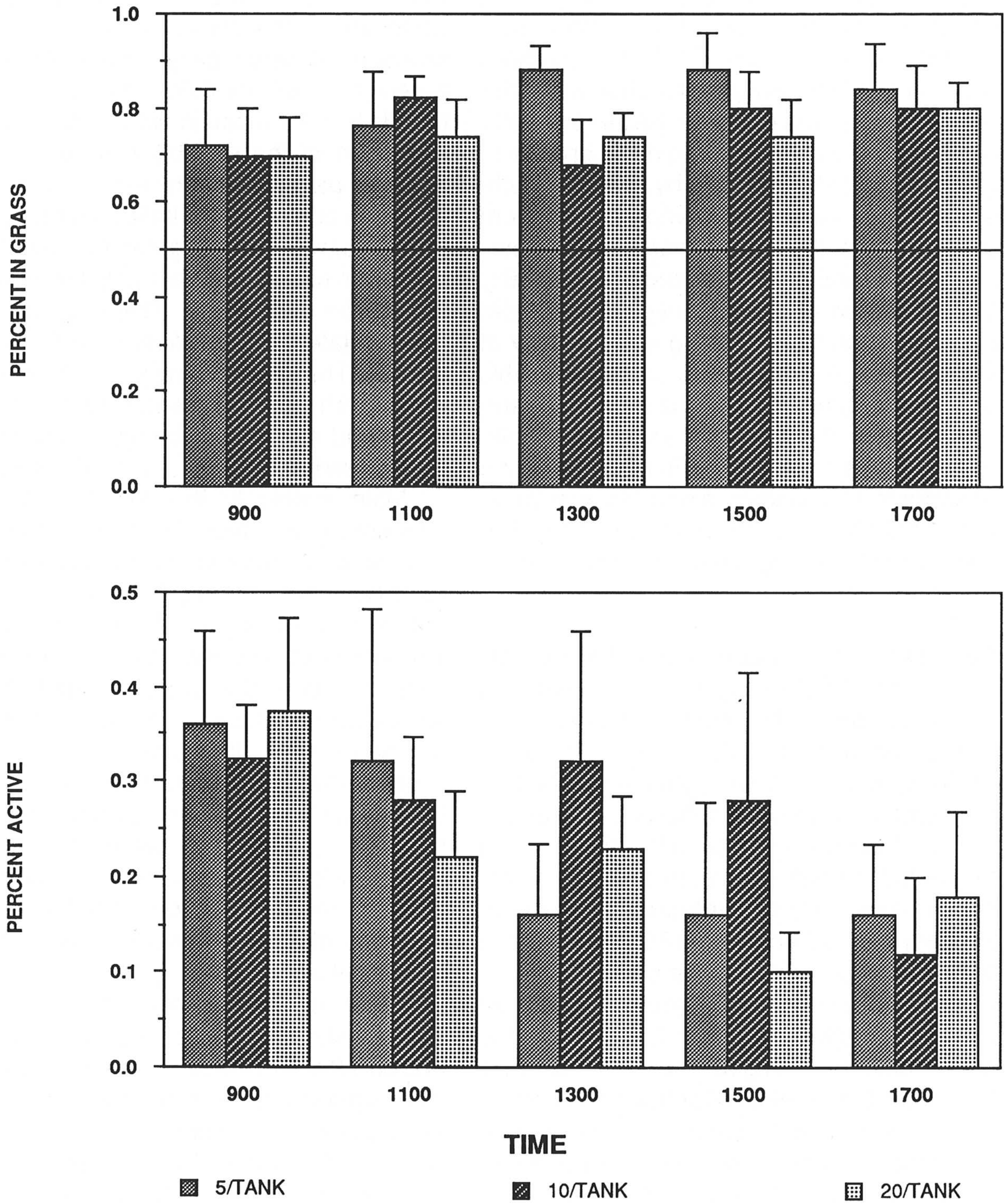


Figure 13. The effect of shrimp density on selection for structure and activity of white shrimp. Each bar is a mean percentage from 5 replicate tanks; error bars represent 1 SE from untransformed data.

Predators

The presence of a southern flounder in the experimental tanks did not significantly affect selection for structure by white shrimp (Figure 14; ANOVA, P=0.36, df= 1,17). The southern flounder generally remained stationary on the bottom in the nonvegetated half of the tank, but the location of the fish did not appear to affect selection for structure by shrimp. Southern flounder were on nonvegetated bottom during 79% of the observations, but the percentage of shrimp in the grass was 87.6% both when fish were on nonvegetated bottom and when fish were in the grass. Activity of shrimp was affected by the presence of this predator (Figure 14), and the mean percentage of active shrimp over the day was significantly reduced from 31.7% in tanks without a predator to 10.5% when a predator was present (ANOVA, P=0.005, df=1,17). Only five shrimp were eaten by the predators during the experimental period.

Control Variability and Within Tank Error

In every experiment, one of the treatment levels was basically a control treatment with similar conditions of salinity (20 ‰), turbidity (0 FTUs), food (no food), substrate (no sand), temperature, and light. Differences in selection for structure and in shrimp activity among these control treatments from the experiments were relatively high. For brown shrimp, control data were collected from 39 tanks over the 9 days of experiments. The daily mean percentages of shrimp in the grass ranged from 64% to 94% ($\bar{x}$=81%, SE=3.2, n=9), and the mean activities ranged from 1% to 39% ($\bar{x}$=12%, SE=4.5, n=9). Control data for white shrimp were collected from 42 tanks over 10 experimental days, and daily mean percentages of shrimp in the grass ranged from 65% to 88% ($\bar{x}$=75%, SE=2.2, n=10) with mean activities ranging from 2% to 44% ($\bar{x}$=28%, SE=4.9, n=10). Selection for structure by both species was associated with inactivity, and there was a significant negative correlation between the transformed percentage in the grass and activity in the control tanks for both brown shrimp (r= -0.44, P= 0.005, n=39) and white shrimp (r= -0.57, P< 0.001, n=42). For white shrimp this correlation was even more pronounced when daily means were compared (r= -0.87, P< 0.001, n= 10), indicating that daily differences in activity could explain over 75% of the variability in selection. In addition, paired comparisons of shrimp activity within control tanks indicated that activity was lower within the vegetation. Only 10% of the brown shrimp were active in the vegetated half of the tanks while 20% were active on nonvegetated bottom (paired t= 3.08, P= 0.004, df= 34). The white shrimp activity pattern was similar with 23% of the shrimp active in vegetation and 42% active on nonvegetated bottom (paired t= 5.58, P< 0.001, df= 40).

Main effects in the ANOVAs for each experiment were tested using an among tank error term, but a comparison of the within tank error (variability throughout the day) and the among tank error was also made. For both species, most analyses (11 of 13) of the percent shrimp in the grass showed that the among tank error was significantly (0.05 level) greater than the within tank error. These data suggest that our observations within a tank throughout the day were probably not independent, and the separation of within tank error from among tank error was necessary in order to meet assumptions of ANOVA. In the analyses of activity, results for white shrimp were similar with 6 of 7 significant differences. However, in the brown shrimp analyses of activity, within tank error was relatively high, and only 2 of 6 of these variance comparisons were significant. This large within tank variability generally reflected a decrease in brown shrimp activity from relatively high levels in the morning to lower levels throughout the day.

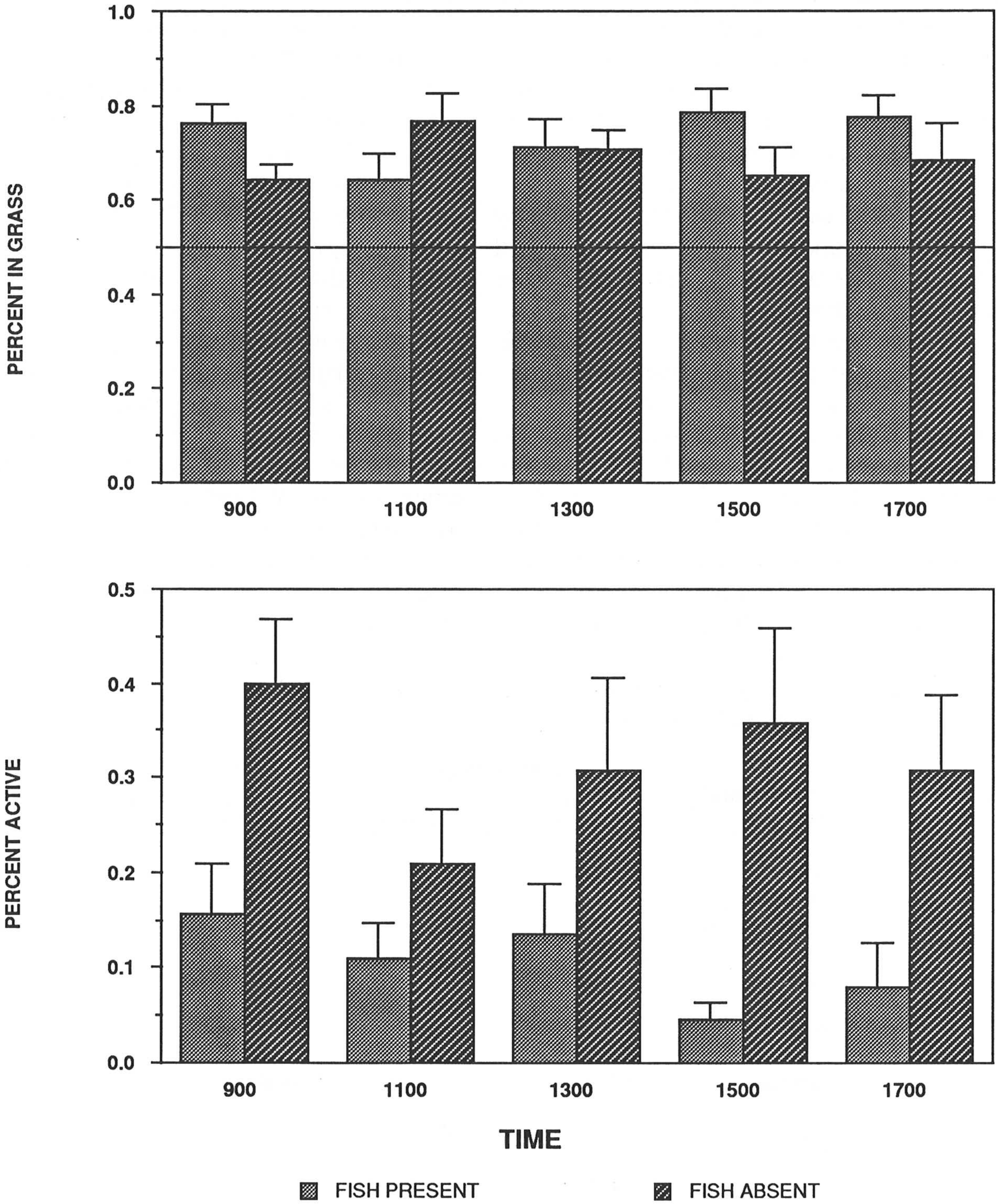


Figure 14. **The effect of fish predator on selection for structure and activity of white shrimp. Each bar is a mean percentage from 10 replicate tanks; error bars represent 1 SE from untransformed data.**

DISCUSSION

Selection for Structure by Brown Shrimp

Brown shrimp exhibited an inherent selection for structure in these experiments as in previous laboratory studies (Minello and Zimmerman, 1985). This selective behavior, however, was readily influenced by environmental conditions (Table 9). Salinity, turbidity, and light interacted with selection for structure by brown shrimp, and the distribution of food and a substrate for burrowing also affected the distribution of this species.

The reduction of salinity to oligohaline levels in our experiments reduced selection for structure. These results suggest that under some conditions, flood events in mesohaline areas of estuaries may result in reduced selection for vegetated habitats. Zimmerman et al. (1990) examined animal distributions in vegetated and nonvegetated habitats of upper Lavaca Bay, Tx, and the percentage of brown shrimp in marsh habitats appeared to decline following flood events. Increased mortality associated with lowering the salinity in our experiments also suggests that effects on selection for structure may be related to increased physiological stress.

Turbidity also affected selection for structure by brown shrimp, and this effect may have been related to the reduction of underwater light levels caused by turbid water. In another experiment, decreased light during the day significantly reduced the percentage of brown shrimp in the vegetation from 89% to 61%. This percentage in the dark was similar to the percentage in the grass during night observations. The light levels used in our experiments (22-27 $\mu E\ s^{-1}\ m^{-2}$) correspond to early morning or late afternoon light in shallow water habitats, and effects of turbidity and perhaps other experimental variables may interact with overall light levels.

Although the overall presence or absence of food or an appropriate substrate for burrowing did not interact with selection for structure,

Table 9. Summary of ANOVA probability values for the main effect of experimental variables on selection for structure and activity.

Experimental Variable	Brown Shrimp		White Shrimp	
	Selection	Activity	Selection	Activity
Salinity	0.052	0.78	0.35	0.90
Freshwater Event	< 0.001	0.29	0.055	0.21
Turbidity	< 0.001		0.39	
Food	< 0.001	0.28	0.62	0.90
Substrate	< 0.001	0.34	0.96	0.84
Size	0.18	0.78	0.16	0.84
Day Length	0.24	0.97		
Light	0.11, 0.008	> 0.3		
Shrimp Density			0.35	0.92
Predator			0.36	0.005

the distribution of these habitat characteristics dramatically affected brown shrimp distributions. Attraction to food or a substrate for burrowing could either enhance or override selection for structure. In salt marshes, abundances of peracarid crustaceans and polychaetes, which serve as food for juvenile brown shrimp, are frequently higher on the marsh surface in relation to nonvegetated bottom, although distributions of these food organisms in the marsh vary considerably in space and time (Kneib 1984; Rader 1984, Zimmerman et al., in press). The distribution of food, therefore, may partly regulate the distribution of brown shrimp in relation to vegetation. Substrate type, however, may also modify selection for vegetation in the field, and the effect of substrate appeared to be closely related to burrowing behavior. The presence of root mats or the compaction of clay substrates in the intertidal zone due to intermittent drying may prevent shrimp from burrowing in vegetated habitats. Under these conditions, selection for vegetation may be reduced as young brown shrimp remain on nonvegetated bottom more appropriate for burrowing. All of the above habitat characteristics can be expected to interact in their influence on selection for vegetated habitats, but our laboratory data would suggest that the distribution of food and substrate are dominant factors.

Selection for Structure by White Shrimp

In direct contrast to brown shrimp results, laboratory experiments on white shrimp showed little effect of environmental variables on selection for structure (Table 9). There was a marginally significant ($P=0.055$) reduction in selection due to salinity reduction, but evidence for any major salinity effect was not persuasive. The lack of a response to the distribution of a substrate for burrowing parallels the relatively low burrowing frequency for this species. Lack of any significant response to the distribution of food, however, is puzzling. The low feeding frequency by white shrimp on the animal food used in the experiment (squid pieces) suggests that either the food was unpalatable or that the group of shrimp used during this experiment was anomalous (supported by unusually low activity levels). There is some evidence indicating that white shrimp are less carnivorous than brown shrimp (Zimmerman et al. in press) and therefore may be less attracted to squid as food, but squid has frequently been used in maintenance diets for white shrimp at the Galveston Laboratory. Additional experiments using different foods and experimental shrimp may be required before we can make any conclusions as to the effect of food on the distribution of white shrimp.

These experiments have provided little insight into the regulation of white shrimp distributions in relation to vegetative structure. Results from our control tanks on each of the nine experimental days revealed an overall selection for structure by white shrimp, unlike previous laboratory experiments with artificial vegetation (Minello and Zimmerman, 1985). This kind of unexplained variability parallels the enigma of white shrimp distributions in the field. The experimental design of this study differed from the design of our previous experiments in overall light levels, substrate type, and the size, shape and material of the experimental containers. In our previous work circular cages of black mesh were used, and the structure of the cage walls themselves or their coloration may have attracted shrimp to nonvegetated areas.

Relationships Between Activity and Selection for Structure

Results from control tanks for both species of shrimp indicated that activity was negatively related to selection for structure. Activity levels for white shrimp were relatively high in relation to brown shrimp, coincident with relatively lower selection for structure by white shrimp. The importance of this relationship is unclear, however, and it may be difficult to determine whether activity affects selection, selection affects activity, or both are responding to some other factor. There is some evidence for independence between activity and selection, especially for brown shrimp, because effects of experimental factors on selection for structure seldom appeared related to any effect on activity (Table 9). Many experimental factors affected selection for structure by brown shrimp, but activity was only marginally affected in the salinity reduction experiment. Reduced selection in salinity treatments with 3 ‰ did coincide with increased activity, but analysis of covariance designed to remove the effect of activity on selection did not have any great effect on the ANOVA results. White shrimp activity was significantly affected in only one experiment, in which activity was reduced by the presence of southern flounder. However, selection for structure was not significantly increased in this experiment.

The highly significant correlation for white shrimp between overall daily activity and selection for structure in controls ($r = -0.87$, $P< 0.001$, $n= 10$), suggests that variability in activity among days may affect selection for structure by this species. If this relationship between activity and selection is not simply an artifact of our experimental design, environmental factors regulating activity may also regulate selection for structure by white shrimp in shallow estuarine habitats. Many environmental factors not examined fully in this study have been shown to affect activity of penaeid shrimp, including light (Moller and Jones 1975, Wickham and Minkler 1975, Bishop and Herrnkind 1976, Moctezuma and Blake 1981), food (Hughes 1968), lunar and tidal phase (Aaron and Wisby 1964, Fuss and Ogren 1966), current speed (Fuss and Ogren 1966, Wickham 1967) water levels (Hughes 1966), temperature (Fuss and Ogren 1966, Aldrich et al. 1968), and shrimp size (Hughes 1968, Moctezuma and Blake 1981).

Evidence from our experiments, however, could also be interpreted to indicate that selection for structure can regulate activity. Activity of shrimp in the nonvegetated half of control tanks was approximately double that in the vegetated half. Environmental conditions affecting activity, unrelated to the presence of structure, should have been similar on both sides of the tanks. Structure may inhibit crawling and swimming or the lack of structure may stimulate these activities. The overall relationship between reduced activity and selection for structure by shrimp should be examined in greater detail. The large ranges in daily means from our experimental controls indicate that factors, not controlled in these experiments, were affecting both selection and activity.

LITERATURE CITED

Aaron, R.L. and W.J. Wisby. 1964. Effects of light and moon phase on the behavior of pink shrimp. Proc. Gulf Carib. Fish. Inst., 16th Ann. Sess. 1963: 121-130.

Aldrich, D.V., C.E. Wood, and K.N. Baxter. 1968. An ecological interpretation of low temperature responses in *Penaeus aztecus* and P. setiferus postlarvae. Bull. Mar. Sci. 18: 61-71.

Bishop, J.M. and W.F. Herrnkind. 1976. Burying and molting of pink shrimp, *Penaeus duorarum* (Crustacea: Penaeidae), under selected photoperiods of white light and U.V. light. Biol. Bull. 150: 163-182.

Fuss, C.M., Jr. and L.H. Ogren. 1966. Factors affecting activity and burrowing habits of the pink shrimp, *Penaeus duorarum* Burkenroad. Biol. Bull. 130: 170-191.

Hughes, D.A. 1968. Factors controlling emergence of pink shrimp (*Penaeus duorarum*) from the substrate. Biol. Bull. 134: 48-59.

Kneib, R.T. 1984. Patterns of invertebrate distribution and abundance in the intertidal salt marsh: causes and questions. Estuaries 7(4A): 392-412.

Loesch, H. 1965. Distribution and growth of penaeid shrimp in Mobile Bay, Alabama. Publ. Inst. Mar. Sci., Tex. 10: 41-58.

Minello, T.J. and R.J. Zimmerman. 1983. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: the effect of simulated *Spartina* structure on predation rates. J. Exp. Mar. Biol. Ecol. 72: 211-231.

Minello, T.J. and R.J. Zimmerman. 1985. Differential selection for vegetative structure between juvenile brown shrimp (*Penaeus aztecus*) and white shrimp (*P. setiferus*), and implications in predator-prey relationships. Est. Coast. Shelf Sci. 20: 707-716.

Minello, T.J., R.J. Zimmerman, and E.X. Martinez. 1989. Mortality of young brown shrimp *Penaeus aztecus* in estuarine nurseries. Trans. Am. Fish. Soc. 118: 693-708.

Moctezuma, M.A. and B.F. Blake. 1981. Burrowing activity in *Penaeus vannamei* Boone from the Caimanero-Huizache lagoon system on the Pacific coast of Mexico. Bull. Mar. Sci. 31: 312-317.

Moller, T.H. and D.A. Jones. 1975. Locomotory rhythms and burrowing habits of *Penaeus semisulcatus* (de Hann) and *P. monodon* (Fabricus) (Crustacea: Penaeidae). J. Exp. Mar. Biol. Ecol. 18: 61-77.

Rader, D.N. 1984. Salt-marsh benthic invertebrates: small scale patterns of distribution and abundance. Estuaries 7: 413-420.

Stokes, G.M. 1974. The distribution and abundance of penaeid shrimp in the lower Laguna Madre of Texas, with a description of the live bait fishery. Coastal Fisheries Project Report, Texas Parks and Wildlife Department. Technical Series, No. 15, 32 p.

Wickham, D.A. 1967. Observations on the activity patterns in juveniles of the pink shrimp, *Penaeus duorarum.* Bull. Mar. Sci. 17: 769-786.

Wickham, D.A. and F.C. Minkler, III. 1975. Laboratory observations on daily patterns of burrowing and locomotor activity of pink shrimp, *Penaeus duorarum*, brown shrimp, *Penaeus aztecus*, and white shrimp, *Penaeus setiferus.* Contr. Mar. Sci. 19: 21-35.

Zimmerman, R.J. and T.J. Minello. 1984. Densities of *Penaeus aztecus*, *P. setiferus* and other natant macrofauna in a Texas salt marsh. Estuaries 7: 421-433.

Zimmerman, R.J., T.J. Minello, and S. Dent. (in press). Habitat-related growth and resource partitioning by penaeid shrimp in a salt marsh. Mar. Ecol. Prog. Ser.

Zimmerman, R.J., T.J. Minello, D. Smith and J. Kostera. 1989. The use of *Juncus* and *Spartina* marshes by fishery species in Lavaca Bay, Texas, with reference to effects of floods. NOAA Technical Memorandum NMFS-SEFC-251, 40p.

Zimmerman, R.J., T.J. Minello, and G. Zamora, Jr. 1984. Selection of vegetated habitat by brown shrimp, *Penaeus aztecus*, in a Galveston Bay salt marsh. Fish. Bull., U.S. 82: 325-336.