ANALYSIS OF THE LOWER DISTRIBUTIONAL LIMIT OF CALLIANASSID SHRIMP IN SOUTH SLOUGH NATIONAL ESTUARINE RESEARCH RESERVE

by

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A THESIS

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"Analysis of the Lower Distributional Limit of Callianassid shrimp in South Slough Estuarine Research Reserve," a thesis prepared by Jonathan N. Miner in partial fulfillment of the requirements for the Master of Science degree in the Department of Biology. This thesis has been approved and accepted by:

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Title: ANALYSIS OF THE LOWER DISTRIBUTIONAL LIMIT OF
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The lower distributional limits (fronts) of callianassid shrimp populations were observed at five sites in South Slough, Coos Bay estuary, Oregon. Fronts at four sites exhibited similar shoreward-seaward movements while the remaining site showed drastic population reductions. Shrimp density and body size were found to be significantly greater above than below the front. There was no consistent pattern found in grain size or interstitial water content across the front.

In a controlled predator-exclusion experiment, resulting shrimp densities were not significantly different among treatments. Front shifts showed no pattern in response to treatments. These results imply that fish predation is not responsible for front placement. Trawls taken on both sides of the front produced similar densities of a predatory fish, <u>Leptocottus</u> <u>armatus</u>. Because predation pressure was

calculated to be roughly equal above and below the front, _Leptocottus_ is not expected to be responsible for position and movements of these fronts.

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TABLE OF CONTENTS

APPENDIX

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

When observing the distributions of intertidal marine species, vertical zonation is extremely common (Lewis, 1964; Paine, 1966; Menge & Sutherland, 1976). Many experiments investigating the reasons for zonation of marine organisms have taken place in the rocky intertidal (e.g. Connell, 1961; Paine, 1974; Menge and Sutherland, 1976; Sousa, 1979). In this environment, patterns of zonation are complex owing to the differing microhabitats afforded by various substrate morphologies. Intertidal areas of estuaries and mudflats are characterized by a more homogeneous surface topography. This permits relatively easy recognition of vertical zonation.

Estuarine mudflats, while lacking in the high energy physical disturbance of a wave-beaten rocky shore, are subject to several other factors which can make them harsh environments in which to live. Salinity fluctuates greatly in these areas. Large amounts of rain can also cause salinity levels to drop significantly at low tide due to riverine input. Salinities are correspondingly high at high tide due to oceanic input. These wide shifts in salinity subject resident organisms to osmotic stresses. Long exposure times during low tide can lead to desiccation, anoxia, increased temperature, and exposure to ultraviolet light. Because few organisms possess the characteristics needed to survive in such a changeable environment, the estuarine mud flat system is inhabited by a relatively low diversity of species (Levinton, 1982). Low diversity among the estuarine species which can tolerate these conditions suggests low levels of interspecific competition for factors such as settling space. R. Black and C. Peterson (1988) showed that interference competition for space was absent between large suspension-feeding bivalves and smaller infaunal macroinvertebrates in western Australia. This was done by using 1 m^2 field enclosures with varying densities of Katelysia sp., Callista sp., Anomalocardia sp. and Circe sp. Even densities that exceeded twice ambient control levels had no significant effect on density or diversity of small bivalves, gastropods, polychaetes or amphipods. Because species in these areas experience little competition for resources, their densities become correspondingly high.

The South Slough, in Coos Bay, Oregon is a good example of the estuarine mud flat systems common on the west coast of the United States. Along with being a habitat for a rich assemblage of bird and terrestrial species, South Slough also supports several infaunal species. These are mainly dominated by bivalves such as Macoma nasuta and Clinocardium nuttallii and polychaetes such as Eteone pacifica and Hesperonoe complanata. Epibenthic species such as Pugettia producta and Cancer magister are also common. Abundant among infaunal species are the ghost shrimp, Callianassa californiensis and C. gigas. Ghost shrimp play a major role in the ecology of the slough due to their burrowing behavior. Being deposit feeders, they construct extensive, interconnecting burrow systems. This intense burrowing activity effectively aerates the soil. Because they are detritovores they rework the sediment as they feed. They have the added effect of increasing the water content of the sediment, and thereby facilitating flushing of the substrate as the tide rises and falls. Ghost shrimp are exploited by man for use as fishing bait, and are viewed as pests by local oyster farmers due to their behavior of resuspending large amounts of sediment into the water column.

The distributions of the ghost shrimps Callianassa californiensis and C. gigas display distinct vertical zonation and density patterns in the coastal estuaries of the Pacific Northwest. Callianassa are found in dense aggregations, or "beds", of up to 500 individuals/m^2 in these intertidal mud flats (Posey, 1985). An abrupt, distinct interface, or "front" is formed in the mid-intertidal below which few Callianassa are found (Thompson and Pritchard, 1969; McCrow, 1971; Swinbanks and Murray, 1981; personal observation). This front is not static, but moves shoreward or seaward 1-10 m during the year (C. Hewitt & M. Posey, personal communication). The factors which maintain this front and cause its movement over time are not well understood.

Previous studies of soft-sediment communities have hypothesized that physical factors such as sediment grain size or current regimes are responsible for determining the lower distributional limit of intertidal populations (Weiser, 1959; Johnson, 1970; Longbottom, 1970; Vassalo, 1971; Grant, 1981; Willason, 1981). Eckman (1983) offered that current regimes through their influence upon larval settlement could be important in determining distribution. Swinbanks (1982) suggested that the lower limit of some plant species is a response to areas of rapid change in submergence time. Thompson and Pritchard (1969) hypothesized that distribution of Callianassa might be determined by interstitial salinity preference.

Among the possible biological factors which might limit lower-end distributions, interspecific competition is the most common. Levin (1981) observed that the polychaete Pseudopolydora sp. aggressively excludes Streblospio sp. in the laboratory. Similar behavior has been observed in intertidal mud snails (Hydrobiidae) by Fenchel (1975, 1977). McCrow (1971) suggested that the lower distribution of ghost shrimp may be determined competition with the burrowing mud shrimp Upogebia pugettensis.

Callianassa sp. have been found in the guts of leopard sharks, dungeness crabs, and Western gulls (Russo, 1975;

Stevens et al., 1982). Posey (1985) identified the staghorn sculpin _Leptocottus armatus_ as a major predator of _Callianassa_ sp. in South Slough and hypothesized that it could play a major role in determining the shrimp's lower distribution. Like many intertidal species, it is generally regarded that the upper maxima of these beds are determined physically by excessive exposure time and desiccation. Similarly, the lower distribution may be determined biologically by the predatory effect of _Leptocottus_ (e.g. Posey, 1985).

The staghorn sculpin is a euryhaline benthic predator which spends a great deal of time in the open water, but feeds in the estuarine intertidal during night high tides (Jones, 1962). When the tide rises, _Leptocottus_ has a greater area over which to feed. As the tide falls, the sculpin returns to deeper water to avoid both the threat of being trapped on the mudflats and exposure to it's avian predators such as the Great Blue Heron (_Ardea herodias_) and the Great Egret (_Casmeroidius albus)_.

Objectives

The purpose of the following study was 1) to monitor the direction and magnitude of the movement of the front found at the lower (seaward) edge of several populations of _Callianassa_ in South Slough, 2) to physically and biologically describe the front and 3) to test the hypothesis that the placement of the front may be determined biologically by the predatory effect of Leptocottus armatus.

Study Area

Five study sites were established in the South Slough arm of the Coos Bay estuary in Coos Bay, Oregon (43°N LAT, 124°W LONG) and were examined from July, 1992 to October, 1993. These sites were selected based on the presence of a distinct interface separating the presence or absence of populations of the Thalassinid shrimp, Callianassa californiensis. Four sites were established within the South Slough National Estuarine Research Reserve (SSNERR) and one in the Joe Ney Slough (see Figure 1). South Slough contains 770 acres of tidelands and the entire drainage basin encompasses 18,370.3 acres (S. Rumrill, personal communication). South Slough joins the Coos Bay estuary 1.6 km east of the mouth of the Bay, and is therefore part of the marine subsystem of the Coos Bay estuary. Site 1 was located at Ferrei Head, site 2 at Long Island Point, site 3 on Senstaken Arm, site 4 on the eastern shore of Valino Island, and site 5 approximately 1 km up Joe Ney Slough beyond it's confluence with the main channel of South Slough. These sites experience a broad range of air temperature (ca. 5°C in winter to 30°C in summer) and a more limited range of water temperatures (10°C in winter to 20°C

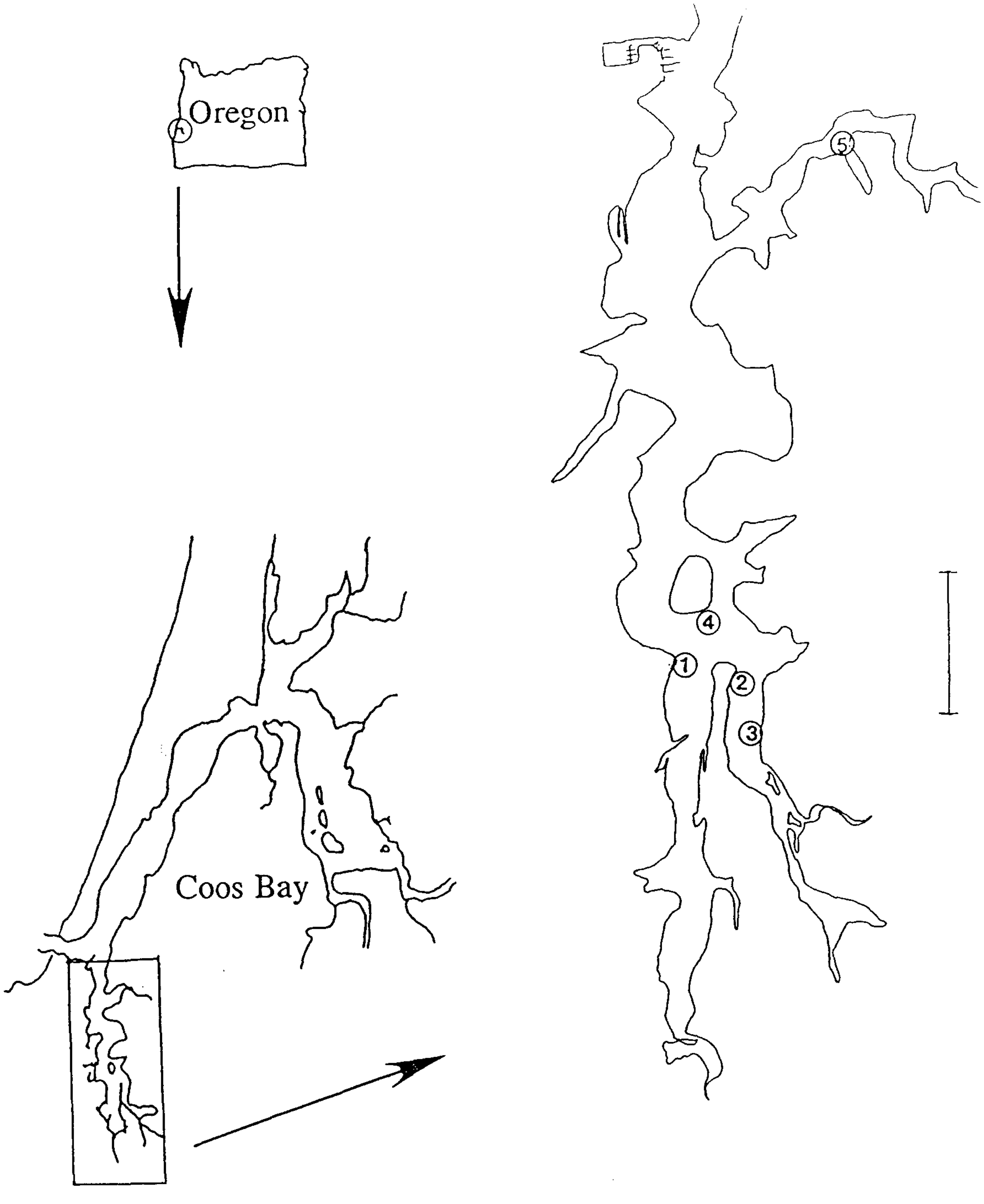


Figure 1. Study sites within South Slough and Joe Ney Slough. 1: Ferrei Head; 2: Long Island Point; 3: Senstaken Arm; 4: Valino Island; 5: Joe Ney Slough. Scale bar represents one kilometer.

in summer (Posey, 1985)). Salinity fluctuates seasonally as a result of precipitation, the majority of which falls between November and May. Salinity at Long Island Point varies between 34 ppt in summer to 17 ppt in winter (S. Rumrill, pers. com.). The year of this study exhibited above average rainfall. Rainfall from September 1992 to September 1993 was 75.45 in. Mean yearly rainfall 1945-1985 was 63.41 in. (North Bend Weather Service, 1993).

CHAPTER II

MATERIALS AND METHODS

Front Movement

The interface between dense shrimp beds located higher in the intertidal and the absence of these populations lower in the intertidal (e.g. the lower end of shrimp bed distribution) was marked with 5 ft long wooden stakes driven 3 ft into the sediment at sites 1, 2 and 3 in July 1992. As at all other sites, the front at site 1 (Ferrei Head) measured greater than 150 m, however only 144 m were marked (12 stakes placed at 12 m intervals). Sites 2 and 3 were each marked along 42 m (7 stakes placed at 6 m intervals). In August 1992, sites 4 and 5 were selected and each marked with 9 stakes. At site 4 stakes were placed at 6 m intervals (54 m total) while site 5 stakes were placed at 10 m intervals (90 m total). At each site, stakes were placed along existing fronts, which were not necessarily straight lines.

Fronts were identified by visual as well as physical inspection. On-site observations of these beds revealed denser aggregations of mound-shaped burrows than seen in surrounding areas. The lower edge of these beds can easily be located by walking in the area. As one passes from outside a bed to inside, the relative firmness of the sediment decreases markedly, taking on a quicksand-like quality. Using this simple measure, the placement of the front can be identified to within 10-20 cm.

The movement of the front was measured at two month intervals between summer 1992 and fall 1993. A tape measure was attached to each stake, and the distance from the stake to the front was measured perpendicular to the original line of stakes. In order to minimize trampling of the shrimp burrows, the stakes were always approached from downshore and perpendicular to the shrimp interface.

In order to investigate a correlation between front placement and submergence/exposure time, intertidal height surveys were carried out at sites 3 (Senstaken arm) and 4 (Valino Island) to determine if the height of the original fronts were coincident across sites. This was done using standard surveying techniques, and measurements were related back to benchmarks of known height within SSNERR. These benchmarks had in turn been related back to a National Geodetic Survey stake of known height at the Coast Guard station in Charleston.

Density Cores

In order to acquire a numerical basis for population changes across the front, ghost shrimp densities were assessed at sites 1 (Ferrei head) and 4 (Valino island) with benthic box cores (25 cm X 25 cm X 40 cm deep) in September 1992 and April 1993. Three 30 m transect lines were established perpendicular to the staked front (15 m above and 15 m below) at equidistant intervals along the staked region of the front (See Figure 2).

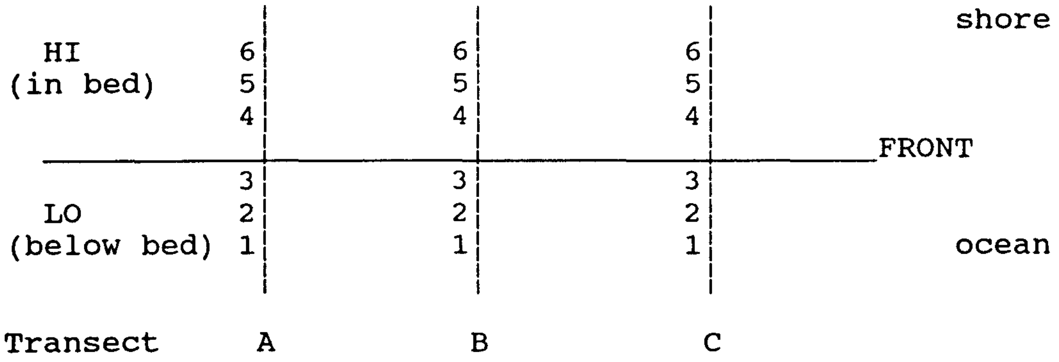


Figure 2. Schematic of distribution of density box cores at Sites 1 and 4. Numbers 1-6 refer to sampling locations along each transect (A-C).

Box cores were taken at 5 m intervals along each transect with 3 cores located above the front (inside the Callianassa bed) and 3 cores were below the front (outside the bed). The number of burrow openings in the sampling area was recorded before each core was excavated. The sediment removed from the cores was sieved through 3 mm mesh in the field and all thalassinid shrimp (whole or in part) were collected, identified and measured. Three morphometric measurements of length were collected; i) eyestalks to telson, ii) cephalothorax length, and iii) abdomen length. For population census purposes, the number of abdomens were counted, while chelae and cephalothoraxes were ignored.

The sampling process had a tendency to dismember about 10.6% of the population, almost exclusively along the abdomen/cephalothorax axis. Cephalothoraxes were therefore discounted and lengths of dismembered abdomens were used to estimate total body lengths based on a regression of total body length on abdomen length. Dismembered chelipeds were also discounted. Population densities, size of ghost shrimp, and size distributions were then determined for areas above and below the front.

Sediment Analysis

In order to determine if sediment grain size distributions were different above versus below the front, sediment samples were taken from three sites. Sediment was collected with a corer fashioned from a 60 cc syringe cores (3.8 cm diam X 8.5 cm deep). The cores were collected in July 1992, at sites 1, 3 and 4. In October 1992, a 6.5 cm diam x 7.5 cm deep cylindrical core was taken at the surface and at 40 cm depth at the same sites. Three pairs of cores were taken along the front, one core 5 m above the front (inside bed) and one core 5 m below the front (outside bed, see Figure 3).

The sediment was oven dried for at least 48 hours at

30°C, gently mortared to break up aggregations and sieved for 30 min. Sieve fractions of 595μm, 417μm, 375μm, 250μm and 125μm were measured to the nearest 0.01 g. Chi-square tests of independence were used to compare sediment grain size distributions above and below the front for surface and subsurface cores.

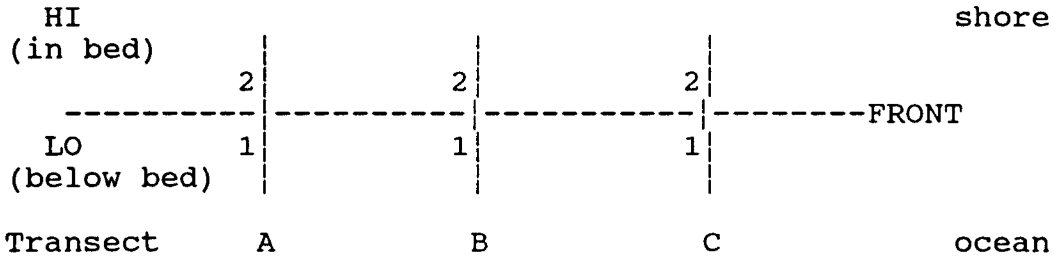


Figure 3. Schematic of distribution of porosity and sediment cores at Sites 1, 3 and 4. Numbers 1-2 refer to sampling locations along each transect (A-C). Shallow and deep sediment cores were taken at each location.

Porosity Cores

In addition to the sediment cores described above, porosity cores were also extracted from six stations at each of sites 1, 3 and 4. Sediment was extracted with a corer fashioned from a 50 cc syringe (3.8 cm x 8 cm). Three pairs of cores were taken along the front, one core 5 m above the front (inside bed) and one core 5 m below the front (outside bed) along each of three transects (See Figure 3). Cores were placed in air-tight bags immediately after extraction and returned to the lab. Samples were then weighed, oven dried at 104°F for 24 hours and reweighed. The difference in the two weights was taken to be the water content.

Sediment Height

To determine changes in sediment height, a grid pattern of stakes was deployed at site 1 in February 1993 and monitored monthly until September, 1993. 25 stakes were placed in a 5 x 5 pattern with 8 meters separating each row of stakes and 24 meters separating each column (see Figure 4). The grid was placed in such a way as to straddle the front so that as the front progressed it would "pass over" several stakes. The level of the sediment at the time of deployment was marked on each stake so as to observe any change in sediment height. Stakes were wooden, four feet long, and were driven three feet into the sediment. Sediment height was then measured monthly, and all variations were recorded.

Caging Experiment

In order to examine the role of fish as predators, an experimental study employing exclusion cages was conducted at site 1. Treatments consisting of full cages, partial cages and undisturbed open plots. All treatments were set in place in February, 1993. Full cages consisted of a wood frame measuring 1.8 x 3.6 x 0.3 m covered on top and all

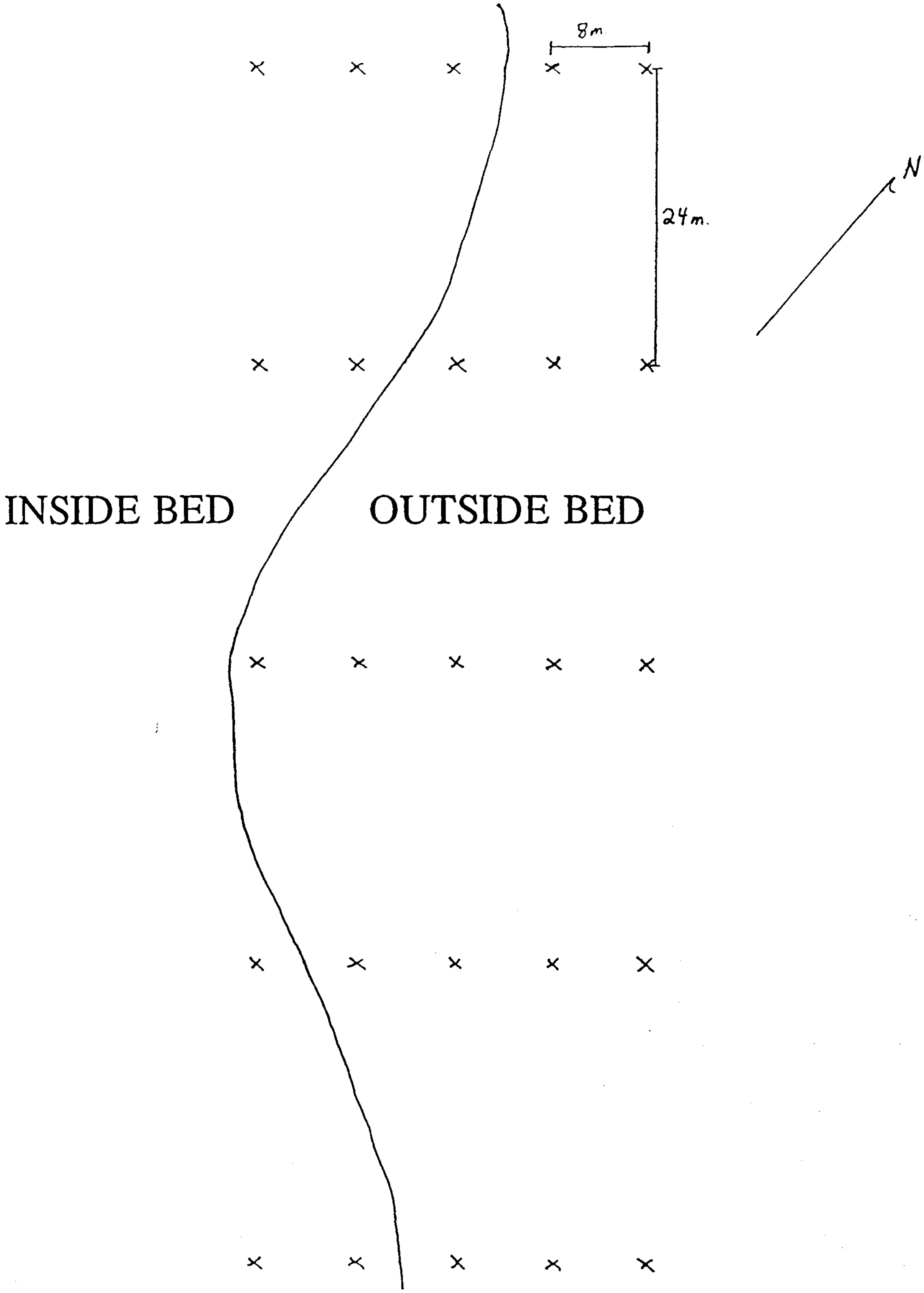


Figure 4. Distribution of sediment height stakes at Site 1. Front position shown corresponds to location at beginning of experiment (2-5-93).

sides with Vexar(tm) plastic 1.3 cm mesh. Three of these cages were placed randomly along the front, and oriented so that half the length of the cage extended above the front and half below (see Figure 5).

Placing cages in the intertidal causes a decrease in current velocity and an increase in sedimentation. Because Callianassa is a detritovore, controls were needed. To accomplish this, partial cages consisting of a top and two sides were placed randomly along the front. In this way, sedimentation changes would still occur while leaving the shrimp open to predation. In addition, three unmanipulated controls were staked out. All random placements were determined through the use of a random number table. Cages remained in the field for 4.5 months and were sampled in early July, 1993. At sampling, each apparatus was removed and six box cores were taken inside the treatment area, three above and three below the location of the front. Recovered sediments were collected and processed in the manner described earlier. Dismembered cephalothoraxes were discarded, while abdomens were measured and used to calculate full body sizes using the regression equation obtained from the density core data. Changes in the position of the front were also recorded by measuring the distance between three equidistant points on the center of each treatment/control and the front.

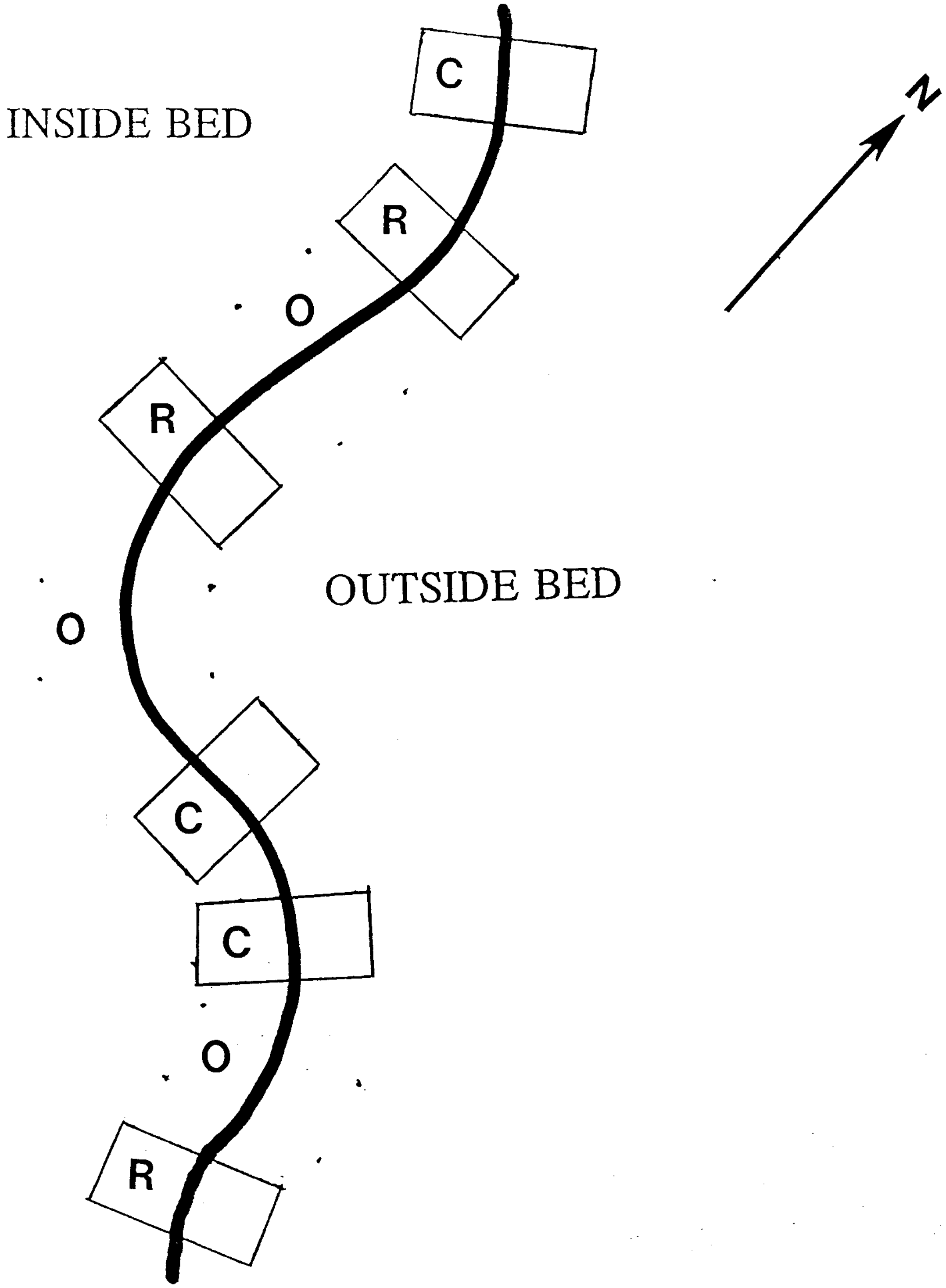


Figure 5. Distribution of cages (C), roofs (R) and open controls (O) at Site 1 (Ferrei Head).

Sculpin Censusing

Sculpins were sampled above and below the front to determine the relative amounts of predation pressure. A small otter trawl (3 m gape, 2 cm mesh) on a 14 m line was used to determine the abundance of sculpins located inside and outside of the existing shrimp bed at sites 1 and 4. Trawls were carried out over a distance of approximately 300 m during evening and night high tides. Two trawls were carried out above and two below the front at each series. A test series of daytime trawls produced no fauna of any kind and was therefore discounted from calculations. Recovered sculpins were placed in seawater and taken back to the lab for morphometric measurements and gut content analysis. All other recovered organisms were removed from the trawl and returned to the water. Guts were examined for the presence or absence of shrimp.

CHAPTER III

RESULTS

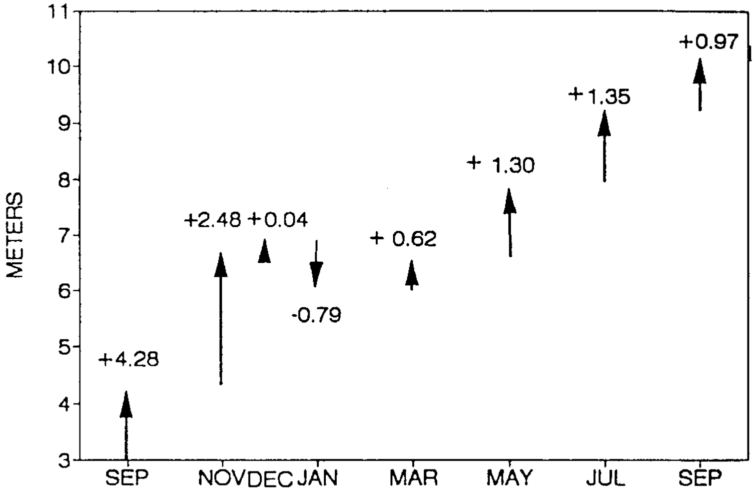
Front Movement

All sites showed similar front movement except site 2 (Long Island Point). Three months after this site was established, the front showed a major regression upshore associated with the disappearance of the bed altogether. Monitoring of this site continued bimonthly for the remainder of the project (11 months) but the shrimp bed never reappeared. At all other sites the front moved up the beach from the original summer 1992 positions (see Figure 6). Complete front movement data is listed in Appendix 1. In all cases, fronts moved up the shore until late December, at which time they started to recede seaward. They continued to move in this direction into spring, at which time all sites reversed and started a constant, uninterrupted climb up the beach, surpassing the peak heights of December. When front measurements were discontinued in fall 1993, the mean locations of each of the four fronts were higher up the beach than on any previous sample dates during the duration of this study.

Site 1 measurements rose to a peak in December 1992 of 6.80 m above the original stakes. Measurements then fell

Figure 6. Front shifts at sites 1, 3, 4 and 5. Arrows and numbers indicate mean distance travelled by the front since the previous measurement. Y-axis values represent the distance upshore from original location of front staked in July 1992 for sites 1 and 3 and August 1992 for sites 4 and 5.

SITE 1



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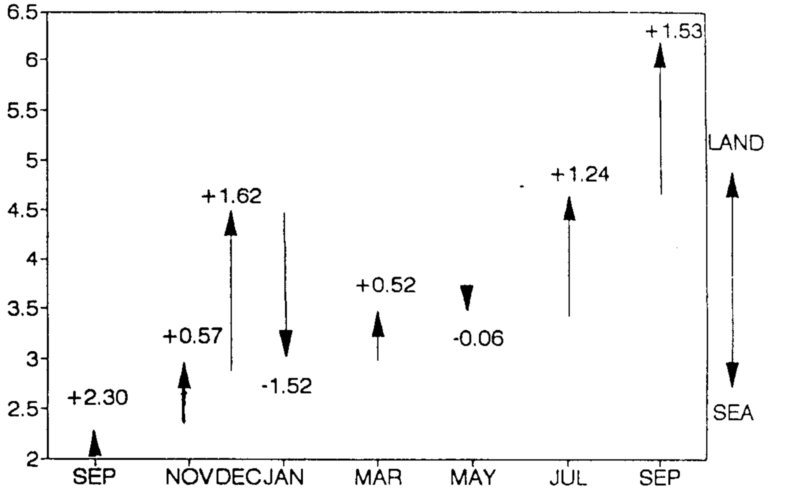
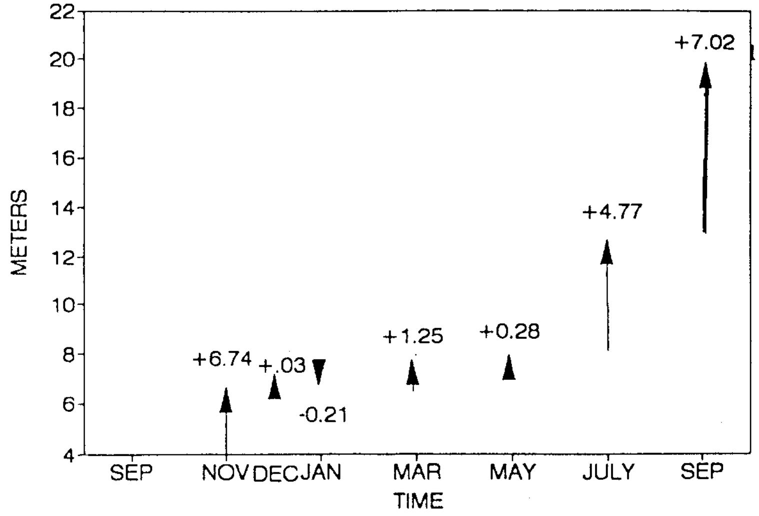
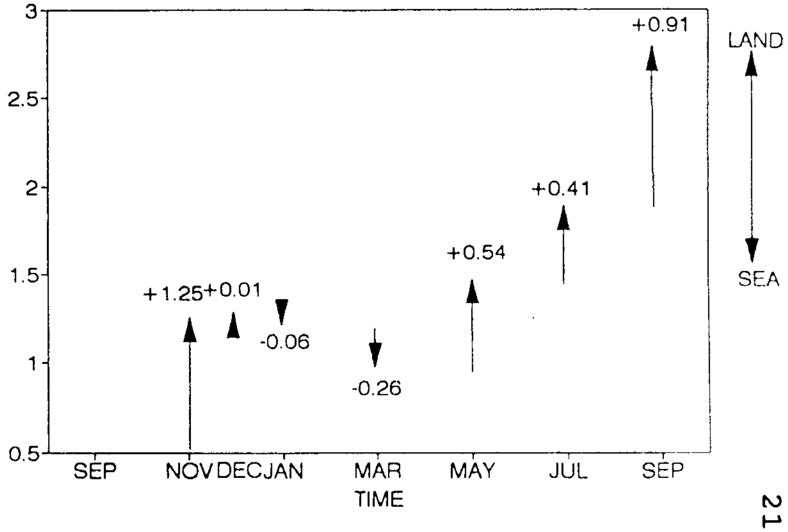


SITE 4



SITE 5



slightly to a low of 5.97 m in January 1993 and rose to a peak of 10.2 m in September 1993. Site 3 measurements rose to a December peak of 4.48 m, fell to a low in January of 2.97 m, and once again rose to a peak in September of 6.2 m. Site 4 also peaked in December at 6.76 m, a low was reached in January at 6.54 m, and a peak in September of 19.8 m. Finally, site 5 reached a peak of 1.27 m in December, a low of 0.94 m in March, and a peak of 2.8 m in September.

Tidal height surveys at sites 3 and 4 showed that the height of the front-delineating stakes at these two sites were similar. Mean height of the stakes at site 3 (± std. err.) was 0.06 m (±0.02) above MLLW (see Appendix B). Mean height of stakes at site 4 was 0.12 m (±0.04) above MLLW. Mean height of the fronts was not significantly different between sites 3 and 4 (t-test, t=2.15, DF=9, p=0.06).

Density Cores

In fall, density cores at site 1 showed mean densities (±1 std. err.) of 8.9 (±1.6) individuals per core (1/16 m^2) above the front and 4.3 (±1.6) individuals per core below the front. Site 4 cores showed mean densities of 9.4 (±1.9) individuals per core above the front and 0.4 (±0.2) individuals per core below the front. Two-way analysis of variance using height and site as factors showed the difference in density to be statistically significant for height on shore but not for site (see Table 1). There was

Table 1. Density of shrimp recovered and two-way ANOVAs for box cores taken in fall, 1992 and spring, 1993 at sites 1 and 4. Dotted line represents the position of the front.

FALL:

	Site 1			Site 4		
Transect	A	B	C	A	B	C
	6	4	6	8	13	2
Above	9	11	12	8	9	12
	8	3	19	13	1	19
	4	9	14	1	1	0
Below	0	1	7	0	1	0
	0	2	1	0	0	0

SPRING:

	Site 1			Site 4		
Transect	A	B	C	A	B	C
	8	13	5	1	4	10
Above	4	8	9	8	6	4
	7	6	9	8	10	12
	8	5	6	0	0	1
Below	0	4	4	0	0	0
	2	0	8	0	0	0

Statistics:

Fall 2-Way ANOVA for density:

Source	DF	SS	MS	F	P
site	1	21.78	21.78	1.10	0.303
ht	1	413.44	413.44	20.81	0.000
site*ht	1	49.00	49.00	2.47	0.126
Error	32	635.78	19.87		
Total	35	1120.00			

Spring 2-Way ANOVA for density:

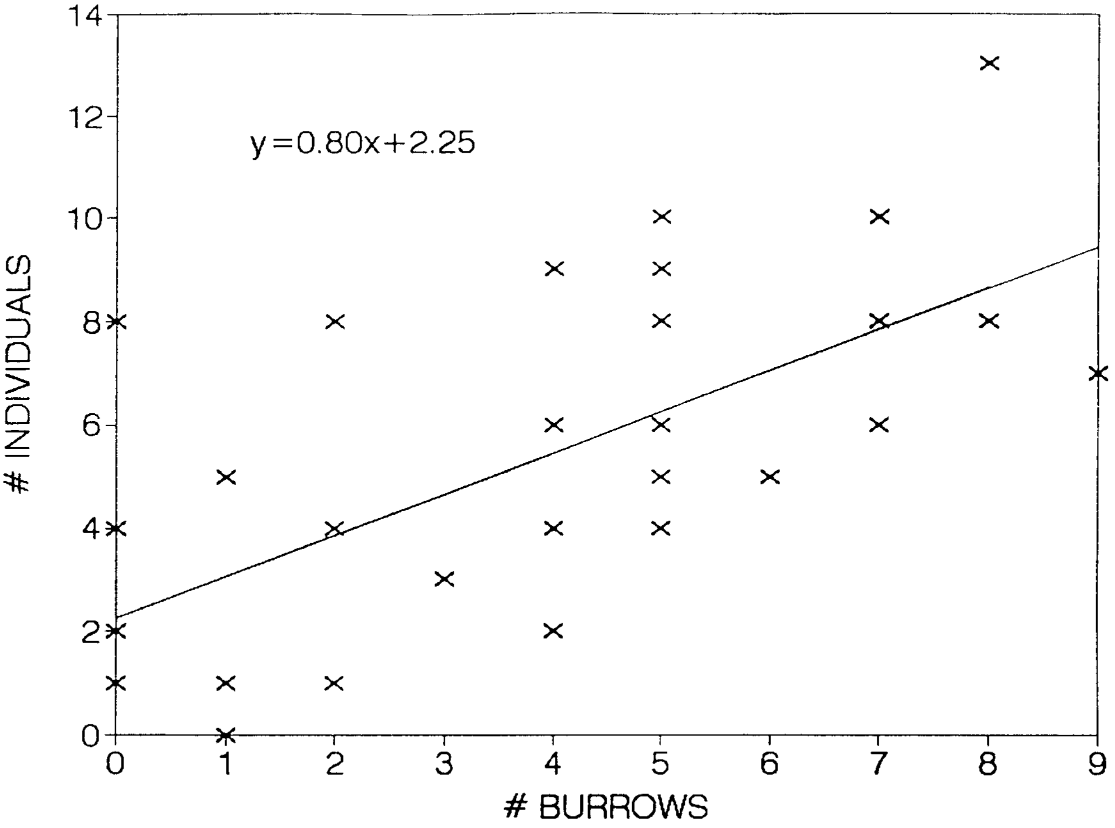
Source	DF	SS	MS	F	P
site	1	75.111	75.111	10.99	0.002
ht	1	196.000	196.000	28.68	0.000
site*ht	1	11.111	11.111	1.63	0.211
Error	32	218.667	6.833		
Total	35	500.889			

also no significant interaction between site and height (Table 1). A two-way ANOVA on spring cores showed the difference in density to be statistically significant for both height on shore and site but not for the site-height interaction ($p=0.21$, see Table 1).

Regression analysis of burrow number as a predictor of density produced $r^2=0.42$ (see Figure 7). The mean burrow number per core is given in Figure 8 for spring cores at sites 1 and 4. Because worm burrows were scored as shrimp burrows during the fall sampling period, this data was discarded.

Body Size

Regression analysis of intact individuals showed a stronger relationship between abdomen length and total length ($r^2=0.97$, see Figure 9) than between cephalothorax length and total length ($r^2=0.84$). For this reason, abdomen lengths were used to estimate total body sizes. An analysis of sizes of animals above the front was conducted by measuring total lengths and estimating total lengths of dismembered animals from abdomen lengths. Because densities below the front were low, individuals were pooled between both sites for body size analysis. Mean total body size for fall samples (±1 std. error) was 4.5 cm (±0.1) above the front and 2.6 cm (±0.2) below the front. This difference was shown to be significant using a standard T-test (observed



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                   Regression Output:
Constant                                       2.25
Std Err of Y Est                               2.58
R Squared                                      0.42
No. of Observations                              32
Degrees of Freedom                               30

X Coefficient(s)          0.8
Std Err of Coef.         0.17
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Figure 7. Plot of regression output of surface burrow number to individual number from spring box cores taken at sites 1 and 4.

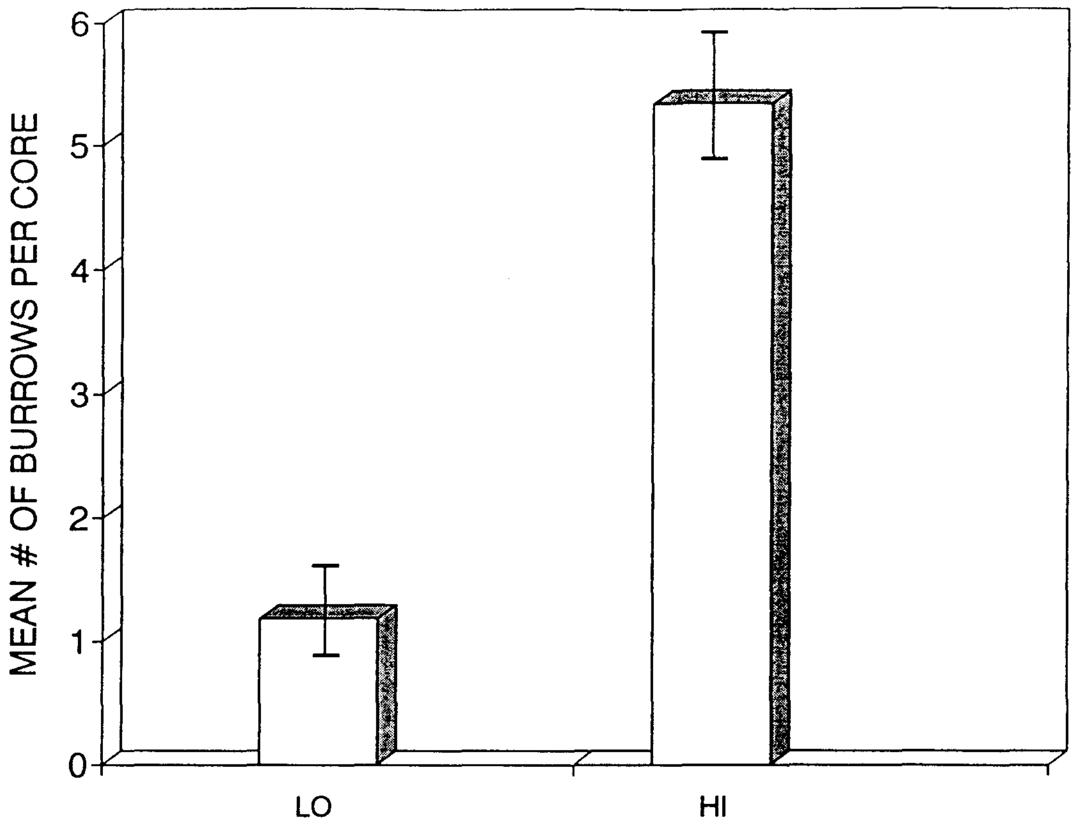
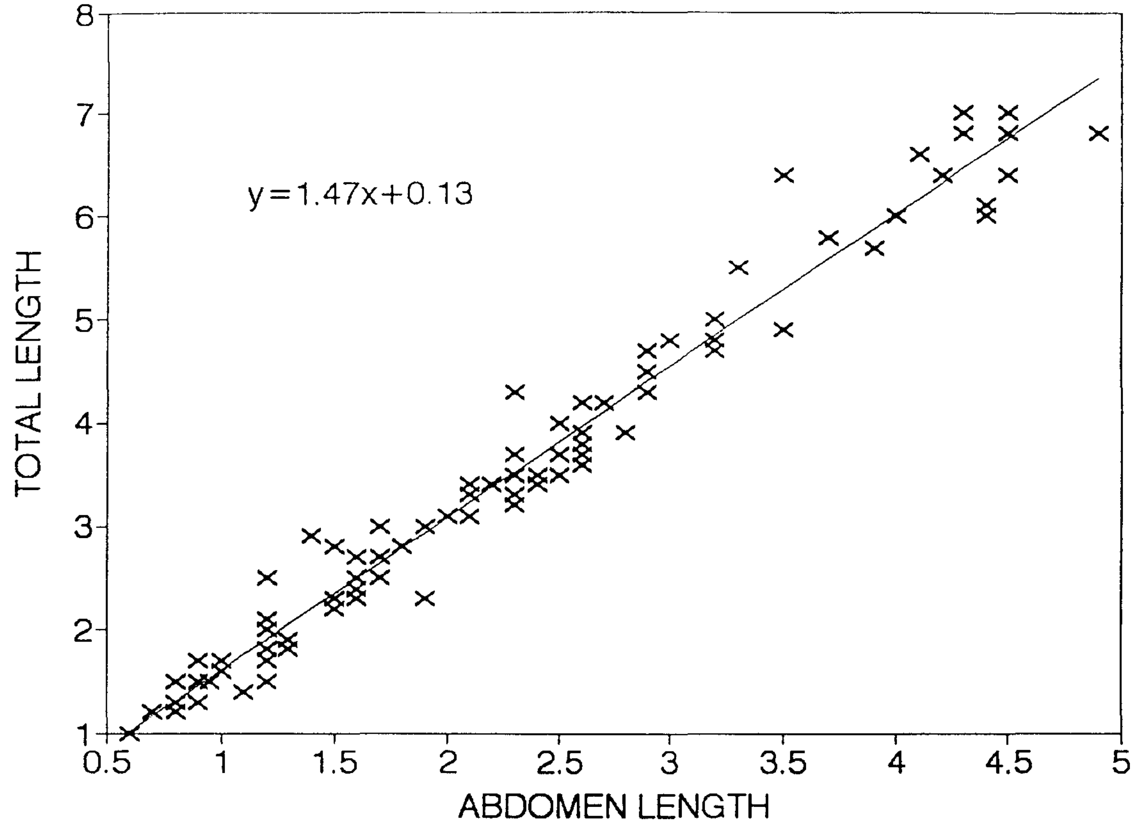


Figure 8. Mean burrow number per core (#/0.063m²) above(HI) vs. below(LO) the front. Data is pooled from spring cores at sites 1 and 4. Error bars represent standard error.



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Constant                              0.13
Std Err of Y Est                      0.29
R Squared                             0.97
No. of Observations                     94
Degrees of Freedom                      92

X Coefficient(s)       1.47
Std Err of Coef.       0.03
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Figure 9. Plot of regression output of abdomen length to total length of <u>Callianassa</u> from individuals taken from fall box cores at site 1.

t=-10.27, DF=101, p<0.001). Mean total body size for spring samples (±1 std. error) was 4.4 cm (±0.2) above the front and 2.0 cm (±0.1) below the front. This difference was also shown to be significant (t-test, t=-10.64, DF=137, p<0.001).

Sediment Analysis

Sediment grain size distributions did not show a discernible pattern. Chi-square analysis indicated a rejection of the null hypothesis (at p=0.05) in 14 out of the 18 samples taken (78%, see Table 2). Half of these samples (7) produced larger grain sizes above the front while half (7) showed larger grain sizes below the front. These differences are noted in Table 2. Grain size distributions are illustrated in Figures 10-12 for sites 1, 3 and 4.

Analysis of sediment samples at site 1 using the chi-square test showed a rejection of the null hypothesis in all cases. Four samples showed larger grain size below the front. These samples were trans A shallow and deep, trans B shallow and trans C deep. The remaining two samples showed larger grains above the front. Site 1 samples showed a high proportion of sediment in the 250μ and 375μ size fractions in four out of the six samples taken. These samples were: trans B shallow, trans B deep, trans C shallow and trans C deep (see Figure 10). A point of note is the fact that the

Table 2. Chi-square test results for sediment grain size distributions at Sites 1, 3 and 4. Transects: A, B, C. Heights on shore: low(1), high(2). Depths: surface(S), 40cm below surface(D). Accept and reject refer to the null hypothesis of no difference in sediment grain sizes at p=0.05.

Surface	X^2 value	40cm Depth	X^2 value
	SITE 1		
A1S vs. A2S	175.27 (reject)	A1D vs. A2D	17.73 (reject)
B1S vs. B2S	63.06 (reject)	B1D vs. B2D	73.12 (reject)
C1S vs. C2S	134.23 (reject)	C1D vs. C2D	157.47 (reject)
	SITE 3		
A1S vs. A2S	214.66 (reject)	A1D vs. A2D	9.62 (accept)
B1S vs. B2S	11.8 (reject)	B1D vs. B2D	171.69 (reject)
C1S vs. C2S	4.54 (accept)	C1D vs. C2D	183.68 (reject)
	SITE 4		
A1S vs. A2S	46.61 (reject)	A1D vs. A2D	110.31 (reject)
B1S vs. B2S	4.17 (accept)	B1D vs. B2D	27.65 (reject)
C1S vs. C2S	164.04 (reject)	C1D vs. C2D	7.77 (accept)

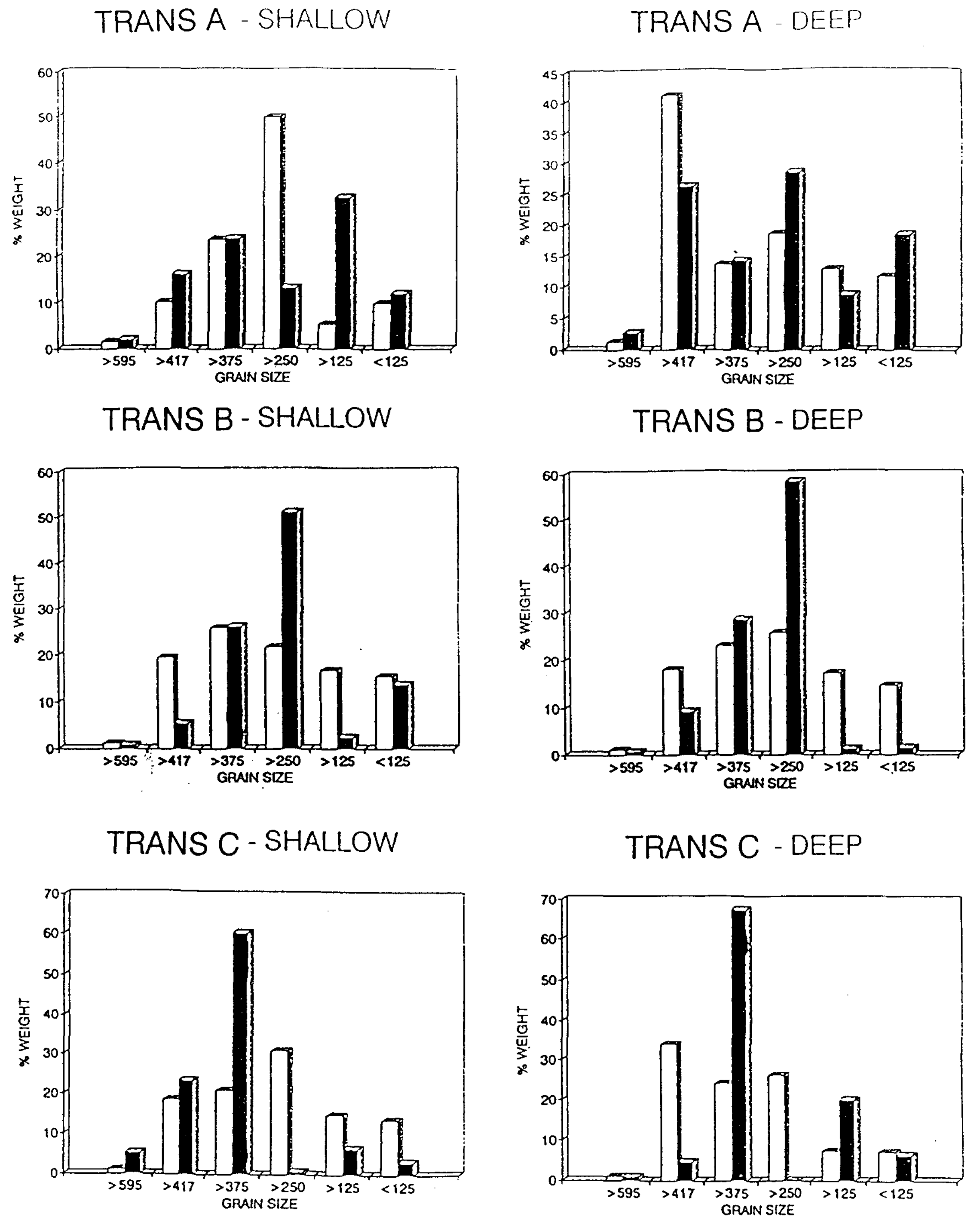

Figure 10. Sediment grain size distributions for Site 1. Empty bars represent samples below the front, filled bars represent samples above the front. Shallow indicates surface samples, deep indicates samples from 40 cm depth.

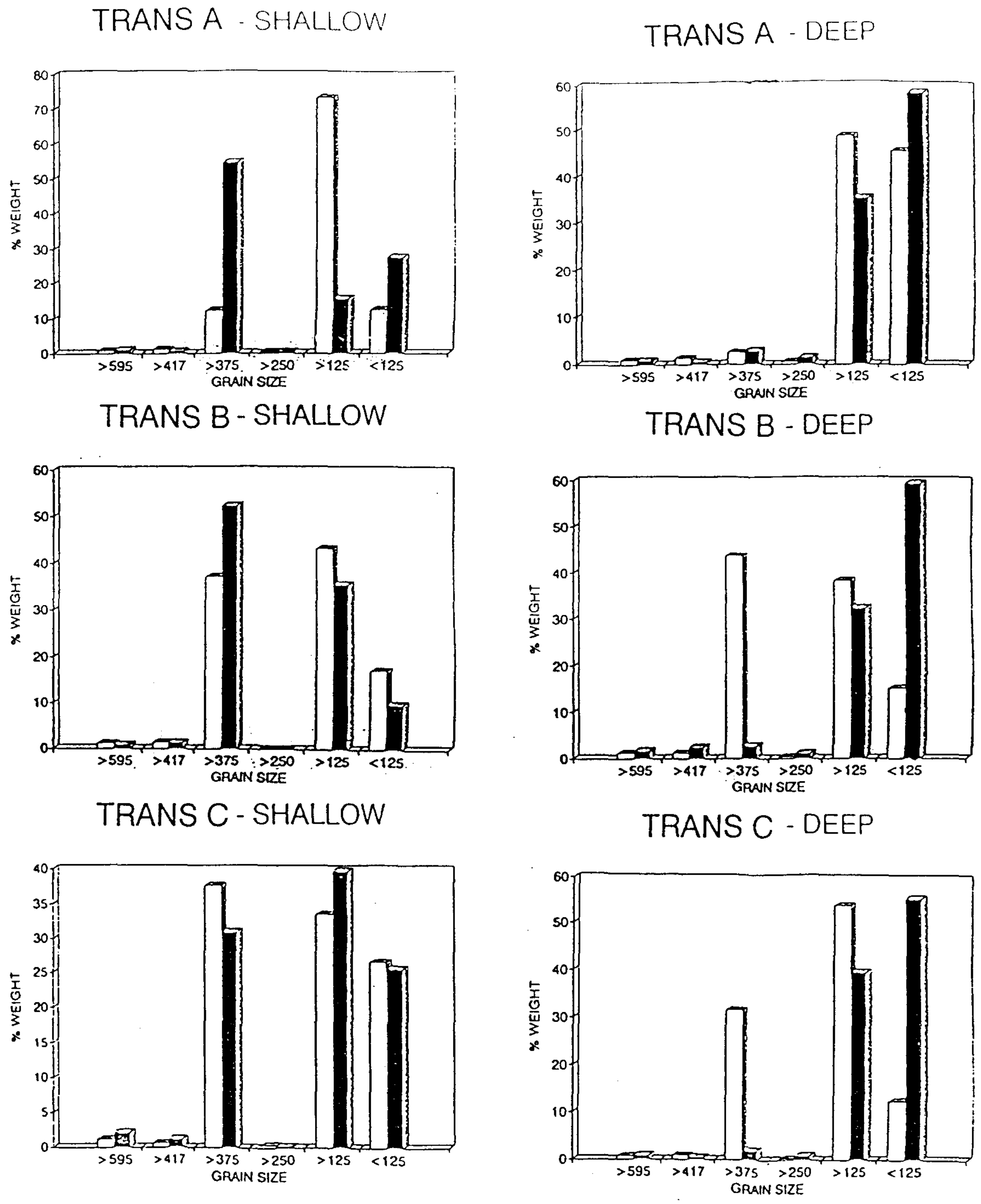

Figure 11. Sediment grain size distributions for Site 3. Empty bars represent samples below the front, filled bars represent samples above the front. Shallow indicates surface samples, deep indicates samples from 40 cm depth.

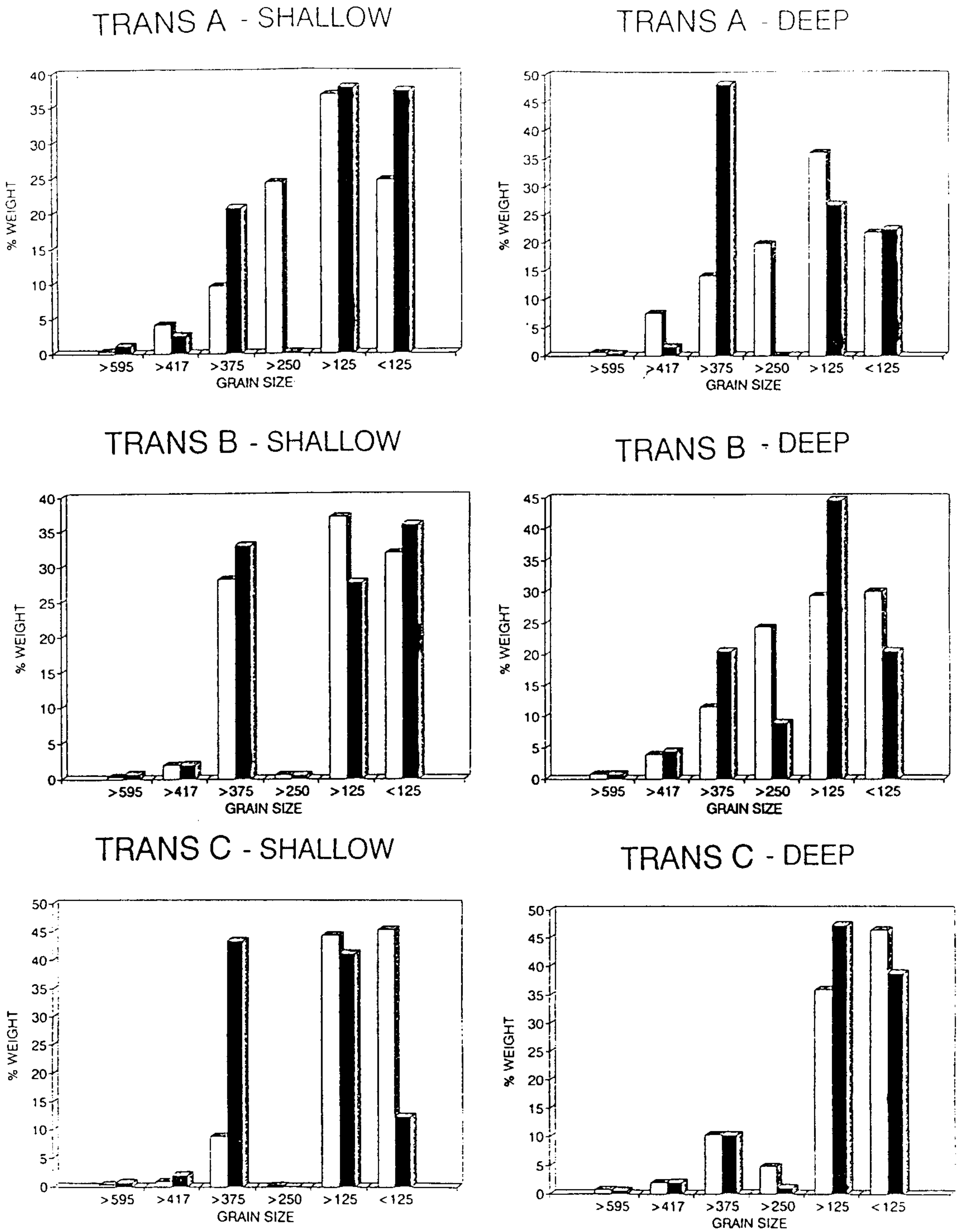

Figure 12. Sediment grain size distributions for site 4. Empty bars represent samples below the front, filled bars represent samples above the front. Shallow indicates surface samples, deep indicates samples from 40 cm depth.

250μ size fraction plays a dominant role in site 1 distributions. This size fraction is consistently smaller in samples taken from sites 3 and 4.

For site 3, chi-square analysis of sediment size distributions showed rejection of the null hypothesis in four out of six samples taken. Two samples showed larger grain size above the front. These were trans A and B shallow. Samples B and C deep showed larger grain size below the front. All samples were deficient in the 250μ size fraction. There was a trend toward high proportions of the 375μ and 125μ size fractions in five out of six samples from below the front. Above-front samples expressed this tendency to a lesser degree.

Site 4 data showed a rejection of the null hypothesis in four out of six cases. All of these four comparisons showed varying tendencies toward larger grain size above the front than below the front. All above-front samples showed a tendency towards sorting grain size into high percentages of 375μ and 125μ and low percentages of 250μ. Samples taken below the front did not produce this result as often.

Porosity Cores

Means water content (±std. errors) was taken above and below the front at sites 1, 3 and 4. The mean water content of the low and high cores at site 1 were 30.7% (±0.6) and 23.7% (±6.7) respectively (See Figure 13). A two-sample t-

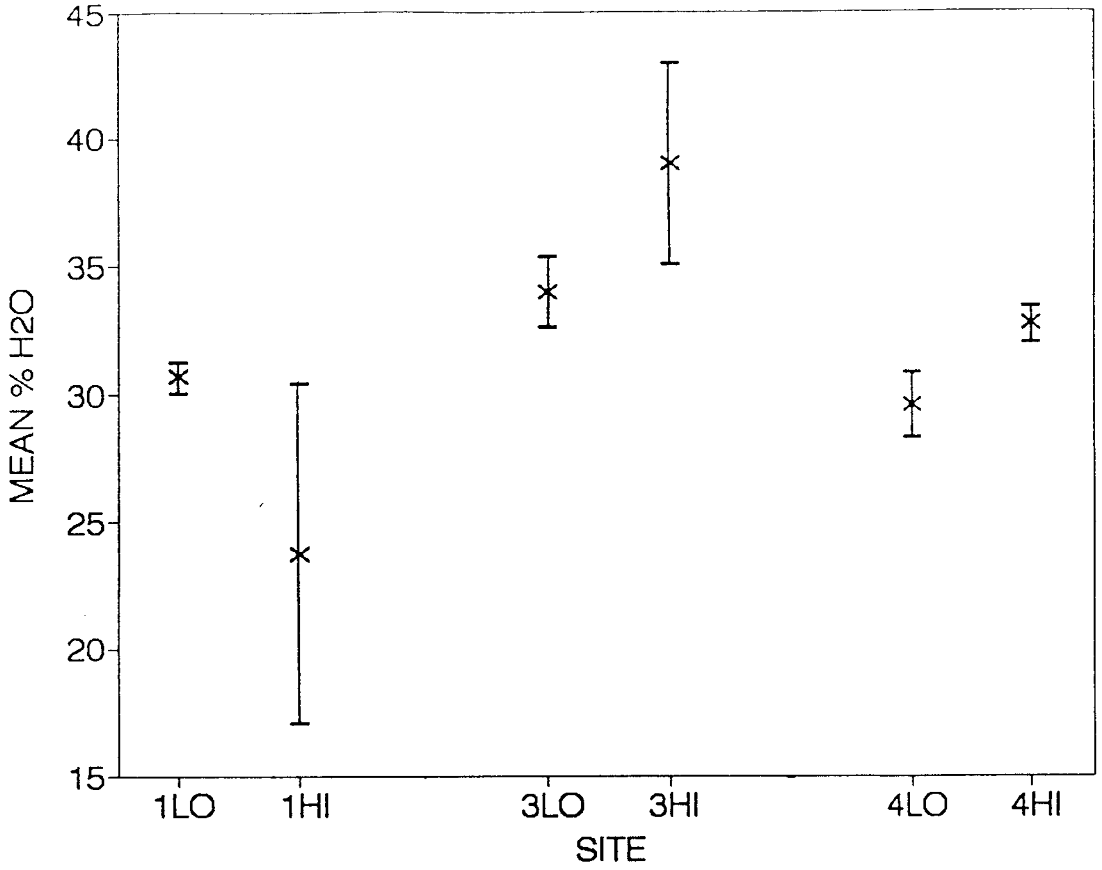

Figure 13. Porosity measurements taken at Sites 1, 3 and 4 above(HI) and below(LO) the front. Bars represent standard error around the mean.

test showed this difference to be insignificant (observed t=1.04, DF=2, p=0.41) Means for low and high at site 3 were 34.0% (±1.4) and 39.0% (±4.0) respectively. A two-sample t-test also showed this difference to be insignificant (observed t=-1.19, DF=2, p=0.36). Site 4 means were 29.5% (±1.3) and 32.7% (±0.7) for high and low respectively. This was also shown to be insignificant with a two-sample t-test (observed t=-2.16, DF=3, p=0.12).

Sediment Height

Complete sediment height data is given in Appendix C. As the tidal currents passed over the stakes of the sediment grid, scouring caused small depressions to be formed in the mud around the base of each stake. Because of this, measurement of the height of the sediment was made on sediments just outside the scoured regions. These measurements were approximate, and because of the nature of this measurement system, human error became a rather significant factor. I estimated my measurement error to be ± 1 cm. This error proved significant for virtually all measurements taken below the front. Sediment heights above versus below the front at the end of the study were compared to those at the beginning of the study (a seven month interval) through the use of a two-sample t-test. Mean sediment levels were found to be lower both above and below the front than levels at the outset of the experiment. The mean shift above the front (±std. error) was 2.25 cm (±0.59). Mean height shift (±std. error) below the front was 0.12 cm (±0.08). This mean falls within my measurement error. T-test analysis showed changes in sediment height above the front to be significantly different than changes below the front (observed t=-3.58, DF=7, p=0.01).

The movement of the front was shoreward throughout this experiment. Stakes above the front registered slight declines in sediment height. Sharp declines were recorded when the front actually traversed a stake.

Caging Experiment

The mean and standard error for the six density cores taken in each treatment are given in Figure 14. Full cage treatments produced densities lower than open plots and lower than open or roof plots in 2 out of 3 cases. Analysis of variance showed no significant difference in mean densities between treatments (p=0.11), replicates (p=0.46) or any interaction between the two (p=0.16, see Table 3). Densities from the upper three cores in each treatment were also analyzed using ANOVA. These cores were above the front (e.g. inside the existing shrimp bed) at the beginning of the experiment. The difference in densities across treatments proved statistically insignificant (p=0.37), while replicate differences and treatment-replicate

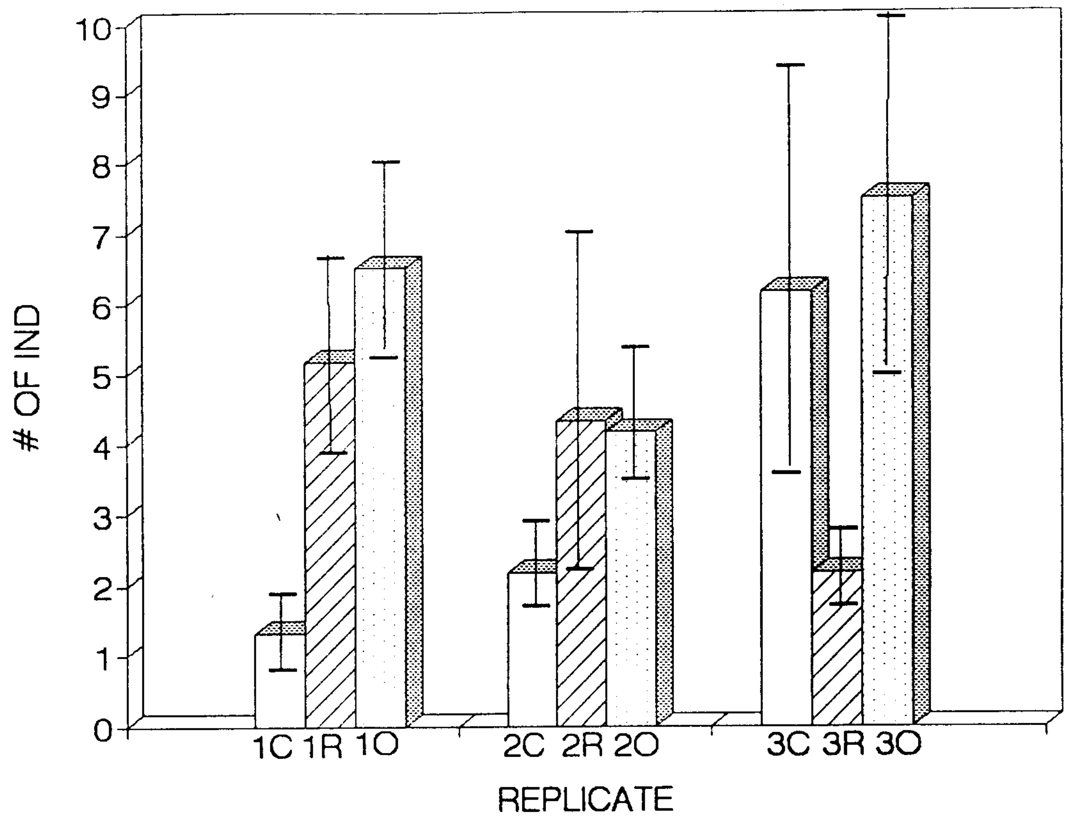

Figure 14. Mean shrimp densities recovered from cage(C), roof(R) and open controls(O) at Site 1. Six cores were summed in each treatment. Cores were taken 4.5 months after treatments were established. Error bars are standard error.

interaction differences both proved significant (p=0.01, p<0.01 respectively, see Table 4).

Table 3. Two-way analysis of variance table for treatment and replicate upon resulting densities from caging experiment. Samples are from six box cores taken from each treatment.

Source	DF	SS	MS	F	P
treat	2	79.00	39.50	2.30	0.11
rep	2	26.78	13.39	0.78	0.46
treat*rep	4	117.22	29.31	1.70	0.16
Error	45	773.83	17.20		
Total	53	996.83			

Measurements of front movement away from it's position at the beginning of the experiment are given with densities in Figure 15 and with average body sizes in Figure 16. Using a random-block design ANOVA, it was shown that there was a highly significant difference in front shift between treatments (p=0.00) and replicates (p=0.00, see Table 5).

Table 4. Two-way analysis of variance table for treatment and replicate upon resulting densities from caging experiment. Samples are from the upper three box cores taken from each treatment.

Source	DF	SS	MS	F	P
treat	2	27.19	13.59	1.04	0.34
rep	2	140.52	70.26	5.39	0.01
treat*rep	4	301.04	75.26	5.77	0.00
Error	18	234.67	13.04		
Total	26	703.41			

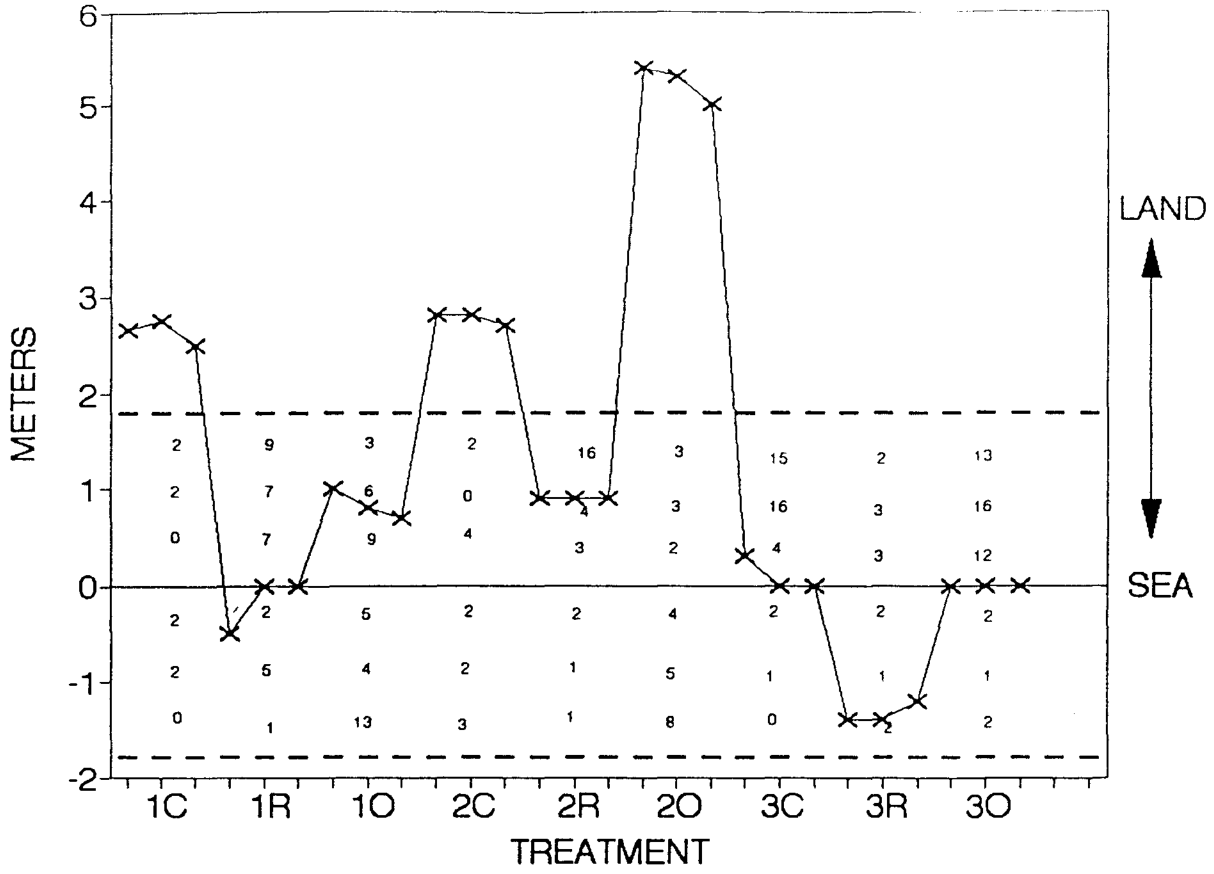

Figure 15. Location of the front and densities of callianassid shrimps (#/0.063m²) within cage(C), roof(R) and open control(O) plots at the end of the experimental period. Densities are rounded off to the nearest integer. Dotted lines represent the upper and lower edges of treatments. 0 on the y axis is the location of the front at the onset of the experiment.

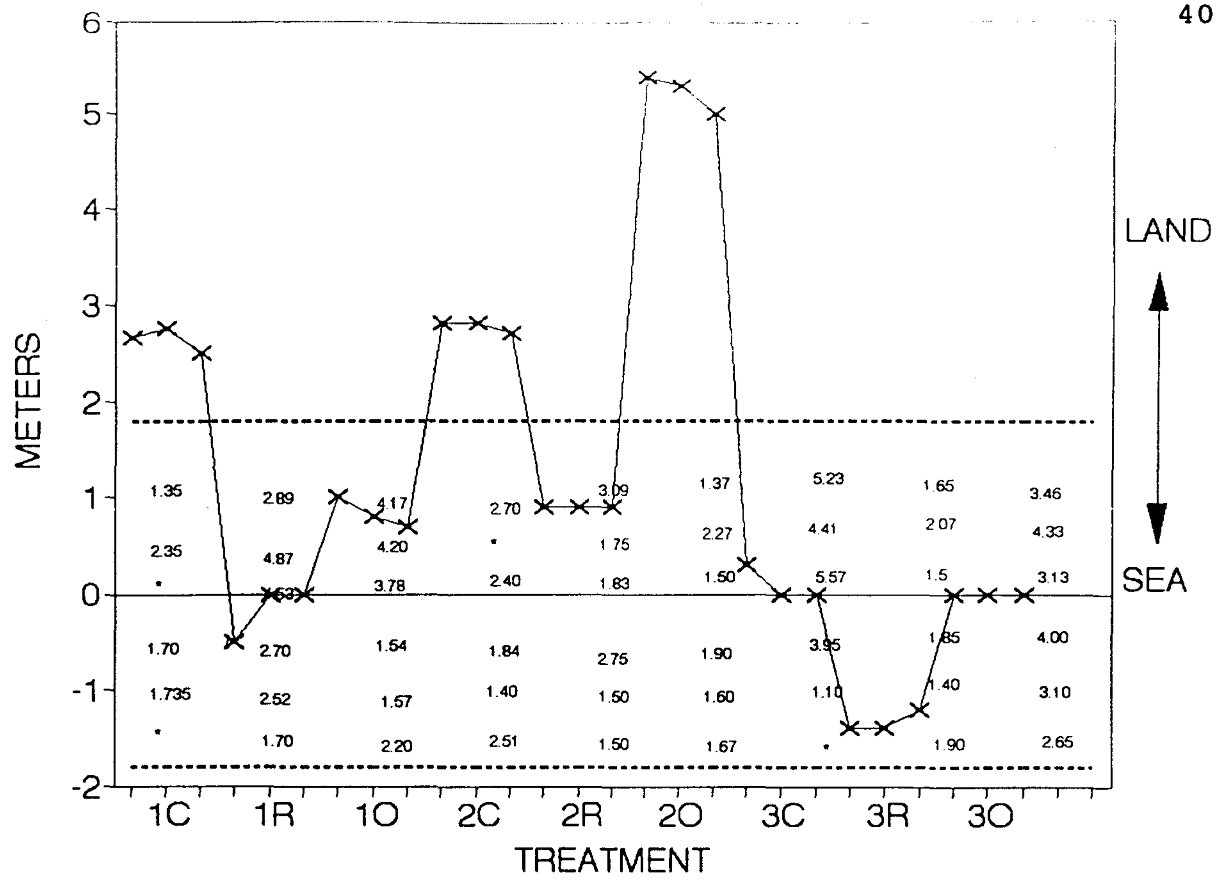

Figure 16. Location of the front and mean size of callianassid shrimps (#/0.063m^2) within cage(C), roof(R) and open control(O) plots at the end of the experimental period. Densities are rounded off to the nearest integer. Dotted lines represent the upper and lower edges of treatments. 0 on the y axis is the location of the front at the onset of the experiment.

Table 5. Random block analysis of variance table for treatment and replicate upon resulting front shift at the end of the cage experiment. Samples are from three measurements taken from each treatment.

Source	DF	SS	MS	F	P
treat	2	27.325	13.663	17.31	0.00
rep	2	51.532	25.766	32.64	0.00
Error	22	17.369	0.789		
Total	26	96.226			

Cores above the new front (e.g. front placement at the end of the experiment) were compared to cores below the new front. Analysis of variance between these two sets of cores showed that shrimp size and density were still significantly different on opposing sides of the front (p=0.00, p=0.00, see Tables 6 and 7).

Table 6. Analysis of variance table for position above or below the front upon size of shrimp recovered at the end of the cage experiment. All above-front core with shrimp were pooled, as were below-front cores. N(above front)=17, N(below front)=33.

Source	DF	SS	MS	F	P
ht	1	19.00	19.00	18.93	0.000
Error	48	48.17	1.00		
Total	49	67.17			

Table 7. Analysis of variance table for position above or below the front upon density of shrimp recovered at the end of the cage experiment. All above-front cores were pooled, as were below-front cores. N(above front)=17, N(below front)=37.

Source	DF	SS	MS	F	P
ht	1	300.2	300.2	20.89	0.000
Error	52	747.3	14.4		
Total	53	1047.4			

Sculpin Censusing

Trawls to estimate the abundance of Leptocottus armatus inside and outside of shrimp beds took place over eight separate dates. An initial and practice daytime trawl was discounted as it produced no fauna of any sort. The total number of recovered sculpins was 45, 22 of which contained shrimp in their guts (49%). Twenty three sculpins were recovered above the front and 22 were recovered below the front. Seventeen of the above-front fish contained shrimp (74%) while 5 below-front individuals contained shrimp (23%, see Table 8). A paired-sample T-test showed this difference to be highly significant (observed t=5.16, DF=20, p<0.001). A standard T-test showed that there was no significant difference between night and evening trawls in terms of number of sculpin recovered (observed t=-1.43, DF=3, p=0.25). A paired T-test for height on shore showed no significant difference in number of sculpin recovered above

Table 8. Abundance and gut contents of Leptocottus armatus taken from September 11 1993 to October 25 1993. Times of trawls: evening(EVE), night(NIG). Height on shore: above front(HI), below front(LO). Percent of catch with shrimp present in gut: (% W/SHRIMP).

Date	Time	Hi	% w/shrimp	Lo	% w/shrimp
9-11	EVE	1	100	2	100
9-12	EVE	1	100	0	-
9-22	EVE	1	0	0	-
9-23	EVE	0	-	5	20
9-24	NIG	7	71	1	100
9-25	NIG	10	90	11	9
10-24	NIG	1	100	2	0
10-25	NIG	2	0	1	0
TOTALS		23	74	22	23

versus below the front (observed t=-0.11, DF=7, p=0.91).

CHAPTER IV

DISCUSSION

Callianassid shrimp in South Slough display distinct intertidal zonation. In this study, I examined the lower limit (front) of several shrimp beds. The main objectives of this study were: 1) to monitor the direction and magnitude of the movement of these fronts, 2) to physically and biologically describe these fronts and 3) to investigate possible evidence supporting the hypothesis that predation by Leptocottus armatus could be acting to determine their placement.

Posey (1985) identified the staghorn sculpin as a major predator upon Callianassa. Warrick (1992) found that the staghorn sculpin, which is the dominant prey item of the Great Blue Heron (Ardea herodias) and the Great Egret (Casmeroidius albus), acted erratically when housed in water less than 20 cm deep. It is reasonable to assume that these sculpins remain below a certain depth to avoid visual detection by these avian predators.

The height on shore of MHHW fluctuates seasonally, displaying a bimodal sin wave with a major peak appearing in December and a minor peak in June (see Figure 17). As the placement of MHHW fluctuates seasonally, the critical depth

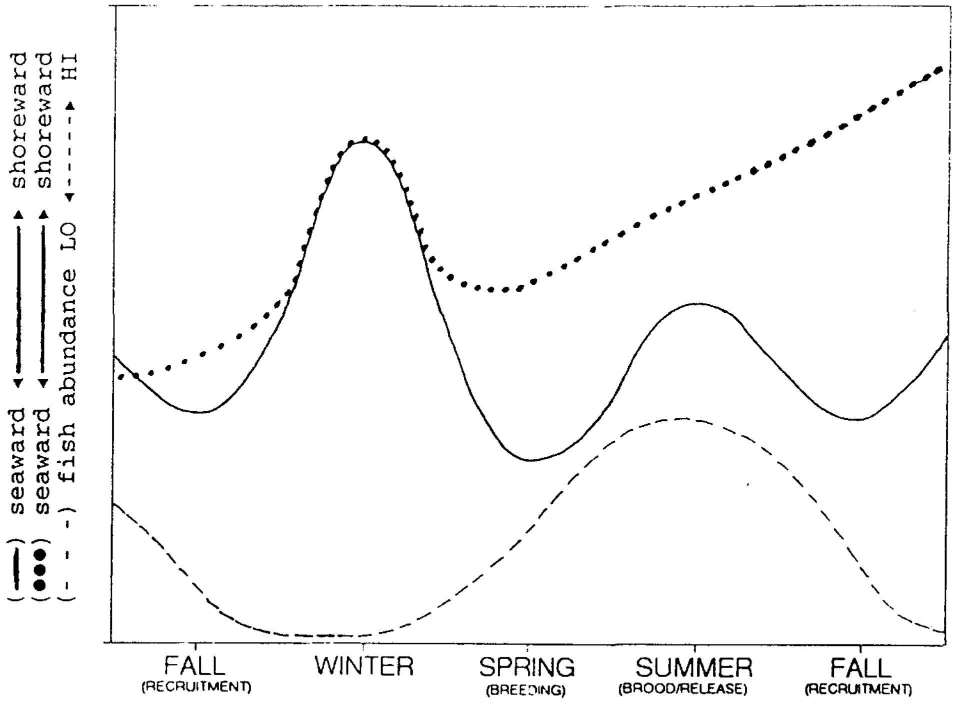

Figure 17. Relative annual trends of tidal height (——), actual front shift (●●●) and sculpin density (- - -). Sculpin density data from Posey (1985).

below which the Leptocottus remains also moves higher or lower in the intertidal. Accordingly, this seasonal change in tidal amplitude affords the sculpin more or less intertidal area over which to feed. If Leptocottus predation is driving front movements, sculpin presence would be reflected in front placement in the intertidal. Therefore, one would expect to find a correlation between seasonal maximum tidal height fluctuations and movement of the lower limit of the shrimp beds.

Figure 17 shows the relative annual trends of tidal height (i.e. expected front shift), actual front shift, and sculpin density. Maximum tidal heights (from NOAA 1993 tables) show a major peak during the winter months and a minor peak during the summer months. Using the hypothesis outlined above, front movements were expected to follow this trend. The actual front shifts followed this trend through the fall 1992 and winter 1992-1993 months, but began to stray from this pattern during the spring of 1993. This rising pattern continued throughout the remainder of the study.

Breeding takes place in spring, young are brooded and released in summer, and recruitment takes place in the fall (McCrow, 1972). If recruitment were strong, this might be a reason for the front to move seaward in later winter and spring, reinforcing the tidally driven pattern. However, the actual front ceased movement upshore or moved downshore only slightly in late winter, suggesting recruitment may have been weak.

Also included in Figure 17 is the annual staghorn sculpin density in South Slough (from Posey, 1985). Sculpin densities display a single peak during the summer months with highest densities found during the summer months.

Front Movement

The pattern of front movements showed significant shoreward migration in fall, slowing and reversing in winter, followed by shoreward movement in spring and summer. The initial movement of the shrimp bed fronts (from June to December 1992) showed a trend which could have easily been interpreted as being a response to changes in tidal amplitude. For instance, this behavior could easily be correlated with the maximum tidal heights in that the peak of MHHW reaches a maximum at or near the winter solstice (December 21, 1993 NOAA tide tables).

If a predator (e.g. Leptocottus armatus) were determining the lowermost distribution of these beds, a similar pattern of front movement would be expected. If sculpins were restricted in their movement over the shrimp beds by tidal height, danger of becoming stranded at low tide, or require a certain depth of water to avoid predation. Krebs (1974) found L. armatus to be a common prey item of the Great Blue Heron Ardea herodias in the estuarine regions of Fraser River, British Columbia. Likewise, Warrick (1992) found L. armatus to be the major prey item of A. herodias as well as a major prey item of the Great Egret Casmeroidius albus. This would explain why the lower front of these beds, though below the maximum tidal height, mirrored it in direction and amplitude of shift. Leptocottus could be said to be driving the shrimp distribution up the beach, while always remaining below this minimum depth. As the maximum high tides grew higher, Leptocottus would be afforded further reach up the intertidal while remaining protected from avian predation.

Movements of the fronts ceased to follow this pattern after spring 1993, however. The position of the fronts during the vernal equinox was different from that of the autumnal equinox. Similarly, front heights during the summer solstice were far above measurements from the previous summer, while tidal heights were not. The overall migration of the front up the shore with relatively minor fluctuations indicates that the seasonality of tides or other factors, such as temperature or salinity, were not obviously correlated with front movement. While annual changes in tidal amplitude may have acted as a factor, effects of tide were masked by other factors.

One possible hypothesis for the behavior of these fronts could be that the animal numbers within these beds were diminishing, due to any number of factors including increased predation pressure, low recruitment, resource competition etc. Callianassa beds were found to encompass a large surface area of the mud flat environment in Yaquina Bay, Oregon, extending to the +1 ft tidal level (Thompson & Pritchard, 1969). Shrimp beds in South Slough appear to be of similar size (pers. ob.). However, because only the lower edge of the shrimp beds were being monitored, I have little data pertaining to the bed as a whole. Analysis of variance shows that there was no significant difference in densities of shrimp within the beds between my fall and spring cores ($p=0.12$). There was also no significant difference between sites ($p=0.73$), or interaction between site and season ($p=0.38$, see Table 9). This does not exclude the possibility, however, that the entire population, and therefore the bed could have been shrinking. Emlet (personal communication) found that a sand dollar (Dendraster excentricus), population in the Puget Sound of Washington state maintained a constant density in response to shrinking population size, through contraction of the overall bed size.

Another observation of note is that the stakes delineating the front at site 1 in this study were approximately 10 m upshore from stakes set out to delineate the front in summer 1990 by C. Hewitt and M. Posey (C. Hewitt, personal communication). This could suggest a longterm upshore migration of the front (and/or a corresponding shrinking of population size). No data exists, however, on location or fluctuations in front during the intervening 2 years.

Table 9. Two-way analysis of variance for site and season upon density of shrimp above the front. Samples are from nine box cores taken above the front per site per season.

Source	DF	SS	MS	F	P
site	1	2.25	2.25	0.12	0.73
season	1	46.69	46.69	2.53	0.12
site*seasn	1	14.69	14.69	0.80	0.38
Error	32	591.11	18.47		
Total	35	654.75			

Another possibly related point lies in the peculiar behavior of the front found at site 3 (Long Island Point). After monitoring front movement of a well-established bed for 3 months, a massive drop in density was observed to the point that the entire bed no longer existed within 50 m of the original. This site was continuously monitored at two month intervals for the remainder of the study, with no apparent repopulation of the area. Whether this could be taken as a local population extinction event or massive migration remains to be seen. This leads one to believe that these beds are not static areas, but rather dynamic in nature.

Tidal height surveys of sites 3 and 4 showed that heights of stakes at both sites were not significantly different. This suggests that a relationship between front placement and exposure/submergence time could exist. This relationship was not pursued, but warrants further study.

Density Cores

Box cores, while work intensive and destructive of microhabitat, provide accurate data for soft-sediment densities. Cores at sites 1 and 4 proved what is inherently obvious from first-hand observation - that these shrimp beds have a strong, distinct edge at their lowermost limit, and below which few individuals are found. It is safe to assume that the remaining two sites, which appear and behave in this same fashion, have similar density differences.

Counts of the number of burrow openings per unit area were poor predictors of the actual numbers of individuals in that area. Burrow counts were made prior to coring in both fall 1992 and spring 1993. After the fall cores were taken, it was determined that field assistants had scored worm burrows as well as shrimp burrows. For this reason, all fall data were discarded. Spring (1993) data showed a weak relationship between burrow number and shrimp density (see Figure 7). This is probably due to the nature of Callianassa burrows. These burrows form a vast, interconnecting network of tunnels and can have multiple openings. The individual residing in any given burrow is not necessarily located directly below the opening. Multiple openings and complexity of burrows probably cause the burrow/individual relationship to be weak.

It has been shown that Callianassa has a high affinity to it's burrow, presumably to avoid predation (MacGinitie, 1934). Given this affinity, it seems highly unlikely that these shrimp would exit their burrows to migrate upon the sediment surface. It does seem plausible, however, that Callianassa could continually extend their burrows seaward, digging vertically periodically to form vents. This would accomplish migration while insuring predation protection. Because smaller individuals are found below the front, however, there is evidence that recruitment is also a mechanism for front movement.

Box cores carried out at sites 1 and 4 showed that when the front is crossed in the downshore direction, along with a significant drop in density, an equally significant drop in mean body size occurred. The distribution of body sizes relative to the front is consistent with a hypothesis that recruitment influences movement of the front.

Large-scale breeding generally begins in the spring, and ovigerous females may be plentiful in the cooler layers of mud until August (McCrow, 1972). The larvae are brooded through the naupliar stages and then released into the plankton as first stage zoea. The carnivorous larvae pass through five zoeal stages and possibly one megalopal stage before metamorphosis and settlement. The estimated duration of planktonic life is six to eight weeks. The duration of each stage is unknown (Johnson, 1981).

If larvae settle both above and below the front and a gradient in mortality occurs with increasing mortality at low intertidal levels, a distribution in sizes such as the one found at sites 1 and 4 would be expected. If recruitment is variable between years and animals maintain a density (#/m^2) within certain limits, then in low recruitment years, mortality should cause the front to recede upshore and in high recruitment years, the front should proceed downshore. The effect of recruitment on movement of the front downshore should depend on intensity of recruitment and the time it takes juveniles to reach a size at which they influence sediment characteristics. Obviously this topic needs to be explored empirically.

These animals have a strong tendency toward aggregation (pers. obsv.). This could be due to the fact that they are internal fertilizers or that they prefer the higher soil porosity and aeration caused by the burrowing activity of conspecifics. As beds become too dense to afford room for new recruits, they may be forced to settle outside the bed into lower density areas. This could explain why juveniles are found on the lower fringe of established beds. Therefore, for a receding front, mortality must exceed recruitment.

Sediment Analysis

In addition to changes in surface morphology with increased burrow density, on-site inspection of *Callianassa* beds provides the observation of greatly decreased firmness inside versus outside the bed. As one moves from the outside of an existing bed to inside, the quicksand-like quality of these areas becomes immediately apparent. Indeed, one can go from ankle deep to knee deep in mud over the course of one step. One factor which could cause this type of result is increased porosity (e.g. water content). Another factor which can be correlated with increased water content is larger sediment grain size. *Callianassa* occur in sediments of fine sands and silts, stable enough to allow the construction of semipermanent burrows (MacGinitie, 1934). The distribution of sediment sizes within the range utilized by *Callianassa* can vary greatly. A survey of sediments was intended to determine if sediment grain sizes were different inside and outside (seaward) of a *Callianassa* bed. A difference might be due to shrimp activity or sediment preferences of shrimp.

Examination of grain size distributions above and below the front with the Chi-square test showed that distributions differed significantly in 14 out of 18 comparisons (78%). However, among these 14 significant comparisons, half (7) produced larger grain sizes above the front while half (7) showed larger grains below the front. Site 4 showed the strongest tendency toward larger grains above the front with 3 out of the 4 significantly different samples larger above the front.

This lack of consistency raises the question of how much of this variation is due to shrimp behavior and how much is random assortment of sediment grains. If Callianassa preferred a certain size fraction, or sorted sediment, discarding particular fractions, distributions would be consistently different above and below the fronts and similar across sites. Because this was not the case, it appears that unless distributions below the front are an artifact of past shrimp activity, fine scale sediment composition is not likely a factor in determining the placement of these populations. The strongest trend in terms of size fraction preference was a tendency for sediments to lack the 250μ size fractions. This tendency was stronger at sites 3 and 4 than site 1. Only half the cases showed a tendency toward larger grain sizes above the front. This analysis of sediments indicates that the decrease in substratum firmness inside these shrimp beds is due more to porosity and burrow presence than larger to grain size.

There is evidence that some species of callianassid shrimp can have some sorting effect in various substrates. McMurtry, et al. (1984) found that callianassid shrimp at Enewetak Atoll lagoon stored coarse-grained sediments ($\geq$1.4

mm) in subsurface refuse galleries. Smaller particles were either used for burrow wall construction or pumped to the sediment-water interface where they were either suspended in the water column or accumulated in mounds. Likewise, Suchanek (1983) found that Callianassa rathbunae in Tague Bay, Virgin Islands sequestered grain sizes ≥1.4 mm in underground burrow galleries and ejected smaller particles.

These cases differ from what was observed in South Slough in that they were in open ocean and sandy bays in the tropics and South Slough is an estuarine mud flat environment. The major difference between these two areas is sediment grain size. In South Slough, Callianassa show no sorting of particles ≥1.4 mm because sediment particles of this size do not exist on a mud flat. The largest grain sizes found in my sediment cores were approximately 600μ. There was also no significant difference between surface and depth cores where such stores of larger particles would be located. C. californiensis and C. gigas do not exist in the tropical areas observed in these studies. These two different sets of species have very different behavior. C. rathbunae and the other tropical species, along with exhibiting this sorting behavior, dig burrows up to 1.5 m deep (McMurtry, et al. 1984). The maximum depth of C. californiensis burrows is 50-60 cm (MacGinitie, 1934). My sediment grain size results also support the theory that C.

californiensis and *C. gigas* do not have a significant effect upon sediment distributions. It appears that while tropical species of *Callianassa* display sorting behavior, it is not a behavior shared across species.

The lack of a consistent trend in sediment distribution inside versus outside of these beds indicates that while *Callianassa* prefers grain sizes within a certain range, no specific size fractions appear preferable, although there does seem to be some evidence that the 250μ fraction might be selected against. Apart from this, *Callianassa* does not appear to preferentially sort the sediment into specific fractions, neither does it seem to settle in areas containing specific sediment sizes.

Porosity Cores

Several different techniques using cores of various sizes were employed during this study in an effort to quantify the factor of porosity. The change in firmness of the sediment described above is caused by the activity of the burrowing shrimp. Because this is an intertidal area with much standing water, it can be assumed that any new interstitial space formed would become occupied by water. Also the vast burrow networks formed by these shrimp populations are also filled with water. Therefore it is reasonable to expect that bulk porosity of sediments above the front should be greater than below the front.

A 50 cc syringe core was used to measure water contents on either side of the front. A trend toward increased water content above the front existed at sites 3 and 4 but was shown to be insignificant. None of sites produced significantly different means above versus below the front at the 95% confidence level (site 1: $p=0.41$, site 3: $p=0.36$, site 4: $p=0.12$). I believe the unexpected results of this experiment were due to improper sampling techniques. Improved methodology for quantifying this type of system is needed. Though I had no success with large cores, it seems a core which could sample burrows as well as surrounding sediment would be more effective.

Sediment Height

The grid of stakes used to monitor sediment height at site 1 was deployed in February 1993. At this point, the movement of the front was seaward and I expected it to continue in this direction into summer, in accordance with the hypothesis that it would continue to follow tidal height variation. Because the front was expected to continue it's seaward movement, the sediment grid was deployed in such an orientation that as the front continued to fall, it would pass over the majority of the stakes. The front, however, ceased it's seaward movement, and instead once again moved shoreward. This caused the majority of the stakes to remain uninfluenced by the movement of the front.

As was explained in the results section, tidal currents caused scouring around the base of the sediment height stakes. Because of this, actual height had to be estimated from surrounding sediment heights. I estimated my measurement error to be ±1 cm. The majority of measurements below the front fell within this margin. The only portion of the sediment grid which produced consistently significant results was the area located above the front. Front movement was in the shoreward direction throughout the period when stakes were sampled. All stakes located below the front showed virtually no change in sediment height.

Visual inspection of these shrimp beds indicates that sediment height above the front is greater than below the front. This is supported by the sediment height experiment results and is intuitive, given the burrowing activity of the shrimp. It was also expected, however, that sediment levels at a point above the front would remain constant until overtaken by the front. Stake measurements showed, however, that stakes above the front showed a slight decrease in sediment height before the actual front reached them. As the front overtook a stake, a sharper drop in sediment level was observed. This result was common throughout stakes crossed by the front.

These data show that distinct changes in sediment height occur at the lower edge of a shrimp bed as it recedes upshore. The behavior of a receding front can easily be compared to that of a receding glacier, which becomes progressively thinner near edge regions while melting. In similar fashion, the sediment height lessens, or "melts", as the front approaches. A possible explanation for this behavior could be variation in shrimp activity or presence near the actual front. As the burrowing activity of shrimp found in the fringing areas tapers off or becomes concentrated in a direction away from the front, the front recedes. Likewise, individuals migrating away from the front area toward the center of the bed could cause the front to recede. One point that should remain clear, however, is that the integrity of the front is still maintained throughout it's movement. That is to say, while the action of the inhabiting shrimp might vary, the front remains clearly delineated. This is interesting, in that while shrimp behavior might be changing, there is still some factor which is causing the front to persist.

There was no evidence of sediment scour or deposition across the site. This is evidenced by the fact that while sediment heights overall dropped above the front, heights below the front remained virtually constant. This seems to imply that large-scale erosion due to runoff was not taking place. This could also be taken as evidence against the hypothesis that intertidal currents could be responsible for determining front placement.

Caging Experiment

Caging experiment results showed no significant difference in resulting shrimp densities across treatments (see Table 3). However, mean shrimp density was consistently lower in cages than in open controls. Resulting front shifts also showed no pattern across treatments (see Figures 15 & 16).

Tasto (1975) reported 4.4% of staghorn sculpins less than 70 mm standard length and 21.5% of those more than 70 mm had Callianassa in their diets. Posey (1985) showed that South Slough shrimp populations transplanted below the front suffered significant mortality by Leptocottus. He also had limited success at inducing shrimp to migrate into predator exclusion cages below the front. This data is supported by the presence of shrimp in the guts of sculpins from my trawling experiment.

It is expected when predation pressure is removed from a prey population that prey densities will increase. This has been shown to be true for infaunal species (Virnstein, 1977). I expected that shrimp densities in cage treatments would increase or remain unchanged while shrimp densities in open controls and roof controls would decrease due to fish predation. This was not the case. Densities of shrimp within cages were consistently less than open controls of the same replicate, though the differences were not significant.

Densities of shrimp in roof controls were both higher and lower than densities beneath cages. These results lead one to believe that if Leptocottus is acting to determine front placement, there must be other stronger factors which are offsetting it's effects. The converse hypothesis would be that sculpins indeed have no impact upon lower distribution of Callianassa.

An alternative could be that the experimental protocol had unforseen effects on shrimp densities in this experiment. One such factor may have been improper controls for the impedance of current flow. As current speed drops and sedimentation increases, sediment level within the treatment also increases. This was observed to occur (albeit slightly) in both the caged and roof-control treatments. If increased sedimentation was a negative factor, then it may have caused a reduction in Callianassa densities. Shrimp burrows could likewise be filled in by this action, causing mortality or migration to a point outside the cage or roof treatments.

Sculpin Censusing

Leptocottus was shown to prey upon Callianassa by the presence of shrimp in their guts. However, there was no pattern of sculpin presence or predation in relation to the position of the front. Sculpin densities showed a tendency to be larger during night trawls than evening trawls.

A significantly larger percentage of sculpin recovered above the front contained shrimp in their guts than those recovered below the front (observed $t=5.16$, $DF=20$, $p \leq 0.001$). This is expected, given the higher density of shrimp above the front. More shrimp in the guts of sculpin above the front also implies that there is a low rate of crossover by fish from one side of the front to the other. Once the tide rises and Leptocottus enters the intertidal zone, it may not change it's relative position much, e.g. after an individual fish arrives on either side of the front, it tends to stay in that general area. This is consistent with behavioral (personal) observation of Leptocottus as a sit-and-wait benthic predator which spends much of it's time motionless on the bottom. This is in contrast to other fish species in this area such as the Shiner Surfperch (Cymatogaster aggregata) which exhibits a highly mobile, pelagic lifestyle.

Before proper methodology was devised, night trawls were not possible for this experiment. Once this was done, larger hauls of fish were recovered for the remaining September (9-24 & 9-25) trawls. The final two sessions, carried out at night in October, failed to produce large catches. One reason for this might have been that the final two sessions were carried out during lower tides than all previous sessions. With lower tides, the outboard motor to rode closer to the sediment and may have startled fish, causing them to move out of the path of the approaching trawl net.

Another possible explanation for the lower returns during the October trawls is the full month time lag between these and the September trawls. Posey (1985) found that Leptocottus densities in Joe Ney Slough and Coos Bay were highest in summer and tapered off to lowest densities in winter. The difference in sculpin catches between my two samples may reflect this decline.

Though these data confirm Posey's (1985) and Tasto's (1975) observations that Leptocottus does indeed prey upon Callianassa, this data does not demonstrate how predation might influence movement of the front. There seems to be evidence that the sculpin is more active at night, but there was no significant difference in sculpin densities above versus below the front.

A rough calculation of shrimp densities, sculpin densities and predation pressures above and below the front produces the following: fall cores produced almost four times as many shrimp above the front as below (163/41). Number of sculpins caught above the front was nearly equal to the number caught below (23/22). The ratio of percent sculpin with shrimp in their guts above the front to below the front is just over 3 (74/23). This means that predation pressure above the front is nearly equal to that below. This leads one to believe that while _Leptocottus_ is having a predatory effect, it is not strong enough, or does not apply ample directional pressure to explain the behavior of the front. This correlates well with the caging experiment results, in that removal of this predator should not cause fronts to shift seaward because it is exerting nearly equal pressure in both directions. While sculpin predation could be working in concert with another factor, perhaps physical, to determine shrimp distribution, it does not appear to be a singular causal factor.

CHAPTER V

SUMMARY

The factors influencing the lower limits of the distribution of Callianassa are complex and interrelated. Previously, several theories concerning physical factors have been put forth in an attempt to explain these distributions. None of these have proved to be the dominant factor in the lower limit of Callianassa in South Slough. Thompson and Pritchard (1968) suggested that salinity might have an effect on Callianassa distribution. Salinity does indeed vary in South Slough with the rise and fall of tides, but Posey (1985) found that interstitial salinities at Valino island did not differ greatly inside and outside of a dense shrimp bed.

C. rathbunae and C. quadracuta were shown to sort sediment grain size in tropical areas (Suchanek, 1983; McMurtry et al., 1984). Grain size analysis of sediments inside versus outside of C. californiensis and C. gigas shrimp beds in South Slough showed no pattern of differences in size fraction distribution on either side of the front. There was also little consistency across sites. This seems to indicate that, while bioturbation caused by burrowing activity may influence the water content and firmness of these beds, sediment grain size does not seem to limit _Callianassa_ distribution.

Eckman (1983) offered that current regimes and their influence upon larval settlement could be important in determining intertidal distribution. No data was taken during this study with respect to relationships between shrimp bed placement and local current regimes. Because there was little evidence of consistent grain size differences across the front, however, currents do not appear to be a factor.

MacGinitie (1935) suggested a cyclical pattern of establishment of _Callianassa_ beds. In this process, sedimentation from riverine input builds up a sandy bottom, creating a habitat for benthic algae such as _Enteromorpha_ sp. As these algae flourish, they cause increased sedimentation until they are smothered and decay. _Callianassa_ then invades the rich bed of detritus and flourishes. The bioturbation caused by the burrowing activity of the shrimp then inhibits further algae establishment. Once the food source is depleted, the shrimp abandon the site, leaving a clean substrate for the process to begin anew. Although this cycle seems possible, evidence of it's presence does not appear to be common. Bird (1982) found no evidence for a cyclic pattern in a northern Oregon shrimp bed. Peterson (1979) likewise found shrimp populations in Mugu Lagoon to be stable in both location and density. Although site 2 displayed abnormal behavior, shrimp populations in South Slough seem to be just as stable on a large spatial scale, with reports from M. Posey (1985) and P. Rudy (unpublished "early 1970s" study as reported by Posey, 1985) showing similar bed positions to this study. This is supported by the fact that the South Slough beds are located above the area of greatest algal growth (Pregnall and Rudy, 1985). My personal observation indicated no affinity of these shrimp populations to algae beds, but data concerning this relationship was not taken.

Tidal height surveys at sites 3 and 4 showed that these fronts correspond vertically in the intertidal, but further analysis was not pursued. The possibility exists that distribution could therefore be a factor of submergence and exposure time. This aspect warrants further study.

Given the nature of this system, it is suspected that the causal factor behind the distribution of these shrimp beds is wholly or partially due to biological factors. McCrow (1972) put forth the hypothesis that competition between Callianassa and the burrowing mud shrimp Upogebia pugettensis could be determining the lower distribution of ghost shrimp beds. This seems unlikely to be the case in South Slough given the low densities of Upogebia in the area. During the course of my study, 132 sampling box cores were taken. These cores produced 626 callianassid individuals and only 2 mud shrimp. Posey's (1985) study in this same area produced similar results. Although Upogebia is common in other estuarine systems in Oregon (Posey, 1985), it's low densities in South Slough seem to indicate that it is not a factor in determining Callianassa distribution.

Devine (1966) put forth the hypothesis that Callianassa filholi distributions may be in response to the intertidal abundance of the diatom Chaetoceras sp., which is one of it's major food sources. Feeding seems to vary quite a bit between different species of Callianassa. C. californiensis and C. gigas have been shown to be predominantly detritovores (MacGinitie, 1935; Powell, 1974). Although stomach contents of shrimp were not analyzed in this study, Posey (1985) found that stomach contents of shrimp collected near Valino island were predominantly detrital.

R. Emlet (personal communication) found that in Ship Bay, Washington, the sand dollar Dendraster regulated it's distribution in response to disturbance factors. In January, 1984, when populations experienced drastic, rapid mortality (20-80%) owing to a winter freeze, distributional borders correspondingly collapsed in order to maintain a constant density. Densities measured in June of 1984 were not significantly different than densities taken the previous June. This case is expected to be similar to Callianassa in South Slough. Because Callianassa exhibits internal fertilization, maintenance of close proximity to conspecifics is imperative. It is also believed that the burrowing activity might also attract new recruits to an existing bed (Posey, personal communication). Establishment of new burrows may be facilitated by the aeration of the sediment resulting in an existing bed, making it easier for new recruits to form burrows.

In support of Posey (1985), my trawl experiment data show sculpin predation to exist in South Slough, but it's patterns do not correspond strongly with the placement of the front. Removal of the predator did not have the an effect on shrimp densities. This could have been a function of season, however. Posey had similar results when predator exclusion cages were used in an attempt to induce migration of shrimp populations. He found the predation effect to be highly seasonal, and that as sculpin densities dropped in fall and winter, there was virtually no difference between exclosures and controls (Posey, 1985). Results from his transplant experiment also showed predation pressure to be stronger in summer. Because my trawls were taken in September and October, predation pressure might have already become insignificant. This hypothesis is not supported by my caging experiment results. This experiment took place in spring and summer, but showed no evidence of predation pressure. While predation by Leptocottus might be working in concert with others factors, it does not appear to be the causal factor in determining the movement of the seaward edge of these shrimp beds.

If we intend to identify the driving forces behind this system, a better understanding of these beds as a whole is required. My study focused on the lower end of these distributions, but this leaves us with only part of the entire picture. It is unknown whether the upper limit of these beds showed similar shifts as the lower limit. Observations of this sort would determine if these populations are in fact shrinking, or simply moving up the beach as a whole.

Growth studies of Callianassa could determine the time frame between larval settlement and the point at which new individuals begin to effect the bed as a whole. This information, when analyzed along with settlement and mortality rates, could shed light upon the mechanism by which the front moves higher or lower in the intertidal.

These estuarine systems are extremely important nurseries for coastal fishes and shellfish. Similarly, the oyster Crassostera gigas is cultured extensively in South Slough. Because burrowing shrimp are the dominant infaunal residents found in these intertidal mudflat systems, they form an important link in estuarine food webs. For this reason, greater understanding of the complexities of their ecology is crucial.

APPENDIX A

FRONT SHIFT MEASUREMENTS

Front shift measurements for sites 1, 3, 4 and 5. Measurements represent shifts away from original stake positions. Positive measurements indicate front movement upshore. Date of measurement is as indicated (MM-YY).

Site 1

Stake#	09-92	11-92	12-92	12-92	01-93	03-93	05-93	07-93	9-93
1	3.4	4.1	3.7	4.0	4.8	4.8	5.5	0.0	-9.0
2	1.6	1.9	2.0	1.8	1.8	1.8	2.3	2.8	5.0
3	1.4	2.8	2.2	1.7	1.8	1.4	1.3	1.6	2.9
4	4.4	4.8	5.7	4.5	5.2	5.1	5.1	7.1	10.2
5	6.0	9.2	8.9	8.9	8.9	9.7	9.4	11.9	14.2
6	3.3	10.2	9.8	10.4	8.5	9.8	10.6	14.0	16.4
7	13.9	14.4	14.7	14.6	14.1	14.0	14.4	20.1	20.5
8	2.9	10.7	11.2	11.5	7.9	8.5	13.5	14.0	14.9
9	6.0	8.5	11.7	7.3	7.2	12.0	14.0	15.7	19.0
10	2.4	6.5	3.7	3.7	3.5	3.2	9.6	11.7	13.5
11	1.3	2.2	2.3	1.9	2.1	2.2	2.5	3.8	5.1
12	4.8	5.8	5.7	4.9	5.9	6.6	6.5	8.2	9.8

Site 3

Stake#	09-92	11-92	12-92	01-93	03-93	05-93	07-93	09-93
1	2.1	2.8	4.1	2.8	2.4	2.4	3.5	5.7
2	2.3	3.5	4.2	3.4	3.6	3.7	4.6	6.5
3	3.1	3.7	4.7	3.7	2.4	4.9	5.4	6.8
4	1.2	4.0	5.4	2.6	2.5	3.7	4.5	6.7
5	2.7	2.2	4.2	2.4	3.8	3.1	4.7	6.4
6	2.1	3.4	4.2	3.1	5.2	3.3	5.3	6.1
7	2.6	0.5	4.6	2.8	4.5	2.9	4.7	5.2

Site 4

Stake#	10-92	11-92	12-92	01-93	03-93	05-93	07-93	09-93
1	6.7	7.3	7.5	5.2	7.6	7.4	9.0	10.6
2	4.1	7.4	7.6	4.6	6.3	6.1	9.2	13.0
3	8.7	8.9	9.0	8.9	9.7	10.0	12.7	18.0
4	7.7	8.6	8.3	10.1	11.3	12.1	14.6	18.2
5	1.9	2.4	2.6	2.6	2.9	2.9	17.3	21.6
6	3.8	4.9	5.3	6.4	7.7	8.4	15.3	22.6
7	5.5	6.7	6.3	7.0	8.6	9.2	13.8	27.2
8	6.4	7.7	7.5	7.5	8.2	8.3	10.7	27.2
9	6.0	11.1	8.6	9.8	11.5	12.5	8.9	29.5

Site 5

Stake#	11-92	12-92	01-93	03-93	05-93	07-93	09-93
1	2.1	2.2	1.8	1.8	1.9	3.5	4.7
2	2.0	1.1	1.1	1.2	1.7	2.4	3.4
3	1.0	1.2	1.1	1.0	1.5	0.0	3.9
4	1.3	1.5	1.2	1.4	1.7	4.0	5.8
5	0.2	0.4	0.4	0.0	0.0	0.0	0.8
6	0.0	0.5	0.5	0.0	0.0	0.0	0.0
7	1.2	0.9	0.6	0.0	0.5	0.5	0.4
8	1.4	1.2	1.7	1.6	3.9	4.0	4.0
9	2.1	2.4	2.4	1.5	2.1	2.6	2.2

APPENDIX B

TIDE HEIGHT MEASUREMENTS OF FRONT STAKES

Stake heights given are meters above Mean Lower Low Water. Site 4 measurements were taken on 6-8-93. Site 3 measurements were taken on 6-9-93.

Site 3		Site 4	
Stake	Height	Stake	Height
1	0.15	1	0.16
2	0.10	2	0.15
3	0.11	3	0.15
4	0.05	4	0.13
5	0.03	5	0.12
6	0.02	6	0.13
7	0.00	7	0.10
		8	0.09
		9	0.04

APPENDIX C

SEDIMENT HEIGHT SHIFTS AT SITE 1 FROM 2-5-93 TO 8-4-93

Positive numbers represent a drop in sediment height (in cm). Missing data is shown by an asterisk (*).

Stake #	3-5-93	4-9-93	4-27-93	5-25-93	7-4-93	8-4-93	9-6-93
1	0.5	0	0	0	0	0	0
2	0.5	0	0	0	0	0	0
3	2	0.4	0.6	1.9	2	2	2
4	1.5	0	0.3	2	2	1.5	3
5	0.5	0.4	0	2	2.5	3	3
6	0.2	*	0	0	0	0	0
7	0.7	*	-0.4	0.2	0.4	0	0
8	0	*	0.2	0	0.3	0	0
9	1	0	0.2	0	0	0	0
10	0	*	-0.1	0.3	1.4	1	1
11	0.4	0	-0.4	0.4	0	0	1
12	0	-0.3	0.1	0	0.3	0	0
13	0.4	0	0.1	0	0.3	0	0
14	0.1	-0.1	0.2	0	0	0	0
15	0.2	0	0	0.4	0	0	0
16	0.2	-0.2	0	0	0	-0.5	0
17	0.9	0.5	-0.1	0.2	0	0	1
18	0.5	0.2	-0.2	0	0	0	0
19	0.3	0	0	0	-0.5	0	0
20	0	-0.2	0	0	0	1.5	1.5
21	0.6	0.2	0	0	0	0	0
22	0.6	0.1	-0.3	0.3	0.3	0	0
23	0.7	-0.2	0	0	0.1	0.5	0
24	-1	0	0.3	1	3	3.5	3.5
25	0.5	0.5	0.5	1.5	1.5	3.5	4

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