THE EFFECTS UPON THE MACROFAUNAL COMMUNITY OF A DOMINANT BURROWING DEPOSIT FEEDER, CALLIANASSA CALIFORNIENSIS, AND THE ROLE OF PREDATION IN DETERMINING ITS INTERTIDAL DISTRIBUTION

by

MARTIN HAROLD POSEY

A DISSERTATION

Presented to the Department of Biology
and the Graduate School of the University of Oregon
in partial fulfillment of the requirements
for the degree of
Doctor of Philosophy

June 1985

I hereby approve of this dissertation by

Martin Harold Posey

Peter Frank

An Abstract of the Dissertation of

Martin Harold Posey for the degree of Doctor of Philosophy

in the Department of Biology to be taken June 1985

Title: THE EFFECTS UPON THE MACROFAUNAL COMMUNITY OF A DOMINANT BURROWING DEPOSIT FEEDER, *CALLIANASSA CALIFORNIENSIS*, AND THE ROLE OF PREDATION IN DETERMINING ITS INTERTIDAL DISTRIBUTION

Approved: Peter Frank

The burrowing, deposit feeding ghost shrimp, *Callianassa californiensis* (Dana), forms dense beds in the mid-intertidal zone of sandflats along the west coast of North America. In most Oregon and Washington embayments, this shrimp displays a distinct zonation with densities declining by an order of magnitude in the low intertidal and subtidal. This investigation focused on the interactions between dense shrimp beds and other infauna of the tideflat, and on the role of predation in limiting the distribution of these beds.

The species composition within a dense shrimp bed and of an adjacent area with low shrimp density were observed from benthic cores taken in the Coos Bay, Oregon, estuary. Sedentary polychaetes and amphipods had significantly lower abundances within than outside a dense *Callianassa* bed. The numbers of most free-burrowing fauna were uncorrelated or positively correlated with increased shrimp density. Sediment resuspension and destabilization have been suggested to explain the effect of deposit feeders on other soft-sediment organisms. My results suggest that sediment destabilization is the primary mode of interaction between *Callianassa* and intertidal fauna.

Exclusion cages were used to study the effect of predation in restricting dense beds to the mid-intertidal zone. The distribution and diets of several potential predators were estimated from laboratory experiments and beach seine collections. The lower edge of the shrimp beds during summer was strongly affected by predation. The staghorn sculpin, *Leptocottus armatus*, was identified as an important predator on adult ghost shrimp during the summer months. Decreased activity of the shrimps contributed to the maintenance of zonation during winter when predation was less intense. These results show that the distribution of a deep-burrowing animal can be significantly affected by predation; previous research on other species had put this into question. Additionally, limitation of a dominant organism, such as *Callianassa*, by predation may affect the overall species composition of the soft-sediment community.

VITA

NAME OF AUTHOR: Martin Harold Posey

PLACE OF BIRTH: Nanjemoy, Maryland

DATE OF BIRTH: December 28, 1959

GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon
University of North Carolina
Charles County Community College

DEGREES AWARDED:

Doctor of Philosophy, 1985, University of Oregon
Bachelor of Arts, 1980, University of North Carolina
Associate of Arts, 1978, Charles County Community College

AREAS OF SPECIAL INTEREST:

Population and Community Ecology
Invertebrate Zoology

PROFESSIONAL EXPERIENCE:

Teaching Assistant, Department of Biology, University of Oregon, Eugene, 1980-85

ACKNOWLEDGMENTS

It is difficult to know how to thank all of the people who have helped with this research. It has benefited from numerous conversations with committee members and fellow graduate students, especially Dr. Paul Rudy, Marshall Pregnall, Robert Graham, and Jeffrey Goddard. Special thanks go to my major advisor, Dr. Peter Frank, who was always willing to discuss problems and whose comments on earlier drafts of this manuscript were invaluable in making it understandable.

Part of this research would not have been possible without the help of many students from the Oregon Institute of Marine Biology. Their willingness to pull beach seines in near-freezing weather, spend long hours observing shrimp behavior, and repeatedly slog through the mud is greatly appreciated.

Finally, I wish to thank my father who patiently introduced me to the wetlands, rivers, and forests of southern Maryland. His continual support has been important throughout this study.

This research was supported in part by funds from Sigma Xi.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

GENERAL INTRODUCTION

A fundamental objective of ecological research is to elucidate the factors affecting the distribution and abundance of organisms (Krebs, 1978). A particular pattern of distribution that has received considerable attention in marine environments is intertidal vertical zonation. Many intertidal organisms have long been recognized to occur in zones with distinct boundaries. Some of these species are largely restricted to this habitat while others are predominately terrestrial or subtidal. Since the vertical profile in the intertidal presents a gradient of physical stresses and biological pressures, studies determining the cause of zonation have provided important information on the role of these factors in restricting the distribution of organisms.

Lower limits to the distribution of rocky intertidal organisms have often been attributed to biological interactions (for reviews see Dayton, 1984; Paine, 1984). Inferior competitors may be restricted to higher tidal levels (Connell, 1961; Dayton, 1971) and predation or herbivory may effectively exclude many organisms from the low intertidal or subtidal (Paine, 1974; Lubchenco and Menge, 1978). Paine (1966, 1974) suggested that predation on a dominant competitor could change the species composition of the community. He found that sea star predation restricted dense beds of the competitively dominant mussel, *Mytilus californianus*, to the mid intertidal. When sea stars were removed, the primary space was slowly invaded by a monoculture of Mytilus. Where this mussel was absent, the low intertidal was dominated by diverse utilizers of primary space, but lacked many of the animals associated with the mussel matrix (Suchanek, 1979).

In soft sediments, by contrast, physical factors generally have been considered more important in determining the lower distribution of organisms. Several studies have noted a change in sediment characteristics (usually particle size) associated with an animal's lower tidal distribution and have suggested that these substrate changes, or the correlated changes in current patterns, may be responsible for zonation (Wieser, 1959; Green and Hobson, 1970; Johnson, 1970; Longbottom, 1970; Morgan, 1970; Vassallo, 1971; Featherstone and Risk, 1977; Grant, 1981; Willason, 1981). Eckman (1983) suggested that local current regimes and passive settlement of larvae are important in establishing zones and Swinbanks (1982) proposed that some lower limits, particularly of certain plant species, are related to zones of rapid change in submergence time (critical tide levels).

There is little evidence that directly implicates competition as a cause of zonation in soft sediments. Levin (1981) showed that the polychaete Pseudopolydora could aggressively exclude a second polychaete, Streblospio, under laboratory conditions. She observed that the densest aggregations of Streblospio existed immediately above those of Pseudopolydora in the field. Fenchel (1975, 1977) has described a possible case of competition among intertidal snails. Exploitive competition (Levinton, 1977) and interference competition (Woodin, 1974; Peterson and Andre, 1980) have been noted subtidally, but do not appear common. Peterson (1979) suggested that competitive exclusion is not important in soft sediments because of the lack of a mechanism for overgrowth or crushing, as seen on hard substrates, and the resistance of most invertebrates to exclusion through exploitive competition.

Distinct assemblages of soft-sediment organisms may result from interactions between functional groups (Rhoads and Young, 1970; Woodin, 1974; Brenchley, 1981, 1982a). Organisms with similar modes of life, such as mobile deposit feeders or tube builders, may alter the environment so that other groups are excluded (see Woodin and Jackson, 1979, for a review). However, while functional group interactions may be responsible for the disjunct distributions of certain species assemblages, they have not been shown to act along a tidal gradient to produce zonation.

Predator exclusion experiments have indicated that predation may reduce the abundance of many epifaunal and shallow infaunal species (Naqui, 1968; Reise, 1978; Woodin, 1978; Virnstein, 1977, 1978; Lee II, 1978; Holland et al., 1980; Wiltse, 1980; Kneib and Stiven, 1982). Higher faunal abundances in seagrass beds have also been attributed to lower predation there than in areas lacking seagrasses (Young et al., 1976; Young and Young, 1977; Heck and Thoman, 1981). Secondary predators may affect abundances of shallow infauna in sub-tropical seagrass beds (Nelson, 1981). Although deeper burrowing fauna may be subject to partial predation, such as siphon snipping in clams (Peterson and Quammen, 1982), their numbers have generally not been observed to change with reduced predator abundances.

Evidence directly implicating predation as a cause of intertidal zonation has also mainly involved epifaunal and shallow infaunal species. Densities of a sand dollar, *Dendraster*, are reduced subtidally by sea star predation (Birkeland and Chia, 1971). The snail *Cerithidia* occurs most commonly in salt marsh pans beyond the tolerance of its predator, *Ilyanassa* (Race, 1982), and *Ilyanassa* larvae appear to be susceptible to *Littorina* predation (Brenchley, 1982b). Dense aggregations of the amphipod *Corophium* have been reported from the upper intertidal above the regions of heaviest predation (Reise, 1978) and other amphipods have been observed to occupy marsh habitats when predators are abundant (Van Dolah, 1978). However, predation has not been reported to cause zonation in deeper burrowing infauna and there is no evidence that predation on a competitive dominant may prevent competitive exclusion, as observed in the rocky intertidal community (Peterson, 1979).

Thus most evidence to date suggests that zonation of soft-sediment organisms is largely in response to physical factors, with predation determining the lower distribution of certain near-surface animals. Competitive exclusion appears unimportant in producing zonation, and keystone predators, such as sea star preying on mussels (Paine 1974) have not been observed.

The ghost shrimp, *Callianassa californiensis*, forms dense beds in the mid intertidal of many Oregon and Washington sandflats, but is usually present in low numbers in the low intertidal and subtidally (Thompson and Pritchard, 1969; McCrow, 1971; Swinbanks and Murray, 1981; personal observation). These mid-intertidal beds occur over a wide range of sediment types. Because of the wide geographical distribution of Callianassa (MacGinitie, 1934) and its presence in a variety of substrate types, predation was suspected as a possible cause of zonation for this shrimp in Oregon estuaries. The following studies have two purposes: 1) to examine the distribution of other tideflat organisms with respect to a dense Callianassa bed and thus to look for possible competitive interactions, and 2) to estimate the role of predation in limiting these beds primarily to the mid intertidal.

CHAPTER II

FAUNAL ABUNDANCES CORRELATED WITH A DENSE CALLIANASSA CALIFORNIENSIS BED

Introduction

Biological interactions as potential organizing forces in silt and sand bottom communities have generated considerable interest during the past several decades. Early work on the distribution of animals in soft substrates concentrated on the effects of sediments (especially sediment grain size) and currents in determining the species composition of these habitats (Allen, 1899; Peterson, 1918; MacGinitie, 1935; Shelford et al., 1935; Jones, 1950; Coe, 1953; Pratt, 1953; Weiser, 1956, 1959). Sanders (1958; Sanders et al., 1962) has suggested that sediment grain size may determine the dominant feeding mode in an area, and numerous recent studies continue to support the contention that sediment characteristics are correlated with large scale (>100 m) patterns in species abundance and feeding type (Pfitzenmeyer and Drobeck, 1967; Longbottom, 1970; Nichols, 1970; Bloom et al., 1972; Boesch, 1972, 1973; Meadows and Campbell, 1972; Driscoll and Brandon, 1973; Featherstone and Risk, 1977; Holland and Dean, 1977; Lawrence and Murdoch, 1977; Levinton, 1977; Mountford et al, 1977; Whitlatch, 1977, 1981; Oliver et al., 1980; Chester et al., 1983). However, it has become increasingly apparent that indirect interactions among soft-sediment flora and fauna, often involving modifications of the immediate environment, may play a dominant role in determining the species composition of the benthic community on a local scale.

Rhoads and Young (1970), with their trophic group amensalism hypothesis, were among the first to examine the effects on the benthic community of physical changes resulting from the activities of soft-sediment organisms. In this theory, they attempted to explain the near absence of suspension feeders (organisms filtering food from the water column) in fine deposits, and their dominance in sandy environments by suggesting that deposit feeders excluded suspension feeders from silty substrates through resuspension of sediment while feeding. The increased amount of resuspended material associated with disturbance from deposit feeding would clog the filtering apparatus of suspension feeding animals and inhibit their filtering capabilities. Moreover, deposit feeders would be uncommon in sands because of a deficiency of detrital material in these areas. Several parts of this trophic group amensalism hypothesis have been supported. A dominance of deposit feeders in finer sediments and suspension feeders in sands has been reported from several areas (Bloom et al., 1972; Driscoll and Brandon, 1973; Myers, 1977; Whitlatch, 1977). Some burrowing deposit feeders appear to increase the amount of resuspended sediment (Brenchley, 1978; Grant et al., 1982; Nowell et al., 1981; Murphy, 1983) and an increase in the amount of suspended sediment affects the filtration rate of at least certain suspension feeders (Stone and Palmer, 1975; Gerrodette and Fleshig, 1979; Murphy, 1983).

However, several studies have described discrete assemblages of soft-sediment organisms that are not easily explained on the basis of a trophic group model alone. These involve functional groups such as tube-building animals, burrowing deposit feeders, or suspension feeding bivalves. Mobile deposit feeders have been found to affect sedentary deposit feeders adversely (Ronan, 1975; Brenchley, 1981; Wilson, 1981; Bird, 1982). Tube-dwelling deposit feeders and tube-dwelling suspension feeders may occur together in high densities (Young and Rhoads, 1971), and deposit feeders or mobile predators may be excluded by sedentary organisms (Woodin, 1974; Brenchley, 1982a; Peterson, 1982).

Brenchley (1978, 1981, 1982a) has proposed that mobile and sedentary organisms represent distinct functional groups which can exclude each other regardless of feeding method. Mobile animals disturb the sediment, thereby preventing the establishment of sedentary forms, while sedentary organisms will tend to bind the sediment and will therefore inhibit burrowing. Since most suspension feeders are sedentary and most infaunal mobile organisms are deposit feeders, Brenchley's mobility mode hypothesis may, in certain cases, lead to the same predictions concerning species associations as Rhoads and Young's trophic group amensalism hypothesis.

A third functional group hypothesis involving sediment modification has been proposed by Woodin (1976). She has suggested that discrete assemblages of burrowing deposit feeders, tube-dwelling polychaetes and crustaceans, and suspension feeding bivalves may occur through adult-larval interactions between these groups. Deposit feeders may prevent the establishment of tube builders or suspension feeding bivalves by continually disrupting the surface sediments. Alternatively, tube builders may occupy most of the available surface space or defecate over the remaining area, thus preventing successful larval colonization. Dense assemblages of suspension feeding bivalves were considered capable of filtering most larvae from the water before they could settle.

Although the mechanism of interaction differs among these three hypotheses, they all seek to explain the occurrence of discrete assemblages of species in soft sediments, and to determine how interactions between functionally different organisms affect the species composition of soft-sediment benthos. The present study constitutes one example where such functional group interactions are possibly a major factor determining the distribution and abundance of tideflat fauna, and it will identify the major functional groups involved and their mode of interaction.

The ghost shrimp, Callianassa californiensis, is a burrowing deposit feeder, often living in burrows up to 0.5 m in depth, on sandflats in embayments of the North American west coast from Alaska to Baja California (MacGinitie, 1934). Dense beds of these animals may have over 500 individuals/m^2 (Bird, 1982) and their activity results in a continual reworking of near-surface sediments (MacGinitie, 1934; Bird, 1982). This bioturbation often gives the sediment in a dense bed a soft, quicksand quality. The intensity of shrimp activity varies seasonally, with higher activity during summer and a decrease in the winter months (see Chapter 3). In Oregon and Washington estuaries, ghost shrimp beds are generally restricted to the high and mid-intertidal zones (Hedgepeth, 1952; Thompson and Pritchard, 1969; Swinbanks and Murray, 1981), the lower limit sometimes being quite abrupt. Density may decrease by an order of magnitude over a horizontal distance of only 1-2 m and a vertical profile of only a few centimeters (personal observation).

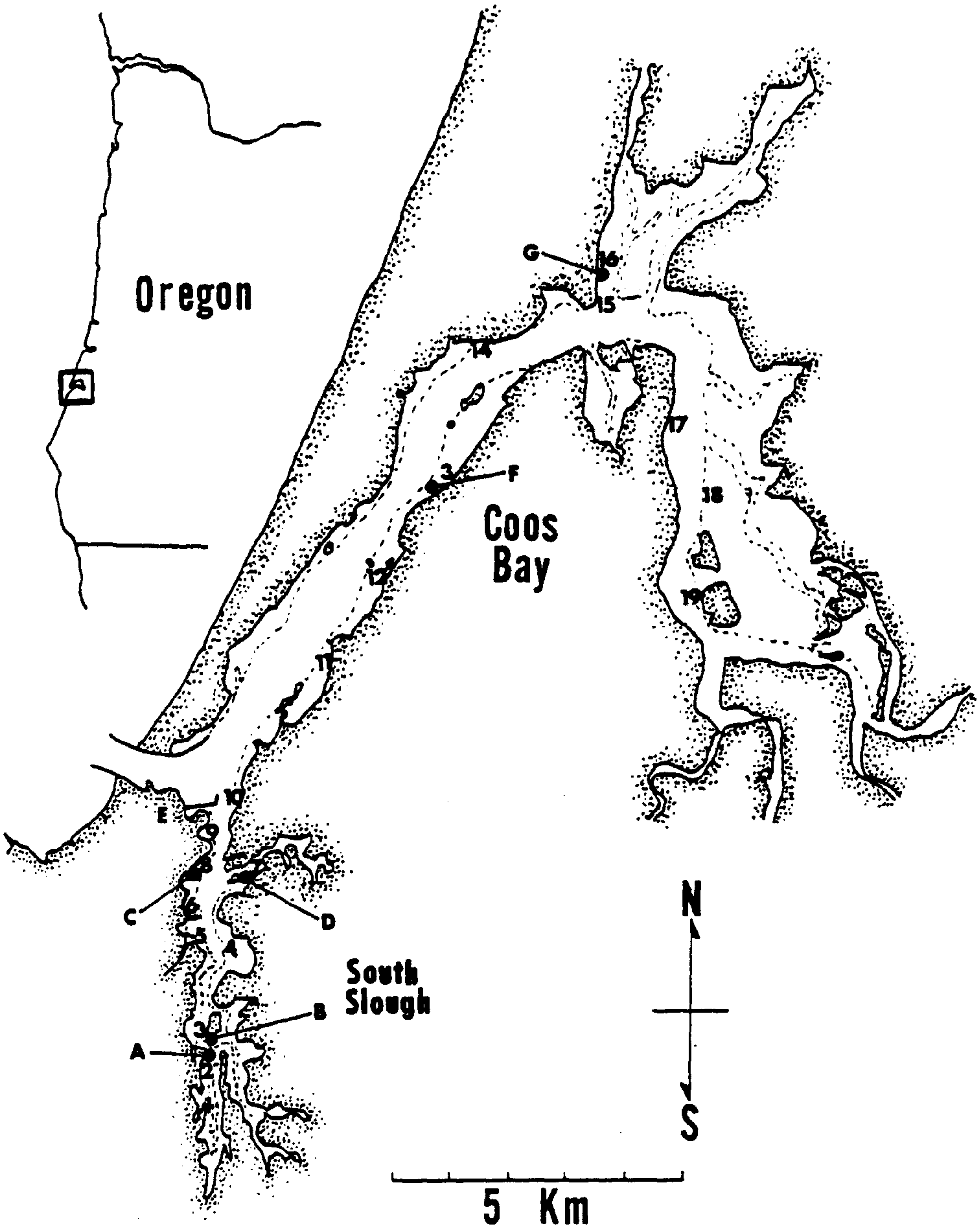
Given the proposed importance of burrowing deposit feeders in soft sediments (Rhoads and Young, 1970, Woodin, 1976; Brenchley, 1978), one might expect dense beds of _Callianassa californiensis_ to have a strong effect on the distribution of the benthic fauna. In the present study, benthic cores from within and outside a ghost shrimp bed were examined to determine if dense _Callianassa_ beds are correlated with changes in faunal species composition and abundance over short distances. If such correlations exist, one would expect seasonal changes in faunal distribution or abundance to be associated with changes in shrimp activity. Further, one should be able to discriminate whether distribution patterns are more easily explained by functional group interactions involving trophic groups or by a mechanism involving physical disruption of the sediment (mobility mode or adult-larval interactions).

Materials and Methods

Study Area

Sampling was conducted intertidally on the south side of Valino Island within the South Slough Estuarine Sanctuary, Coos Bay, Oregon (Figure II-1). This area experiences mild temperature fluctuations, air temperatures during the study usually remaining between 5°C and 30°C and surface water temperatures ranging from 10°C in winter to 20°C in summer (personal observation). Rainfall varies seasonally, with most

FIGURE II-1. Study sites within Coos Bay. A: Long Island Point; B: Valino Island; C: Battle Flats; D: Joe Ney; E: Oregon Institute of Marine Biology; F: Empire; G: Causeway. Numbered areas represent sites of hole density transects of examine zonation of dense shrimp beds.


Oregon
G
16
15
14
3
F
Coos Bay
17
18
19
12
11
10
E
9
8
C
D
7
6
5
A
South Slough
B
3
A
2
1
N
S
5 Km

falling during November through May. Low-tide surface water salinities ranged from a low of 4 $^{o}/oo$ during winter freshets to 31 $^{o}/oo$ during July and August. Interstitial salinities ranged from 16 $^{o}/oo$ to 31 $^{o}/oo$, suggesting that the occurrence of extreme low salinities during winter freshets does not last for extended periods.

Benthic samples were taken around a dense shrimp bed adjacent to a small Salicornia marsh. The substratum consisted primarily of fine sands (.125-.250 mm) with slightly coarser sediments within the ghost shrimp bed. The lower boundary of the bed marks an abrupt change in shrimp numbers with densities declining from $100/m^2$ to $2\text{-}3/m^2$ over a horizontal distance of less than 2 m. Although this lower edge of the shrimp bed became somewhat less abrupt during winter, the position of the bed remained relatively constant throughout the study.

Sampling

Benthic cores were collected in three areas: within the ghost shrimp bed; along the transition zone from high to low Callianassa density (intermediate density); and in an area of low shrimp abundance approximately 3 m from the ghost shrimp bed. All three areas were approximately 1 m above mean lower low water (MLLW). The distance between areas of high and low density was 5-6 m. Samples within each of the three areas were chosen haphazardly with the toss of a shell. Three replicates were taken in each area at roughly bimonthly intervals (March, June, July, September, October, January) from March 1982 to January 1983 and five samples were taken from each area at quarterly intervals from February 1983 to February 1984. In order to examine seasonal variations in faunal abundance and the effect of disturbance by shrimp, the 1982 data were combined into seasonal categories for analysis (Spring: March-May; Summer: June-August; Fall: September-November; Winter: December-February). These intervals roughly correspond to the rain and upwelling cycles prevalent along the Oregon coast (such as maximum rainfall between December and February and strong upwelling in June and July).

Cores were 12.5 cm in diameter and 15 cm deep. They were immediately preserved in 4% formaldehyde with rose bengal dye added, seived after 4-5 days on a 0.5 mm screen, and transferred to 70% ethanol for storage (Gonor and Kemp, 1978). Counting was done under the 10x power of a dissecting microscope, recording only the number of whole organisms or heads present. Identifications were made using Fauchald (1977), Hartman (1968a, 1968b), and Smith and Carlton (1975). The identifications were kindly checked by Lynn Rudy from the Oregon Institute of Marine Biology and by Howard Jones from Oregon State University.

Statistical Analysis

A two-way analysis of variance (ANOVA), blocking for differences between years, was used to test the effect of ghost shrimp density, season, and interactions between season and shrimp density on species abundances. Blocking for years was considered necessary because of the unusual sea conditions associated with the 1983 El Niño/Southern Oscillation event. Since a significant interaction, effect may be expected if shrimp activity varies seasonally, it should be noted that in a model I ANOVA, such as used here, the presence of significant interactions does not invalidate an examination of main effects (Sokal and Rohlf, 1981).

F-max tests (Sokal and Rohlf, 1981) for the ten most abundant species indicated that variances were heterogeneous between sampling dates and a $\log_{10}(x+1)$ transformation was applied to achieve homogeneity. The absence of some species from a sampling location on a particular date (resulting in a zero variance for that cell) was not considered to be a major problem since recalculation of the ANOVA substituting small artificial variances in these cases did not yield noticeably different results. All ANOVA's were calculated with the General Linear Models Procedure of the Statistical Analysis System (Ray, 1982).

Results

Forty-nine taxa were identified from the South Slough study site, 37 to the generic or species level (see Appendix). A single species, the tanaid *Leptochelia dubia*, constituted 44-75% of the animals during each sampling period. Over 95% of the individuals collected were represented by only seven taxa.

To examine the relationship between the number of species and ghost shrimp density, the number of species in the three sampling areas (Table II-1) was compared using a G-test, blocking for seasonal variations (Sokal and Rohlf, 1981). Differences were not significant (G=3.58; 16 d.f.). Since higher taxa may contain several species with independent distributions, their inclusion may bias the results of this statistic.

TABLE II-1. Number of taxa collected near a dense *Callianassa californiensis* bed.

	Spring 1982	Summer 1982	Fall 1982	Winter 1983	Spring 1983	Summer 1983	Fall 1983	Winter 1984	2 year total
number of samples per area	3	6 (5 below bed)	6	8	5	5	5	5	43 (42 below bed)
number of taxa taken per area:									
within bed	20	25	23	19	15	13	18	18	39
transition zone	18	21	24	20	17	20	17	18	35
below bed	15	25	26	22	20	22	22	25	39

Repetition of the analysis using only organisms identified to the generic or species level also indicates no relationship between shrimp density and species number (G=2.41; 16 d.f.). There is likewise no difference in the total number of taxa from areas of high and low shrimp density pooled for the two year sampling period (Table II-1).

Even if high *Callianassa* density does not affect the number of resident species, it may produce changes in the abundance of some. In particular, one might expect negative effects on suspension feeding (Rhoads and Young, 1970) or sedentary organisms (Woodin, 1974; Brenchley, 1981). The effects of *Callianassa* abundance in South Slough were examined for the ten most abundant taxa (Table II-2), representing over 98% of the animals collected during this study.

Three of these ten were polychaete worms belonging to the family Spionidae: *Pseudopolydora kempi japonica*, *Pygospio elegans*, and *Streblospio benedicti*. All three are sedentary, tube-dwelling deposit feeders that collect detrital material from the tideflat surface using ciliated palps (Fauchald and Jumars, 1979); although *Pygospio* and *Pseudopolydora* may also be facultative suspension feeders under certain current regimes (Taghon et al., 1980). *Pygospio elegans* and *Streblospio benedicti* are common constituents of soft-bottom communities along the Atlantic coast of North America and have often been considered as opportunistic colonizers (Boesch, 1973; Grassle and Grassle, 1974; McCall, 1977; Whitlatch, 1981; Kneib and Stevens, 1982; Dauer, 1984). Densities of *Pygospio*, *Streblospio*, and *Pseudopolydora* in this study were negatively correlated with that of *Callianassa californiensis* (Table II-3; Figure II-2). Only with *Pseudopolydora* was there a

TABLE II-2. Mean numbers per .01 m^2 (and standard error of mean) for the ten most abundant taxa collected from spring 1982 to winter 1984. Sampling locations are abbreviated as H (within bed), T (transition zone), and L (below bed).

Taxon, mobility, and feeding mode	% of fauna	Sampling location	Spring 1982 n=3	Summer 1982 n=6(L=5)	Fall 1982 n=6	Winter 1983 n=8	Spring 1983 n=5	Summer 1983 n=5	Fall 1983 n=5	Winter 1984 n=5
Crustacea										
Tanaidacea										
Leptochelia dubia	63.5	H	674.3	223.3	946.5	831.8	169.0	450.5	950.6	453.6
m-d.f.*			(32.9)	(96.8)	(243.5)	(53.1)	(20.4)	(52.8)	(65.6)	(71.6)
		T	659.0	627.8	952.2	1048.3	249.0	645.6	448.8	906.4
			(35.8)	(279.1)	(106.8)	(53.7)	(30.3)	(81.7)	(39.9)	(51.9)
		L	895.3	560.4	655.3	686.5	105.4	280.2	391.6	654.4
			(9.0)	(97.6)	(203.6)	(131.9)	(9.1)	(24.6)	(30.4)	(65.1)
Ostracoda	7.1	H	44.7	21.0	30.5	41.1	74.4	34.2	27.4	4.6
m-?			(17.7)	(5.8)	(6.1)	(6.6)	(10.4)	(5.0)	(3.4)	(0.9)
		T	16.7	110.8	177.7	101.3	6.8	166.2	48.4	10.6
			(8.4)	(46.6)	(46.7)	(12.4)	(1.5)	(24.3)	(9.4)	(1.7)
		L	39.3	255.4	182.8	136.6	71.6	16.4	1.8	0.8
			(28.2)	(44.4)	(33.8)	(20.5)	(8.4)	(2.2)	(0.6)	(0.6)
Amphipoda										
Eobrolgus spinosus	6.6	H	100.7	24.0	34.3	99.9	112.0	55.0	76.6	44.4
m-s			(26.3)	(10.9)	(5.8)	(6.8)	(21.4)	(9.7)	(8.0)	(3.8)
		T	102.7	66.7	129.5	110.4	82.4	112.6	50.6	41.6
			(9.7)	(31.6)	(63.4)	(7.4)	(6.2)	(23.0)	(5.6)	(2.9)
		L	135.3	70.4	27.5	12.8	1.2	0.4	1.4	1.8
			(10.7)	(27.3)	(6.6)	(3.8)	(0.4)	(0.2)	(0.7)	(0.7)

TABLE II-2. Continued.

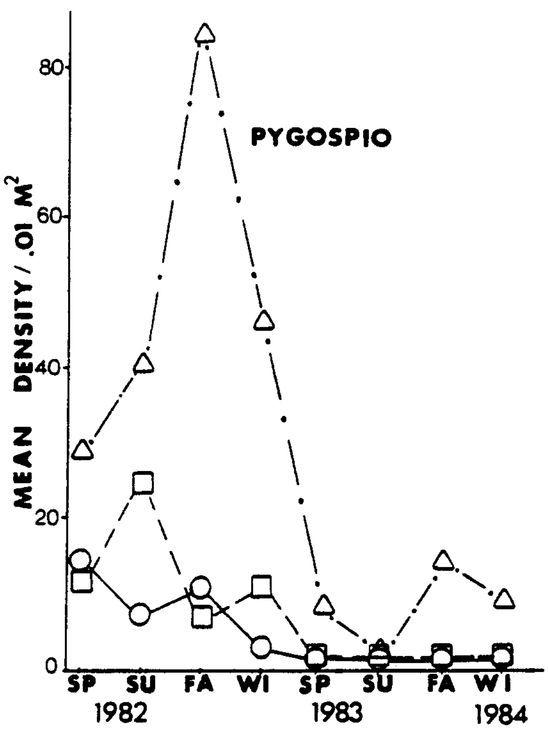
Taxon, mobility, and feeding mode	% of fauna	Sampling location	Spring 1982 n=3	Summer 1982 n=6(L=5)	Fall 1982 n=6	Winter 1983 n=8	Spring 1983 n=5	Summer 1983 n=5	Fall 1983 n=5	Winter 1984 n=5
Corophium	2.8	H	2.3	4.0	73.2	16.5	4.6	4.2	6.6	1.8
spp.			(1.4)	(1.2)	(12.4)	(3.0)	(2.4)	(1.6)	(1.5)	(0.7)
s-?		T	3.7	64.8	50.2	31.9	5.4	12.8	19.2	3.0
			(1.8)	(25.5)	(7.1)	(3.5)	(0.8)	(4.7)	(3.0)	(1.0)
		L	7.3	197.8	63.8	5.1	0.6	3.2	57.2	0.8
			(1.8)	(48.0)	(12.7)	(1.4)	(0.4)	(1.0)	(15.7)	(0.4)
Grandidierella	1.2	H	0	0	0.2	3.3	0.6	10.8	9.4	3.0
japonica			-	-	(0.2)	(0.8)	(0.4)	(2.4)	(0.9)	(1.0)
s-d.f.		T	8.0	0.2	1.0	6.4	6.4	26.4	52.2	18.4
			(3.5)	(0.2)	(0.8)	(1.4)	(1.4)	(6.0)	(9.9)	(5.7)
		L	0	1.2	0.3	9.3	1.2	27.6	71.0	7.6
			-	(1.2)	(0.3)	(2.1)	(0.6)	(5.5)	(3.7)	(2.6)
Cumacea	2.1	H	3.7	3.0	1.8	38.9	0.8	1.0	1.2	0.6
m-d.f.			(1.7)	(0.9)	(1.2)	(6.3)	(0.6)	(0.3)	(0.6)	(0.2)
		T	43.3	28.3	7.2	43.1	33.4	3.8	2.0	2.8
			(18.2)	(12.6)	(2.0)	(8.0)	(17.5)	(1.2)	(0.4)	(0.5)
		L	94.0	67.4	18.8	26.1	24.2	21.6	5.4	0.6
			(9.1)	(6.3)	(1.8)	(4.3)	(5.0)	(7.6)	(1.8)	(0.4)
Oligochaeta	11.1	H	108.0	197.7	77.7	80.1	37.8	24.2	57.6	119.8
m-d.f.			(13.1)	(61.1)	(12.9)	(11.3)	(5.5)	(1.5)	(12.3)	(13.1)
		T	98.5	245.2	78.0	129.1	48.4	119.2	114.6	225.0
			(12.5)	(73.9)	(19.7)	(14.6)	(23.6)	(47.2)	(29.4)	(63.9)
		L	218.7	85.8	75.3	98.5	58.4	45.6	76.6	98.4
			(81.7)	(27.5)	(27.4)	(9.9)	(5.5)	(3.9)	(4.5)	(8.9)

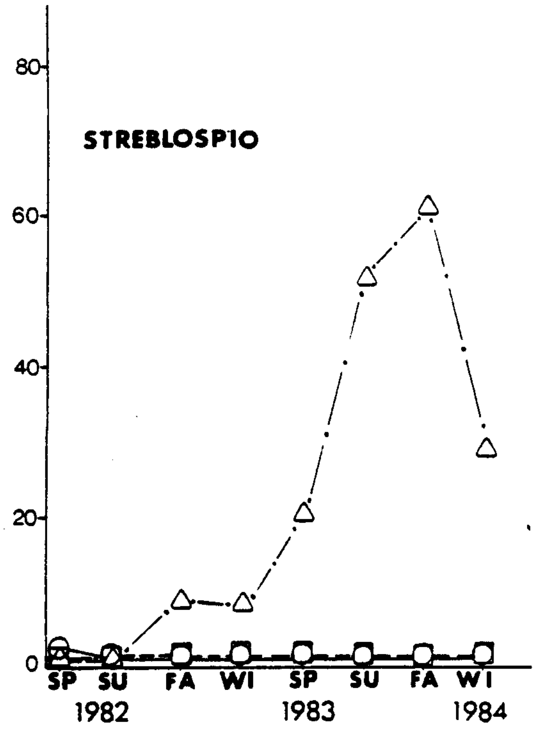
TABLE II-2. Continued.

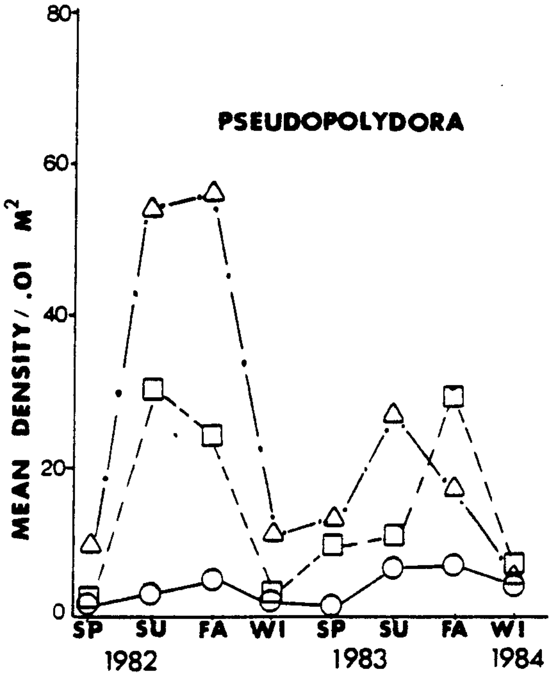
Taxon, mobility, and feeding mode	% of fauna	Sampling location	Spring 1982 n=3	Summer 1982 n=6(L=5)	Fall 1982 n=6	Winter 1983 n=8	Spring 1983 n=5	Summer 1983 n=5	Fall 1983 n=5	Winter 1984 n=5
Polychaeta										
Spionidae										
Pseudopolydora	1.5	H	9.7	54.4	56.3	11.0	13.0	26.8	17.2	5.8
kempi			(6.2)	(5.1)	(4.5)	(1.8)	(2.8)	(4.7)	(3.5)	(2.0)
s-d.f.		T	2.0	30.2	24.0	3.4	9.8	11.4	29.8	7.8
			(0)	(14.4)	(6.4)	(0.8)	(2.3)	(3.0)	(7.7)	(2.6)
		L	9.7	54.4	56.3	11.0	13.0	26.8	17.2	5.8
			(6.2)	(5.1)	(4.5)	(1.8)	(2.8)	(4.7)	(3.5)	(2.0)
Pygospio	1.5	H	14.7	7.2	10.7	3.0	0	0.6	0.4	0.2
elegans			(7.7)	(0.9)	(1.9)	(0.9)	-	(0.2)	(0.2)	(0.2)
s-d.f.		T	11.7	24.7	7.8	11.4	1.6	0.4	0.8	0.8
			(2.2)	(7.1)	(1.1)	(3.3)	(0.4)	(0.2)	(0.4)	(0.4)
		L	29.0	40.6	84.3	46.0	8.6	1.6	14.0	9.0
			(7.6)	(18.9)	(38.8)	(9.8)	(1.8)	(0.9)	(2.8)	(2.8)
Streblospio	0.8	H	2.3	0.2	0.5	0	0	0	0	0.2
benedicti			(0.7)	(0.2)	(0.3)	-	-	-	-	(0.2)
s-d.f.		T	0	0.5	1.2	0	0	0.2	0	0.4
			-	(0.2)	(0.7)	-	-	(0.2)	-	(0.4)
		L	0	0.4	9.0	8.1	20.6	52.0	60.8	29.2
			-	(0.2)	(3.6)	(1.8)	(5.1)	(7.0)	(10.6)	(3.6)

*m=mobile; s=sedentary; d.f.=deposit feeder; s.f.=suspension feeder; ?=feeding mode not known.

FIGURE II-2. Seasonal abundance of spionid polychaetes. Exact values for means and standard errors are given in Table II-2. Circles: within Callianassa bed; squares: transition zone; triangles: below Callianassa bed.


PYGOSPIO
MEAN DENSITY/.01 M^2
0
20
40
60
80
SP
SU
FA
WI
SP
SU
FA
WI
1982
1983
1984


STREBLOSPIO
0
20
40
60
80
SP
SU
FA
WI
SP
SU
FA
WI
1982
1983
1984


PSEUDOPOLYDORA
MEAN DENSITY/.01 M^2
0
20
40
60
80
SP
SU
FA
WI
SP
SU
FA
WI
1982
1983
1984

significant seasonal effect on abundance, and this species showed a slightly significant interaction between season and shrimp effects (Table II-3). The abundance patterns of the other two spionid species indicate strong yearly fluctuations that may have obscured seasonal variations.

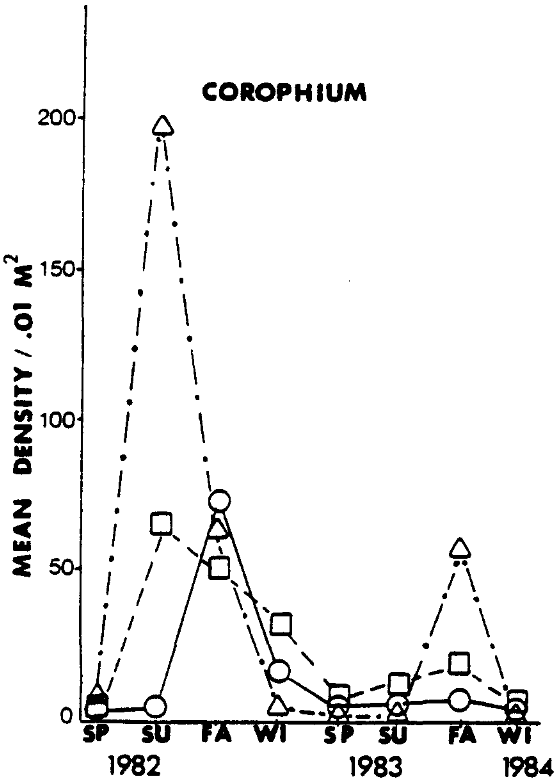
Three tube-building crustaceans were also commonly observed in this study, the amphipods _Corophium_ and _Grandidierella japonica_ and the tanaid _Leptochelia dubia_. Several of the _Corophium_ were identified as _Corophium brevis_; however, the small number of individuals and lack of female specimens on certain dates made it difficult to ascertain whether this was the only species of _Corophium_ present. Since members of the genus _Corophium_ use filtering mouthparts to collect detritus from the tideflat surface (Rudy and Rudy, 1983; Miller, 1984), they do not easily fit into the usual trophic categories and have been variously classified as both surface deposit feeders and suspension feeders (Brenchley, 1978, 1981; Bird, 1982). _Grandidierella_ and _Leptochelia_ deposit feed or scavenge (Smith and Carlton, 1975; Mendoza, 1982).

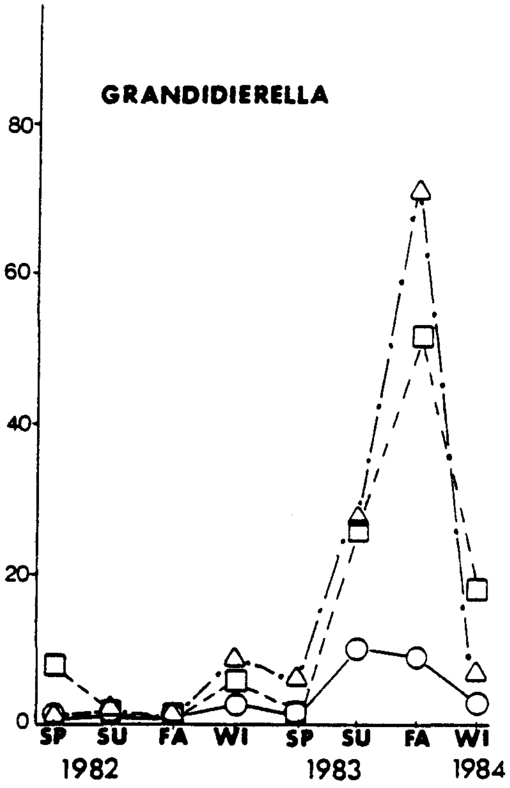
Corophium and _Grandidierella_ exhibited a spatial pattern similar to that of the tube-dwelling polychaetes, with lower abundances within the ghost shrimp bed and higher numbers in areas of low _Callianassa_ density (Table II-3; Figure II-3). The numbers of both amphipods varied seasonally. Strong seasonal variation in the effect of shrimp density on abundance was observed for _Corophium_. The interaction between shrimp density and seasonality was only slightly significant for _Grandidierella_.

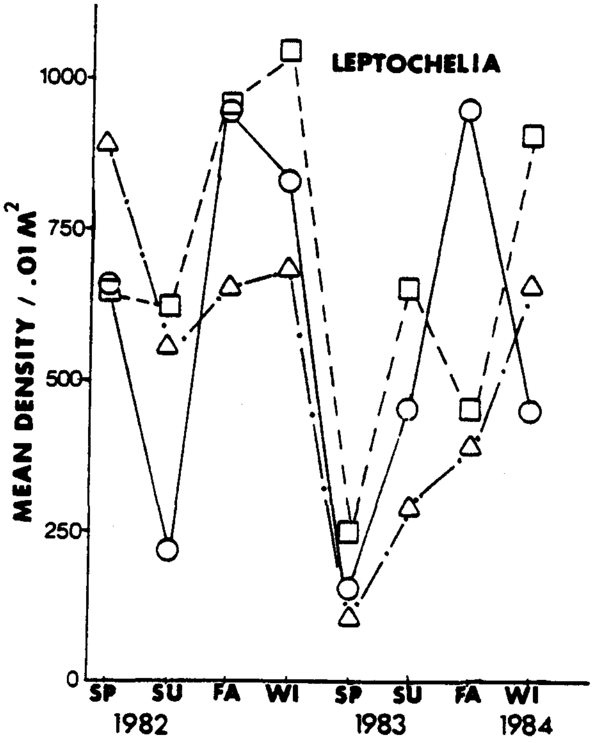
TABLE II-3. F-statistics for the effect of shrimp density, season and shrimp*season interactions on the abundance of the ten most common taxa sampled at Valino Island. Degrees of freedom are 2 for shrimp density, 3 for season and 6 for interaction.

Taxon	Shrimp Density	Season	Season*Shrimp Density Interaction
<u>Leptochelia dubia</u>	.99 N.S.	11.52 p<.0001	1.38 N.S.
Ostracoda	9.68 p<.0001	2.50 N.S.	.61 N.S.
<u>Eobrolgus spinosus</u>	32.77 p<.0001	3.29 p<.025	.99 N.S.
<u>Corophium</u> spp.	6.79 p<.005	32.50 p<.0001	6.56 p<.0001
<u>Grandidierella japonica</u>	11.52 p<.0001	10.61 p<.0001	1.68 N.S.
Cumacea	37.02 p<.0001	10.79 p<.0001	8.18 p<.0001
Oligochaeta	1.04 N.S.	2.79 p<.05	2.40 p<.05
<u>Pseudopolydora kempi</u>	42.10 p<.0001	20.68 p<.0001	2.20 p<.05
<u>Pygospio elegans</u>	39.03 p<.0001	.86 N.S.	2.54 p<.025
<u>Streblospio benedicti</u>	96.50 p<.0001	2.27 N.S.	1.34 N.S.

FIGURE II-3. Seasonal abundance of tube building crustaceans. Exact values for means and standard errors are given in Table II-2. Circles: within _Callianassa_ bed; squares: transition zone; triangles: below _Callianassa_ bed.


COROPHIUM
MEAN DENSITY / .01 M^2
200
150
100
50
0
SP
SU
FA
WI
SP
SU
FA
WI
1982
1983
1984


GRANDIDIERELLA
80
60
40
20
0
SP
SU
FA
WI
SP
SU
FA
WI
1982
1983
1984

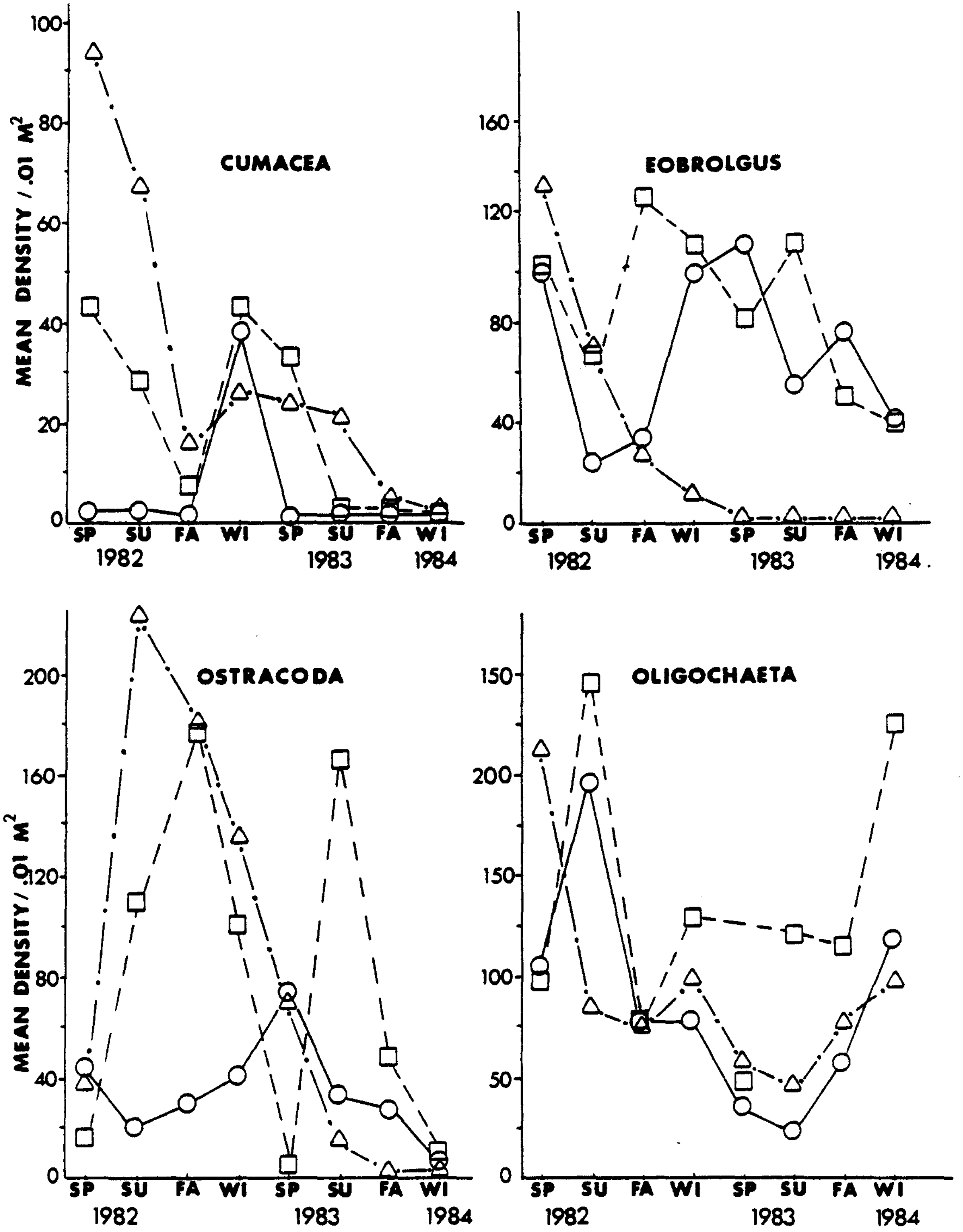

LEPTOCHELIA
MEAN DENSITY / .01 M^2
1000
750
500
250
0
SP
SU
FA
WI
SP
SU
FA
WI
1982
1983
1984

In contrast to the tubicolous amphipods, the tanaid Leptochelia dubia did not have lower numbers within a dense ghost shrimp bed than outside the bed. Highest abundances occurred in the zone of transitional (intermediate) ghost shrimp density during seven of the eight seasons sampled.

The four remaining taxa, cumaceans, ostracods, oligochaetes, and the amphipod Eobrolgus spinosus, are generally considered mobile forms (Smith and Carlton, 1975; Brenchley, 1978; Barnes, 1980). The dominant cumacean species were Cumella vulgaris and Hemileucon comes, of which at least Cumella is a deposit feeder (Weiser, 1956). The two are not dealt with separately because of problems in distinguishing them in early samples, but they showed similar distributions with respect to shrimp density during the second year of sampling. Total cumacean abundance showed a decreasing trend over the two years, while varying with both season and Callianassa density (Table II-3; Figure II-4). Highest numbers during summer, fall, and the first spring were observed in areas of low ghost shrimp abundance; however, the densities within the ghost shrimp bed and along the transition zone increased dramatically in winter, suggesting seasonal variation in the effect of ghost shrimp disturbance.

Ostracods proved difficult to identify and classification is only to the class level. As a group, ostracods are generally mobile, but display a diverse array of feeding types, including carnivory, herbivory, scavenging, filter feeding, and deposit feeding (Devine, 1980). Ostracod numbers were initially high in areas of low Callianassa

Figure II-4. Seasonal abundance of mobile organisms. Exact values for means and standard errors are given in Table II-2. Circles: within *Callianassa* bed; squares: transition zone; triangles: below *Callianassa* bed.


CUMACEA
EOBROLGUS
OSTRACODA
OLIGOCHAETA
MEAN DENSITY / .01 M^2
MEAN DENSITY / .01 M^2
100
80
60
40
20
0
160
120
80
40
0
200
160
120
80
40
0
150
200
150
100
50
0
SP
SU
FA
WI
SP
SU
FA
WI
1982
1983
1984

abundance but declined steadily after the summer of 1982 (Figure II-4). During the second year of sampling, highest ostracod abundances were along the lower edge of the shrimp bed. Density did not vary significantly with season.

The gammarid amphipod, Eobrolgus spinosus (=Paraphoxus, see Barnard and Barnard, 1981), is an active burrower (Smith and Carlton, 1975; Brenchley, 1978, Bird, 1982) classified by Brenchley (1978, 1981) as a suspension feeder. Eobrolgus abundance in areas of low Callianassa density showed a pattern similar to that of the ostracods, with initially high abundances declining steadily throughout the two year period (Figure II-4). During most sampling periods, highest Eobrolgus density was observed from within the ghost shrimp bed or from the transition zone. Although numbers of this amphipod varied seasonally, interactions between season and shrimp density did not appear important.

Dr. R. O. Brinkhurst (Institute of Ocean Sciences, British Columbia, Canada) identified oligochaetes from several of the South Slough samples as Limnodriloides victoriensis Brinkhurst and Baker (written communication). It is not possible to determine if other species of oligochaetes also occurred commonly in the study area. Macrofaunal marine oligochaetes are generally considered to be mobile deposit feeders (Smith and Carlton, 1975; Brenchley, 1978). No significant pattern of abundance was observed for these worms with respect to Callianassa density (Table II-3; Figure II-4).

To summarize the results, distributional patterns for eight of the ten most abundant organisms observed in this study were correlated with Callianassa density. Seven of these showed highest abundance with low or intermediate shrimp numbers. They included four sedentary, deposit feeding species, one mobile, deposit feeding taxon, and one sedentary and one mobile taxon of uncertain feeding mode. One mobile, suspension feeding species achieved highest densities within the ghost shrimp bed. The two most abundant taxa, oligochaetes and a tanaid, did not seem significantly affected by ghost shrimp activity. Interactive effects between season and ghost shrimp density were strong for two species.

Discussion

Although marine animals have often been thought to have little effect on their environment, *Callianassa* activity appears a potentially important structuring agent in certain habitats. Bird (1982) suggested that *C. californiensis* reduces sediment organic content and affects sediment grain size and sorting. A similar effect has been noted for a Caribbean species (Suchanek, 1983). Increased resuspension rates associated with *C. californiensis* have been reported from laboratory experiments (Brenchley, 1978; Murphy, 1983) and from field studies on a tropical species of *Callianassa* (Aller and Dodge, 1974). Records of *Callianassa* bioturbation also appear in geologic studies of near-shore sediments (Picket et al., 1971; Dewindt, 1974; Moreno and Curros, 1979).

Several studies have discussed the effects of *Callianassa* activity on the infaunal community. Brenchley (1978) and Bird (1982) noted a negative correlation between the abundance of several sedentary organisms and dense *C. californiensis* beds, including spionid polychaetes, the amphipod *Corophium*, and the tanaid *Leptochelia dubia*. Highsmith (1982) also provided evidence that *Leptochelia* was susceptible to bioturbation. Peterson (1979), Murphy (1983), and Stevens (1928) found that *C. californiensis* may exclude certain bivalve species and Ronan (1975) showed that the ghost shrimp may inhibit a tube-dwelling phoronid. Aller and Dodge (1974) observed a negative effect of a tropical species of *Callianassa* on suspension feeding organisms. Turtlegrass growth was reduced in the presence of a Caribbean species (Suchanek, 1983). Spionid polychaete distributions were negatively correlated with that of *C. ceramica* in Australia (Dorsey and Synnot, 1980). Bird (1982) also observed significantly fewer species within a *C. californiensis* bed compared to beds of the sedentary burrowing shrimp, *Upogebia puggettensis*, but no data were provided from habitats in which neither species was common.

This study of *C. californiensis* at South Slough differs from others in observing community changes on the scale of only a few meters. Yet even along the lower edge of the shrimp bed examined here, abundances of several species were strongly correlated with ghost shrimp density. However, the number of species did not change along this gradient, as might have been expected from Bird's (1982) results. Since Bird compared samples from within a *Callianassa* bed to those taken within a *Upogebia* bed, the difference in number of species may be partially a result of positive effects associated with *Upogebia*, such as increased area for surface contact and increased sediment stability (Thompson, 1972). Also, Bird used sampling locations separated by more than 100 meters along an estuarine gradient. The greater distance between samples could imply greater habitat heterogeneity that may have contributed to differences in species number.

The results from the benthic samples presented thus far have been correlative, involving comparisons of samples taken in different areas. In order to demonstrate a causal relationship between shrimp density and faunal abundances, it would be desirable to manipulate shrimp numbers and observe the response patterns of other members of the community. Bird (1982) placed containers of defaunated sediment within a northern Oregon ghost shrimp bed and, after six months, observed an almost five-fold increase in spionid and capitellid polychaete densities as compared to the surrounding bed. *Corophium* densities increased to three or four times that of a dense bed. After 24 to 36 months, *Callianassa* had successfully invaded the exclosures and the abundances of polychaetes and amphipods declined to those of the surrounding area. Bird's results, along with laboratory observations of the effect of ghost shrimp disturbance on selected organisms (Brenchley, 1978; Murphy, 1983), suggest that the distribution patterns seen in this study are at least partially a result of *Callianassa* activity.

The effect of a decrease in *Callianassa* activity during winter is unclear. Assuming some migration of benthic fauna, one might expect a reduction in the differences between areas of low and high ghost shrimp density with a decrease in their bioturbating activities. Such a pattern occurred among the cumaceans and the amphipod *Corophium* (although for *Corophium* this coincided with a period of generally low numbers). However, for other species interactive effects were either nonsignificant or slight in comparison with the main effects of season and shrimp density. One possible explanation for this result may be that the application of a transformation masked interactive effects.

Since one effect of a transformation is to produce additivity in the data, nonadditive interactions may not be apparent after its application. However, examination of the abundances of the ten organisms over time (Figures II-2, II-3, II-4) does not suggest interactions between season and shrimp density which were not detected by the statistical analysis. A second reason for this lack of an interactive effect may be an error in assuming that adult migration occurs over several meters. Among spionid polychaetes, both Streblospio benedicti and Pygospio elegans have been reported to emigrate in response to stress (Levin, 1982). If there is no such emigration under low stress conditions in the field, if it involves only short distances, or is limited in the winter months, little reduction in spionid zonation would occur. Also, winter and spring represented a time of low abundance in all three areas for several species, suggesting low settlement or survival at this time.

The presence of both mobile and sedentary deposit feeders in the South Slough community allows an examination of the extent to which functional group models based on mobility mode or trophic group interactions explain the influence of Callianassa on species abundance. Five deposit feeding organisms reached highest numbers outside a shrimp bed, whereas numbers of one suspension feeder were positively correlated with Callianassa abundance. Two other deposit feeders did not show a significant difference in distribution with respect to the shrimp bed. The trophic group amensalism hypothesis (Rhoads and Young, 1970) would not predict a negative effect of a deposit feeding shrimp on other deposit feeders, but would predict a negative effect upon suspension feeders. A mobility mode hypothesis predicts a negative effect by ghost shrimp on sedentary organisms and a neutral or positive effect on mobile animals. Five of the six sedentary organisms examined in this study were negatively correlated with Callianassa density, as were two of the four mobile taxa. One mobile species was positively associated with the shrimp bed, and one mobile and one sedentary form were not significantly affected. Most of these relationships appear consistent with predictions of a mobility mode hypothesis; however, the exceptions underscore the need for a more thorough understanding of species' habits and other potential interactions on community composition. Levin (1981, 1982) has shown that aggressive competition among spionid polychaetes (Pseudopolydora and Streblospio) is important to the spatial distribution of these worms. Similar interactions may provide an explanation for the lack of an increase of Leptochelia in areas with low Callianassa density, as was observed in this study. This relatively small crustacean may be particularly susceptible to aggression from larger polychaetes or amphipods. Levinton (1972, 1977) proposed that deposit feeding bivalve communities may be regulated by exploitive competition for food. Although exploitive competition would not explain the rapid response of many species to Callianassa under laboratory conditions (Brenchley, 1978), it could be important in specific cases, in this study possibly for cumaceans.

While the distributions of most infauna examined here tend to support a mobility mode of interaction, these conclusions should not be generalized beyond this habitat. Rhoads and Young (1970) suggested that trophic group amensalism may occur only in subtidal areas, although several researchers have noted distinct assemblages of deposit and suspension feeders in intertidal regions as well (Bloom et al., 1972; Myers, 1977; Whitlatch, 1977). As discussed previously, several studies, mostly from subtidal areas, have provided support for the trophic group amensalism hypothesis while Aller and Dodge (1974) and Murphy (1983) have found evidence that Callianassa spp. can affect flora and fauna subtidally through resuspension of particles rather than strictly via sediment disruption. It is becoming increasingly apparent that several modes of interaction among functional groups may be important, depending on the physical environment or species involved.

CHAPTER III

EXAMINATION OF ZONATION AND BEHAVIORAL PATTERNS IN *CALLIANASSA CALIFORNIENSIS*

Introduction

Because ghost shrimp live within relatively deep burrows, their density is difficult to measure directly without the excavation of large quantities of sediment. Aside from being time consuming and labor intensive, excavation prevents the monitoring of an area over time. Several researchers have used counts of burrow holes or mounds to estimate ghost shrimp density (MacGinitie, 1934; Aller and Dodge, 1974; Ott et al., 1976; Swinbanks and Murray, 1981; Suchanek, 1983). While some of these studies have provided estimates for the number of holes per shrimp, ranging from 1 to 4 among the various species of *Callianassa* (Pohl, 1946; Biffar, 1971; Ott et al., 1976; Swinbanks and Murray, 1981; Suchanek, 1983), they have not confirmed a statistically significant relationship between the density of burrow holes and ghost shrimp density. Devine (1966) and Frankenberg et al. (1974) have suggested that the number of holes/burrow may be highly variable, and Thompson and Pritchard (1969) and Ott et al. (1976) considered holes to be relatively impermanent structures that collapse during each tidal cycle.

Behavioral patterns of ghost shrimp are likewise difficult to observe outside of narrow glass tanks (limnoria) or artificial tubes. However, several authors have provided field observations of *Callianassa* behavior that suggest that some members of this genus are susceptible to predation by epibenthic animals. Torres et al. (1977) observed C. californiensis activity near the burrow entrance immediately after submergence and McCrow (1971) found that this ghost shrimp moved towards the surface when the tide covered the burrow. Carson (1955) noted that C. major can be enticed out of its burrow with small pieces of meat and Pohl (1946) suggested that C. major may leave its burrow for short periods. C. longiventris remained near the entrance of their burrows until disturbed (Biffar, 1971) and C. filholi feeds on the surface layer of sand (Devine, 1966).

This chapter will examine the relation between hole and shrimp density in nature as well as observations of Callianassa behavior within laboratory aquaria. Hole densities will be used to examine zonation patterns in four estuaries. A specific aim of the behavioral observations was to determine whether C. californiensis spends appreciable time near the burrow entrance. Potential seasonal variations in activity will also be examined in relation to temperature fluctuations and through laboratory tests of the effect of reduced salinity on activity.

Methods

Hole/Shrimp Correlations and Zonation Patterns

The relationship between the density of burrow holes and the number of ghost shrimp was examined by counting the number of holes in a haphazardly placed 0.5 m^2 quadrat and then taking three 50 cm deep by

12.5 cm diameter cores within the same area. The contents of the cores were combined and sifted by hand to determine ghost shrimp density. A few samples were reseived through a 1 mm mesh screen to ensure the accuracy of the hand seiving method. Samples were taken at low tide during four time periods: 1) July 9 to August 10, 1982; 2) November 10, 1982 to March 4, 1983; 3) June 21 to July 10, 1984; and 4) July 29 to August 4, 1984. All samples came from the Valino Island and Battle Flats areas (Figure II-1). Holes were counted monthly in three replicate 0.25 m^2 quadrats in a dense shrimp bed at Valino Island.

Hole density was observed qualitatively at several locations within Coos Bay that contained dense aggregations of *Callianassa* (numbered areas in Figure II-1) between 1982 and 1984. Surveys were made only during daylight tides lower than mean lower low water and generally involved walking from the wrack line down to the water's edge. Tidal levels were not measured directly, but were estimated for some areas by repeatedly comparing observed high and low tides with those predicted from a tide table and with a tide gauge in the Charleston boat basin. During 1983, ghost shrimp beds were also surveyed in Winchester Bay (at the mouth of the Umpqua River), along the south causeway of Tillamook Bay, the eastern side of Sand Lake, and in several areas of both North and South Bay, Humboldt Bay, California.

Behavioral Observations

General observations of *Callianassa californiensis* behavior were made in a 190 l aquarium. The aquarium had a flow-through water system and was filled to a depth of 0.4 m with sifted sand from a moderately dense shrimp bed. The substrate surface remained oxygenated throughout the study. Daylight observations were in natural light and a red light was used at night.

Because of difficulties in observing and timing behaviors of shrimp burrowing in sediment, ghost shrimp behavior was quantitatively observed in an artificial mudflat aquarium that simulated burrow conditions (Hoffman, 1981). The aquarium was divided into two compartments, each with three suspended U-shaped clear plastic tubes (2 cm inner diameter). One compartment received seawater (30-33 ^{o}/oo salt during the duration of the study) pumped from the mouth of Coos Bay. The salinity of the water entering the other compartment could be varied from that of the bay down to 0 ^{o}/oo. The entire apparatus was located out-of-doors and the temperature was allowed to vary. Since ghost shrimp normally receive light only from the surface, a black plastic skirt was used to reduce light exposure to the plastic tubes.

Ghost shrimp were exhumed from Battle Flats and were transferred directly from the field to the observation aquarium. One shrimp was added to each of the plastic tubes. They were left undisturbed for 1-2 days and then were observed for a single 20 minute period. Because of occasional rapid changes between behaviors, timing of a given pattern was not begun until it had lasted at least 10 seconds. General observations of behavior patterns in this chapter are presented only for salinities of 30 ^{o}/oo.

In examining the effect of salinity on activity, salinity in the experimental compartment was changed gradually and the shrimp were allowed to acclimate for 3-4 days before observations were begun

(Thompson and Pritchard, 1969). Observation periods were 20 minutes as described above. Linear regression, blocking for time of observation (morning, midday, or evening) was used to examine the effect of decreasing salinity on the time shrimp spent actively moving within the tubes. The data were recorded as percentages of the total observation time and were arc sine transformed before analysis (Sokal and Rohlf, 1981). The regression was calculated using the General Linear Models Procedure of the Statistical Analysis System (Ray, 1982).

Results

Hole-to-Shrimp Ratios

For both July/August periods, hole density and number of ghost shrimp recovered in the cores were relatively well correlated (Table III-1, Figure III-1, $r \geq .88$ for both periods). The relationship between holes and shrimp density was also highly significant during the longer 1982/1983 winter period, although the correlation is lower ($r=.79$). The slope of the line for the winter data is higher than that for the 1982 summer ($F=8.22$; $p<.01$), suggesting that there are fewer holes per individual between November and March. Monthly monitoring of hole density at Valino Island also suggests a seasonal variation (Figure III-2). Hole densities were lowest during mid-winter and increased to a peak during mid-summer. As discussed in Chapter 5, peak recruitment of <u>Callianassa</u> generally happened during late summer.

In contrast to the other three periods, the relationship between hole and shrimp density was not significant during late June and early

TABLE III-1. Statistics for regression of shrimp density on hole density.

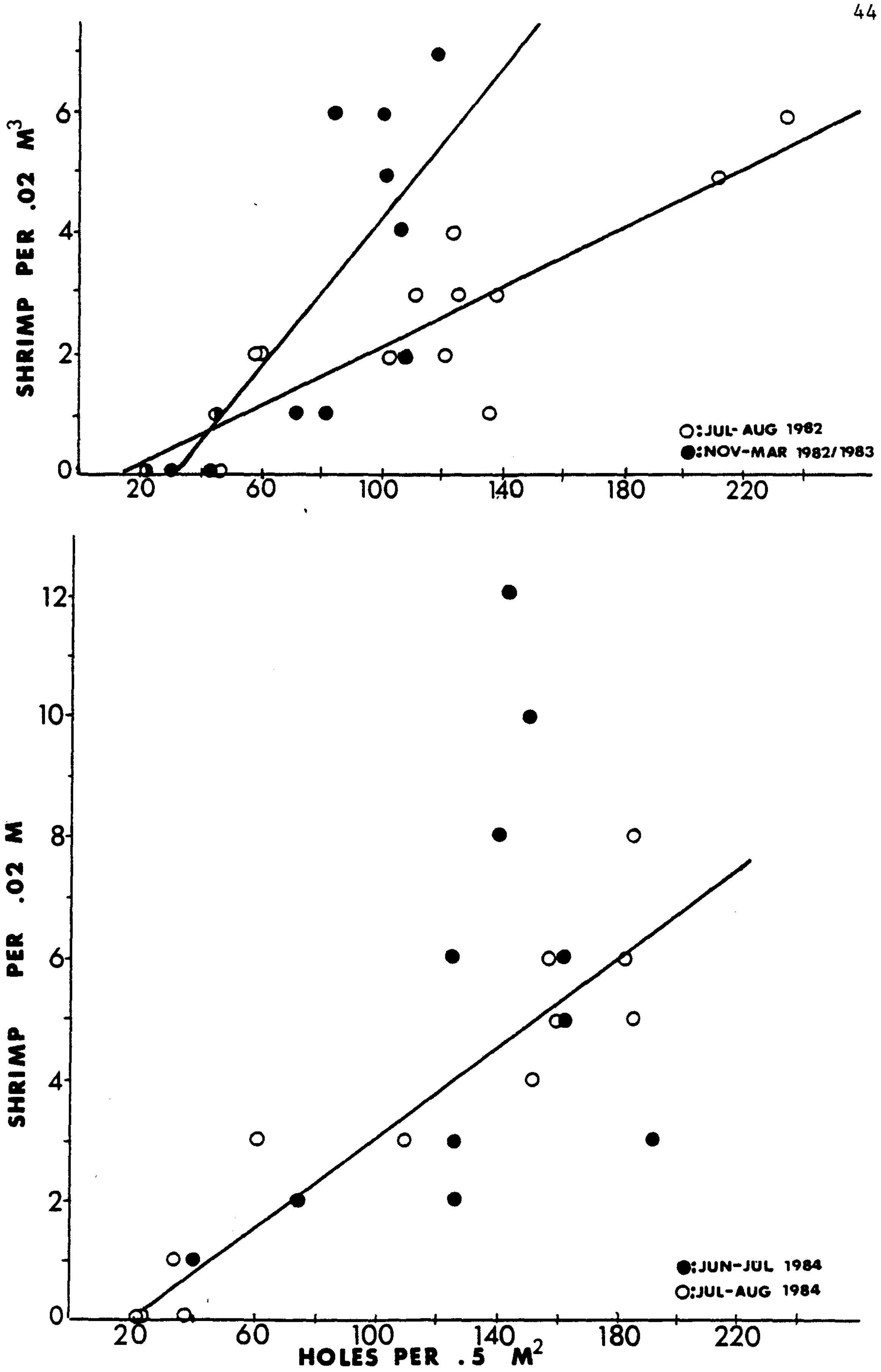
Period	Source of Variation	Sum of Squares	d.f	F	p	r
July 9-Aug. 10, 1982	Hole Density	30.24	1	39.46	.0001	.88
	Error	9.43	12			
Nov. 10-March 4, 1983	Hole Density	49.01	1	16.76	.005	.79
	Error	29.24	10			
June 21-July 10, 1984	Hole Density	26.13	1	2.35	.2	.45
	Error	100.05	9			
July 29-Aug. 4, 1984	Hole Density	71.67	1	77.53	.0001	.94
	Error	9.24	10			

July, 1984. However, higher shrimp numbers were still associated with higher hole density and most of the points lay between the July/August and winter values.

Zonation

Using holes as an indicator of relative density, there was a distinct zonation of dense Callianassa beds in 18 of the 19 sites examined in Coos Bay (Figure II-1). The beds occurred predominantly in the mid intertidal with a lower limit in many areas between +0.3 and +0.9 m above mean lower low water (MLLW). The vertical position of the lower edge often varied by as much as 0.3 m within a site. Short transects taken across the lower boundary indicate that the transition from high to low density is relatively abrupt in some areas (Figure III-3). However, this abruptness appears to vary seasonally and between areas.

Figure III-1. Relationship between hole density and Callianassa abundance. Lines represent best fit regression lines. F-statistics and correlation coefficients are given in Table III-1.


SHRIMP PER .02 M^3
0
2
4
6
20
60
100
140
180
220
○:JUL-AUG 1982
●:NOV-MAR 1982/1983
SHRIMP PER .02 M
0
2
4
6
8
10
12
20
60
100
140
180
220
●:JUN-JUL 1984
○:JUL-AUG 1984
HOLES PER .5 M^2

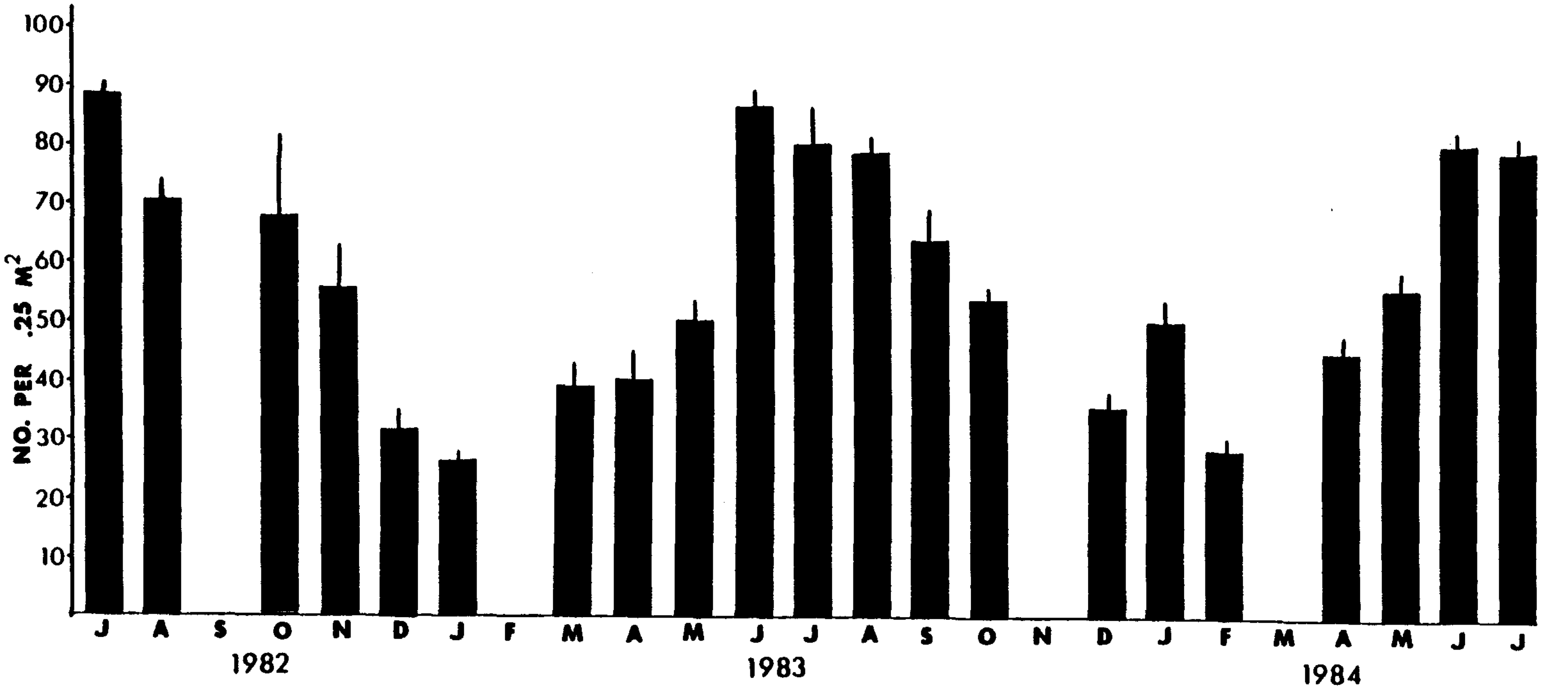
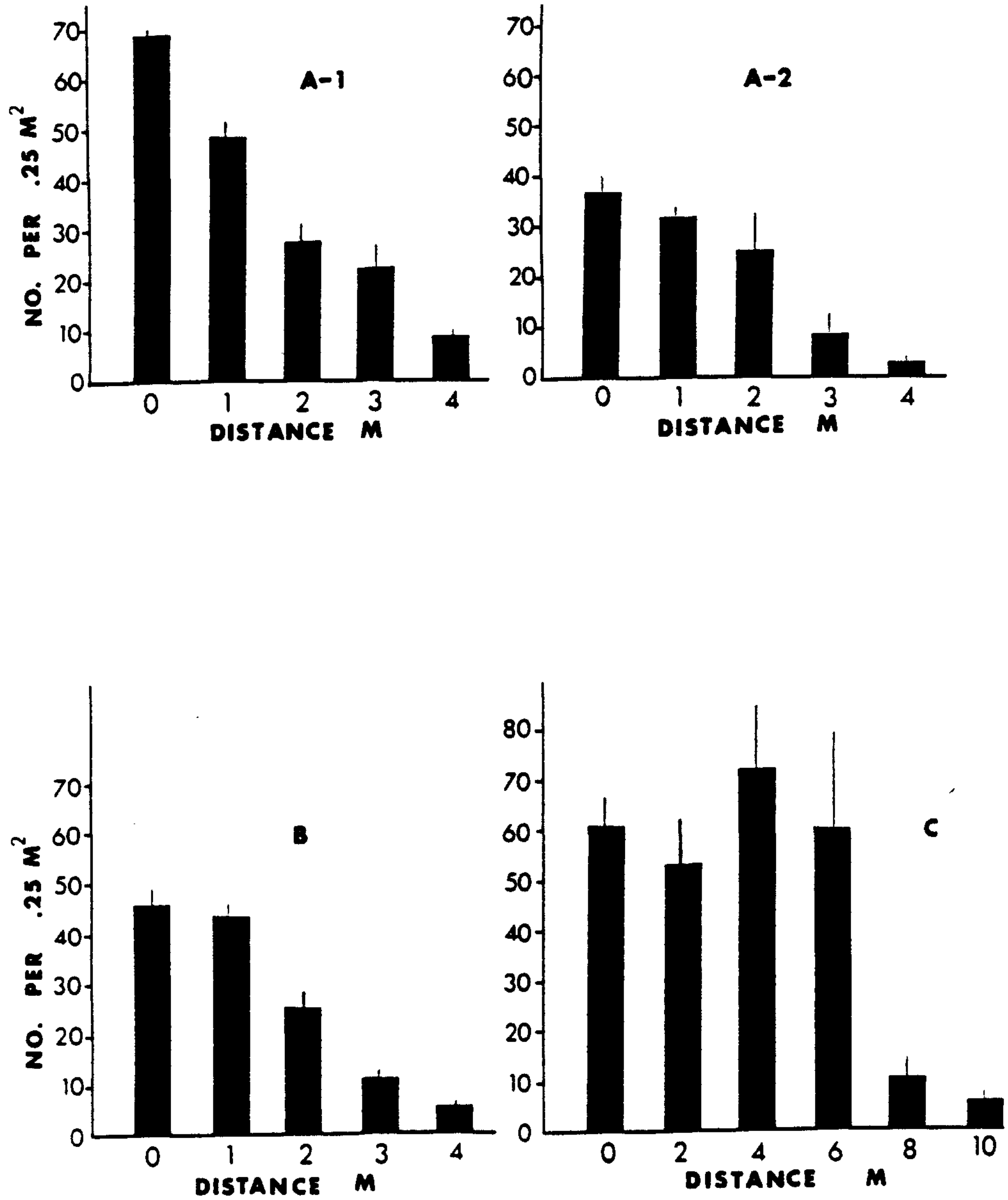


Figure III-2. Monthly fluctuations of hole densities in a *Callianassa* bed. Small bars represent 1 standard error (n=3 for all dates).

Figure III-3. Hole densities from transects taken across the lower edge of three _Callianassa_ beds. Small bars indicate 1 standard error (n=4 for all means) and 0 m represent an arbitrary starting point in the lower portion of the bed. A-1: Battle Flats, north bed, August 1984; A-2: Battle Flats, north bed, February 1984; B: Valino Island, January 1984; C: Battle Flats, south bed, August 1984.


A-1
A-2
B
C
NO. PER .25 M^2
DISTANCE M
0
10
20
30
40
50
60
70
80
0
1
2
3
4
0
2
4
6
8
10

The one site that did not show a pronounced intertidal zonation was near a causeway at the mouth of North Slough Coos Bay (designated "causeway" in Figure II-1). A Callianassa bed of moderate density at this site extended below 0 m MLLW. The area appeared to receive seepage from a nearby paper mill and the sediment had a high concentration of wood fragments.

A single site examined in Winchester Bay had a dense bed that extended to just above MLLW. In Tillamook Bay, dense beds were limited primarily to the mid intertidal and numbers declined in the low intertidal and subtidally. In the site examined at Sand Lake, however, dense Callianassa beds extended subtidally. Within Humboldt Bay, California, C. californiensis were generally less common with no beds approaching the densities seen in Oregon.

Behavioral Observations

Callianassa showed a varied repertoire of behaviors within the sediment-filled tank. For the purposes of this study, these behaviors were grouped into five general categories: burrowing; cleaning; pleopod movement (ventilation); aggressive interactions between shrimp; and sedentary behavior. Burrowing involved the excavation of sediment, packing of burrow walls using the walking legs, and transport of particles (often to the substrate surface). Feeding, which often involved sifting sediment with the maxillipeds, could not be readily distinguished from nonfeeding activities. The most common method of transporting sand out of the burrow was to carry the sediment to within 1-3 cm of the substrate surface and then to expel it forcibly with a burst of pleopod activity. Plumes of sediment coming from ghost shrimp burrows could also be seen while diving over a dense bed at high tide. This activity resulted in cones similar to those reported from other *Callianassa* beds (Aller and Dodge, 1974; Ott et al., 1976; Suchanek, 1983). If the burrow was in the initial stages of construction, the shrimp often pushed the sediment out of the burrow rather than using its pleopods to blow the sediment out. This technique was used even after shrimps had constructed a turn-around chamber and usually resulted in an individual being partially exposed.

Cleaning was most commonly directed at the gills, antennae, feeding appendages (maxillipeds), and the egg masses of females. Pleopod movement often occurred simultaneously with cleaning and burrowing. Aggressive interactions happened when two burrow systems met and usually ended where one of the shrimp walled off the opening into its burrow. A lack of detectable movement was classified as sedentary behavior.

Most of the patterns seen within the sediment-filled tank were also observed within the artificial burrows, including pleopod movement, cleaning, and sedentary behaviors (Table III-2). Burrowing was not possible within the plastic tubes; however, shrimp spent a considerable amount of time moving within these tubes and often carried sediment that had fallen into them. Since ghost shrimp often tried to carry sediment or "pack" the tube walls while moving, it is likely that this behavior is related to burrowing in sediment. Active movement was the most frequently observed behavior.

As mentioned earlier, several field observers have noted ghost shrimp near the entrance of their burrow. Ghost shrimp within the

TABLE III-2. Duration of behaviors observed in artificial burrows.

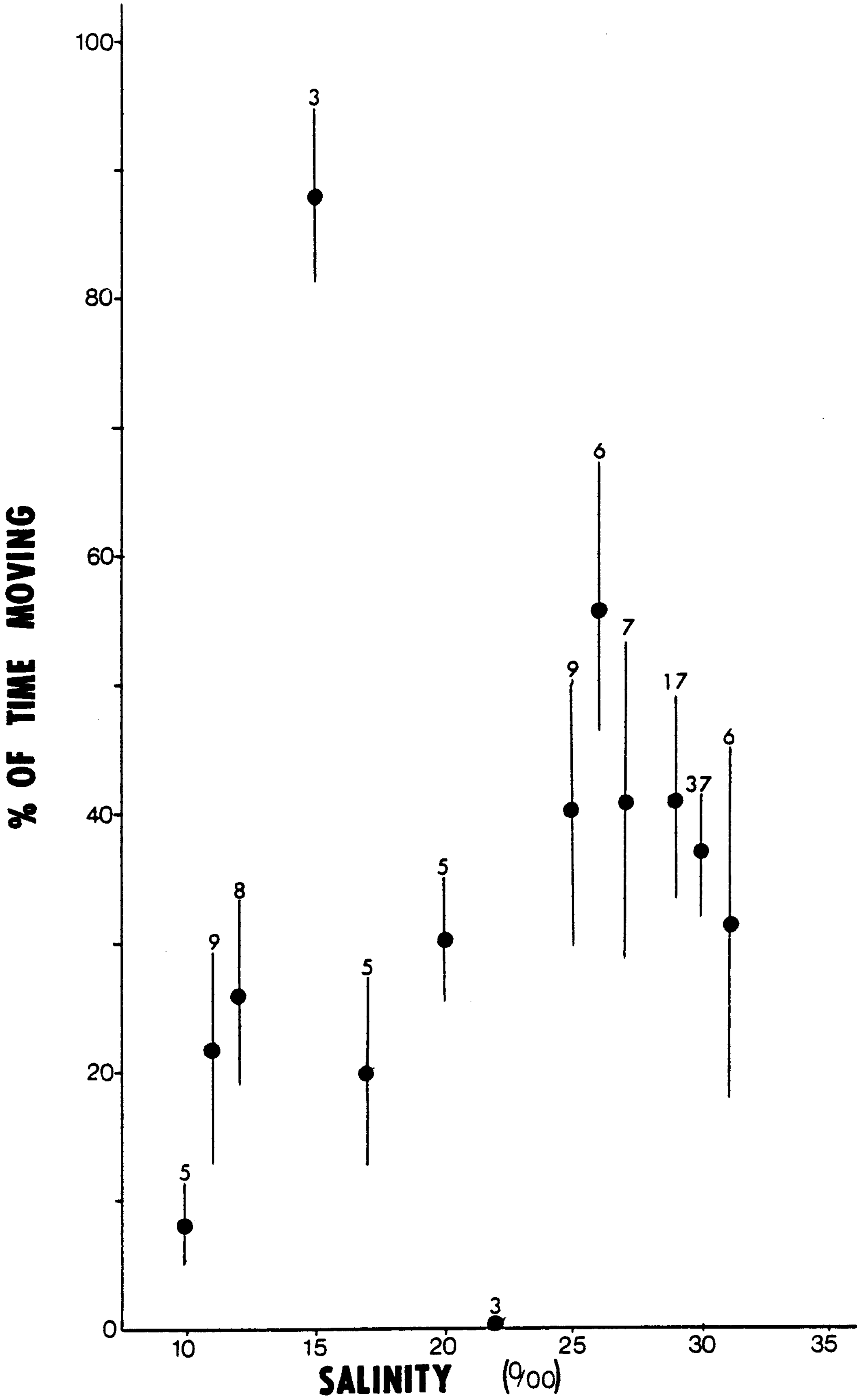
Behavior	Number of Observation Periods	Mean Min. Per 20 Min. Period	S.E.	% of time
Active Movement	119	9.3	.7	46.6
Sedentary	116	5.5	1.1	27.5
Pleopod Movement	115	3.7	1.2	18.3
Cleaning	55	6.0	.8	29.7
Near Burrow Entrance	120	5.4	2.0	27.0

plastic tubes spent over 25% of the observation time within 2 cm of the burrow entrance. Although they were seldom seen outside the burrows, shrimp occasionally moved from one tube to another. This required a shrimp to expose itself on the surface. When hanging near the burrow entrance, a shrimp often exposed part of its chela above the substrate surface.

When Callianassa in the artificial burrows were exposed to lowered salinity, 75%-100% died between 8 and 9 $^{o}/oo$ salt, a value that agrees closely with the results of Thompson and Pritchard (1969). These shrimp, which apparently died of osmotic stress, all showed signs of swelling in the gill areas. No salinity related mortality occurred at 10 $^{o}/oo$ salt. Only observations at higher concentrations were used to examine the effects of salinity on behavior.

An apparent trend towards decreasing activity with decreasing salinity (Figure III-4) is not significant at the .05 level ($p<.066$).

Figure III-4. Relationship between salinity and the per cent of time spent actively moving within artificial burrows. Bars represent ± 1 standard deviation, and sample sizes are given above the bars.


% OF TIME MOVING
100
80
60
40
20
0
3
6
7
9
17
37
6
5
8
9
5
5
3
10
15
20
25
30
35
SALINITY (‰)

However, much of the deviation is due to the high activity seen at 15 $^{o}/oo$. Unlike most of the other salinity levels, these three values all stem from a single mid afternoon observation period. Since the tank is located outdoors, unusual conditions, such as warmer temperatures, could have contributed to the higher activity. Dixon's test for extreme observations (Snedecor and Cochran, 1980) indicates that this mean is an outlier when compared to the other data (ratio=.593; $p<.05$). Recalculation of the regression excluding these three values suggests a significant decline in activity with reduced salinity ($F=6.15$; $p<.015$; $r=.35$).

Discussion

Holes appeared to be a relatively good estimator of shrimp density within a given time period. The one sampling period that did not show a significant relationship, June 21 to July 10, 1984, did show a concordant trend, although the points appear to fit an exponential distribution better than a linear one. In previous studies of the number of holes per shrimp in C. californiensis beds, Swinbanks and Murray (1981) reported a mean of 2.5 holes per shrimp and MacGinitie (1934) "two to several openings to a burrow." In this study, the number of holes per shrimp ranged from a high of 4.2 during the summer of 1982 to a low of 3.8 during the 1982/1983 winter. Since ghost shrimp may burrow below the 0.5 m sampled by the corer (MacGinitie, 1934) and some individuals may be able to evade a corer, these values probably overestimate the number of holes per individual.

Although holes provide a good estimate of relative shrimp density within the same time interval, the number of holes per shrimp varies seasonally. This is shown both by the lower hole-to-shrimp ratios and lower hole densities in the field during the winter months. The spring and early summer increase in hole densities cannot be attributed to recruitment, since peak settlement of *C. californiensis* in Oregon estuaries appears to occur in late August (Bird, 1982; Johnson and Gonor, 1982; personal observation).

Since holes are produced in association with burrowing and may collapse if not maintained (MacGinitie, 1934; Thompson and Pritchard, 1969), the winter decline in hole densities and hole-to-shrimp ratios may indicate reduced burrowing activity at this time. Ghost shrimp in Yaquina Bay move deeper into their burrow during winter (McCrow, 1971) and *C. californiensis* produces fewer eggs between December and March (Bird, 1982). Hailstone and Stephenson (1961) and Devine (1966) similarly found that several species of *Callianassa* in Australia and New Zealand have reduced reproduction and lowered growth rates during the Southern Hemisphere winter (June-through August). During winter in Oregon, lower air and water temperatures (Table III-3) can be expected to lead to lower activity in the ectothermic ghost shrimp. Although salinity has only a small effect on movement, as indicated by the low correlation, lower winter salinities would also tend to contribute to reduced activity.

Surveys of *Callianassa californiensis* burrows in Coos Bay and two other estuaries indicate that a mid-intertidal peak in ghost shrimp abundance is common in Oregon estuaries. However, the two examples of low-intertidal and subtidal beds suggest that *C. californiensis* is not

TABLE III-3. Tideflat and surface water temperatures at Valino Island. All temperatures were measured during low tide.

Date	Water Temperature (°C)	Tideflat Temperature (°C)
1983		
February 19	10.0	10.5
March 3	12.0	12.0
March 13	12.5	11.5
April 6	15.5	15.5
May 4	16.0	-
May 14	12.5	-
May 23	20.0	18.5
June 19	17.0	-
June 26	18.0	-
July 2	17.0	-
July 12	17.5	-
July 16	20.0	-
August 13	18.0	-
August 25	18.0	-
September 24	16.0	-
October 10	12.0	-
October 23	13.5	-
November 28	12.5	12.5
December 13	12.5	-
1984		
January 11	11.0	11.5
February 25	10.0	10.0
March 10	13.5	-
April 22	13.5	-
May 5	12.0	13.0
June 13	15.0	-
June 24	21.0	-
July 3	18.0	-
July 12	17.0	14.5

physiologically prevented from inhabiting these areas. In the Boundary Bay tide flats of British Columbia, densest aggregations of ghost shrimp occurred between +2.2 and +1 m above MLLW, with low densities below this level (Swinbanks and Murray, 1981). McCrow (1971) noted that densest beds occurred between +0.6 and +1.2 m above MLLW in Yaquina Bay. Thompson and Pritchard (1969) observed them in a zone between 0 and +0.3 m in the same estuary, although their reference to this as "higher intertidal" makes it unclear whether the heights are relative to mean sea level or MLLW. MacGinitie (1934) reported densest beds between 0 and +0.3 m in Elkhorn Slough, California and Ronan (1975) observed that _Callianassa_ occurred in the upper intertidal of Bodega Bay. However, Millicent Quammen (University of California, Santa Barbara, personal communication) has indicated that dense aggregations of _Callianassa californiensis_ may extend subtidally in Mugu Lagoon. References to a mid-intertidal distribution of _C. californiensis_ also exist in Bybee (1969) and Smith and Carlton (1975).

One problem associated with a hypothesis that predation limits the lower distribution of these beds is how a burrowing shrimp may become vulnerable to surface predators. The presence of ghost shrimp near the entrance of their tubes in the artificial mudflat aquarium suggests a possible mechanism. One can often collect adult _Callianassa_ during high tide by scraping the sediment by hand, indicating that they are relatively close to the surface, and on two occasions shrimp were seen at the entrance of their burrow in the field. During observations at high tide of a dense bed in June, a few shrimp were also observed out of their burrows on the substrate surface. Such behavior in the field, as well as reports by others, suggest that the behavior observed in the plastic tubes also represents field conditions. The explanation for this pattern is less clear, but feeding (Bird, 1982) and mating activities may be involved.

CHAPTER IV

PREDATORS OF *CALLIANASSA CALIFORNIENSIS* IN COOS BAY, OREGON

Introduction

Although *Callianassa californiensis* is a popular bait item of sports fishermen in Oregon and California, little is known about the natural predators of adult shrimp. Russo (1975) reported *C. californiensis* and *Upogebia* from the stomachs of leopard sharks, *Triokis semifasciata*, while Stevens et al. (1975) found that *C. californiensis* constituted the major portion of the diets of Dungeness crabs in Gray's Harbor on at least one date. Biffar (1971) and Darnell (1958) have noted cases where Caribbean species of ghost shrimp have been eaten by bottom-feeding fish. The presence of *Callianassa* in Western Gull fecal pellets from Coos Bay (personal observation) also suggests that intertidally foraging birds may occasionally take this shrimp.

For predation to restrict dense ghost shrimp beds primarily to higher tidal levels, a situation analogous to sea star limitation of mussel beds (Paine, 1974), an aquatic predator would have to be capable of consuming significant numbers of this burrowing shrimp. Within Coos Bay, and particularly at the Valino Island study site in South Slough, bottom-feeding fish and crabs are the predominant large epibenthic predators. Benthic cores (Appendix) and random samples taken with a shovel indicate that most infauna immediately below the Valino Island shrimp beds are relatively small. The only common infaunal predator large enough to prey upon even juvenile ghost shrimp (8-12 mm length; Bird, 1982) is the nemertean, Cerebratulus californiensis. In this chapter, the potential importance of fish, the crab, Cancer magister, the epibenthic feeding shrimp, Crangon, and the infaunal nemertean, Cerebratulus, as predators on Callianassa californiensis will be examined through a series of laboratory and field studies.

Methods

From 1982 to 1984, fish were collected with beach seines near the Empire boat landing and in Joe Ney Slough, Coos Bay (Figure II-1), in conjunction with Estuarine Biology and Vertebrate Ecology classes taught by Daniel Varoujean at the Oregon Institute of Marine Biology. Dense mid-intertidal ghost shrimp beds, with patchy Zostera marina beds subtidally, were present at both sites. The net was 40 m long by 2 m high with 1.5 cm mesh and a centrally located catch bag. Seines were placed parallel and approximately 50 m from shore using a motorboat and were pulled in by hand using ropes attached to the ends. In order to sample less common fish for stomach content analysis, two beach seine hauls were made at each site during a sampling period; however, these consecutive seines were not considered replicates because of disruption to the fish fauna after the first seine and microhabitat differences (such as vegetated versus unvegetated areas) that may occur if samples are taken far enough apart to prevent disturbance effects. Therefore, only the first seine at a site was used to estimate relative densities of fish. Most samples were taken during neap low tides.

Subsamples of the fish caught in beach seine hauls during 1982 and 1983 were immediately preserved in 10% formalin for later examination of stomach contents. In addition to the samples from Coos Bay, stomachs were also analyzed from fish collected during a 1981 study of the Umpqua River estuary, Oregon.

Because beach seines sample a relatively large area, fish traps were used to observe local fish distributions associated with dense shrimp beds at Battle Flats and the Causeway (Figure II-1). All traps were of 1.2 cm galvanized wire mesh and were not baited. They were set out only after all areas were covered by at least 0.3 m of water and were retrieved before exposure. This helped to ensure that differences in the number of fish caught in the various zones were not due to differences in fishing time. Shrimp beds at Battle Flats showed a typical pattern with highest densities in the mid intertidal while the causeway was the only site examined in Coos Bay where a dense bed extended throughout the intertidal (see Chapter III). The distribution of fish in three zones at Battle Flats was studied by placing traps over a dense bed, approximately 1 m above the lower edge, along the lower edge of the bed, and approximately 1 m below the shrimp bed (Figure IV-1). Traps were placed during 9 time periods, and equal numbers were put into each zone (Table IV-1). A second study involving traps was begun to determine whether the lower extension of the shrimp bed at the causeway site was due to lower predator abundance. Four traps were placed at both the causeway and Battle Flats at a tidal level corresponding to approximately 1 m below the Battle Flats bed. Comparisons were made for two consecutive days during July 1984.

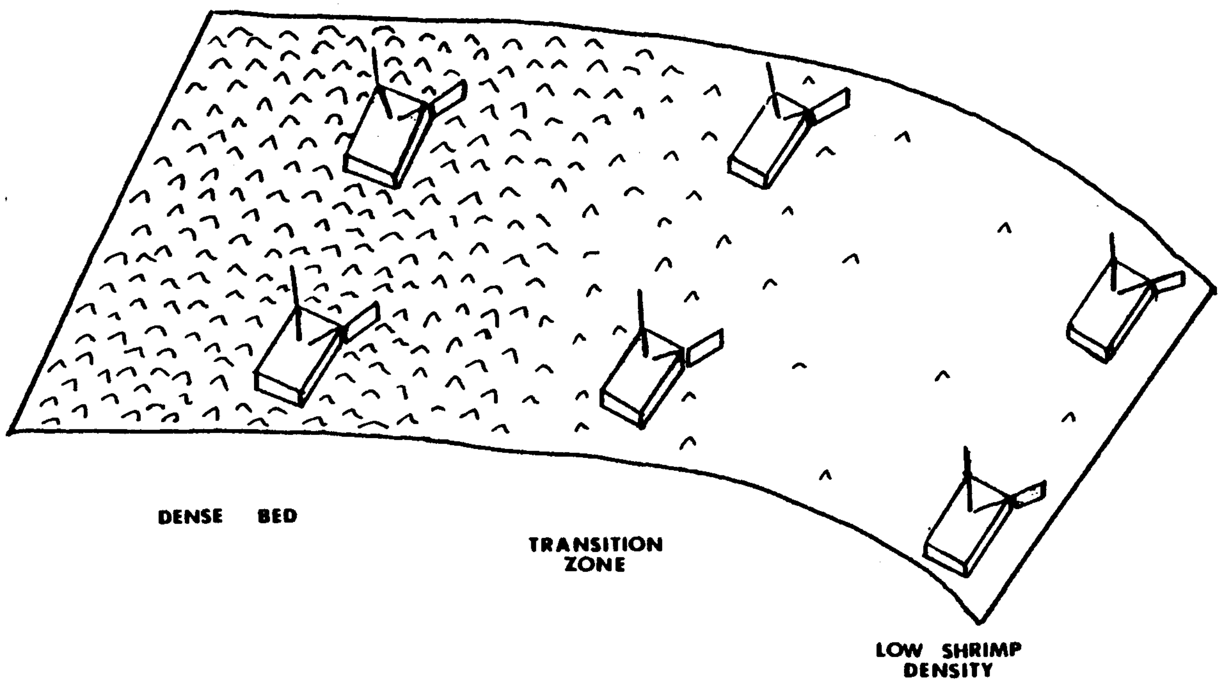


Figure IV-1. Placement of fish traps relative to a dense ghost shrimp bed.

TABLE IV-1. Number of staghorn sculpins caught in fish traps during a single high-tide period on each of nine dates. B=over dense bed; T=over transition zone; L=below dense bed.

Date	n	B	T	L
1983				
23 July	1	2	9	6
7 August	1	0	0	2
22 August	1	0	1	0
1984				
19 May	2	0	0	7
13 June	3	2	5	11
21 June	2	0	0	9
12 July	2	0	2	2
28 July	2	0	1	4
29 July	2	7	4	2

Laboratory tanks were used to observe Dungeness crab (*Cancer magister*) predation because of difficulty in catching large numbers of adults near dense shrimp beds and problems in identifying stomach contents (many of the items seen in *Cancer* stomachs were mascerated and unrecognizable). Adult and juvenile *C. magister* were fed live ghost shrimp of various sizes in clean 380 and 57 liter tanks, respectively. Predation by adult Dungeness crabs was also observed under simulated tideflat conditions in a second 380 liter aquarium filled to a depth of 0.4 m with sifted sand from a ghost shrimp bed. The tank had a flow-through water system that allowed percolation of water through the sediment and was divided into two halves with 1.2 cm screening. Equal numbers of ghost shrimp were added to each side at a density of 30-50/m^2. The shrimp were allowed to burrow for 3-4 days before a single crab was added to one side. The other side was periodically disturbed by hand as a control for disruption due to the crab's movements. Crabs were observed from a darkened blind which covered one side of the tank. Daytime observations were under natural light and a red light was used at night.

Predation by Crangon spp. and the nemertean, Cerebratulus californiensis, was observed in a 57 liter tank without sediment. Crangon were observed during summer using ghost shrimp 30-40 mm long while Cerebratulus were observed in early fall using newly settled shrimp (10-15 mm length).

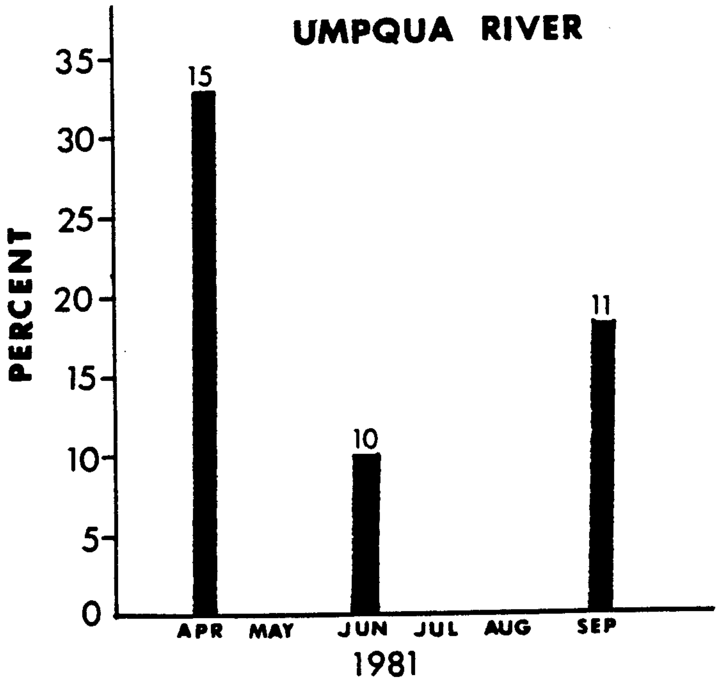
Results

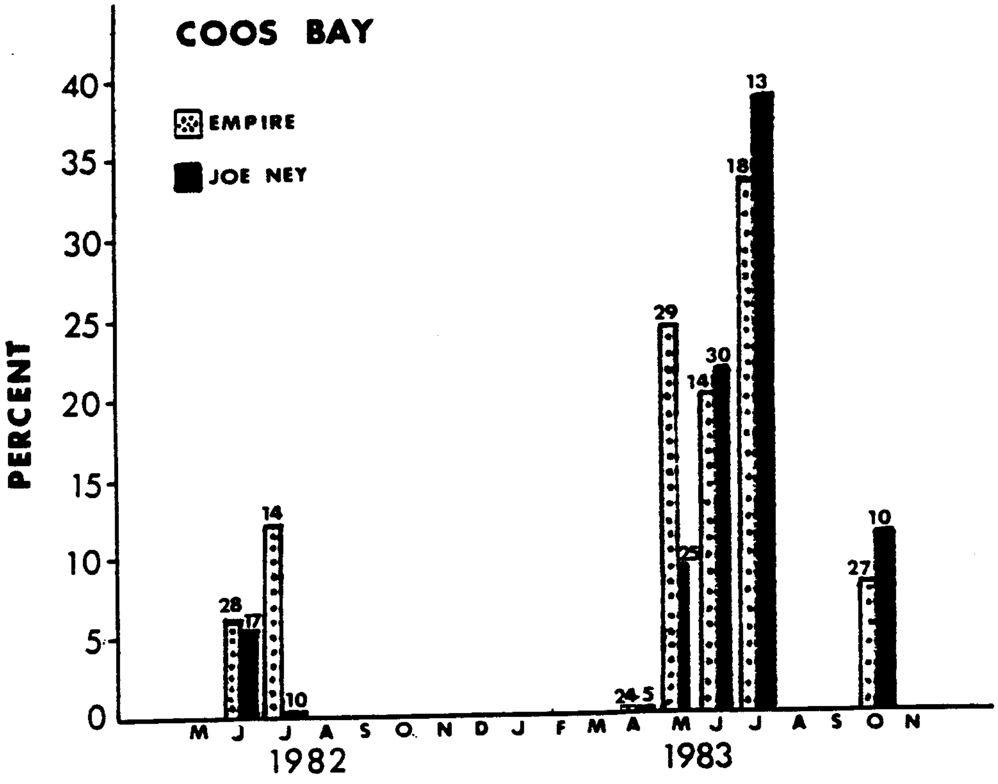
Predator Diets

Only two species of fish commonly ate Callianassa californiensis: the cutthroat trout, Salmo clarkii, and the staghorn sculpin, Leptocottus armatus. Since fewer than 20 cutthroat trout were caught during the 3 years of sampling, this fish is probably unimportant to the distribution of C. californiensis.

Ghost shrimp formed a significant portion of the diet of staghorn sculpins from both Coos Bay sites as well as from the Umpqua River (Figure IV-2). Over the first two years of sampling in Coos Bay, an average of 15.9% of the staghorn sculpin had eaten ghost shrimp.

Figure IV-2. Percent of staghorn sculpins having Callianassa as part of their diet. Numbers above bars indicate sample sizes.


UMPQUA RIVER
PERCENT
35
30
25
20
15
10
5
0
15
10
11
APR
MAY
JUN
JUL
AUG
SEP
1981


COOS BAY
EMPIRE
JOE NEY
PERCENT
40
35
30
25
20
15
10
5
0
28
17
14
10
24
5
29
25
14
30
18
13
27
10
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
1982
1983

Predation on *C. californiensis* appears to increase as summer progresses (Figure IV-2). At the Joe Ney and Empire stations in 1983, relatively few fish had ghost shrimp in their diets during April. The percentage had increased by a factor of four at the two Coos Bay sites in July 1983. Within the Umpqua, however, highest consumption was observed in April 1981, decreasing in June, and then increasing again in September.

Consumption of ghost shrimp by staghorn sculpins also depended upon the size of the fish. No sculpins less than 70 mm standard length contained *C. californiensis*, even though this size class contributed 58 of the 276 stomachs examined from Coos Bay. The average standard length of *Leptocottus* that had eaten *Callianassa* in the Coos Bay samples was 110.5 mm (S.E.=3.8 mm; n=44).

Predation on *C. californiensis* by the three invertebrate predators was less evident. Within tanks that lacked sediment, adult Dungeness crabs rapidly moved their antennae and maxillipeds and began searching even when a shrimp was placed where it was not visible. Similarly, juvenile *Cancer magister* attacked both juvenile and adult ghost shrimp, although they were usually unsuccessful when attacking adults and appeared to have difficulty piercing the exoskeleton of these larger shrimp. The juvenile crabs also tended to retreat from frontal confrontations with the adults. Occasionally, juvenile *Cancer* were successful in stripping the eggs from berried females. Despite the readiness of adult crabs to attack ghost shrimp in clean tanks, no *C. magister* tried to excavate *Callianassa* in the sediment-filled tanks, none of the adult crabs in this tank had shrimp in their stomachs at the end of the experiment, and there was no significant difference in number of holes or in numbers of shrimp recovered as compared to the control side.

Neither _Crangon_ shrimp nor nemerteans were observed to attack ghost shrimp even after several days of exposure. All ghost shrimp appeared active at the end of observations.

Sculpin Distribution

Since peak numbers of juvenile staghorn sculpins occurred several months earlier than adults and juveniles are not effective predators, the examination of seasonal and spatial distributions of _Leptocottus_ will be limited to fish longer than 70 mm standard length. Within both Coos Bay sites, this size class was most plentiful during summer. At Joe Ney, highest catches of sculpins were usually between May and July, although July 1983 and May 1984 are exceptions (Figure IV-3). The four samples taken between November and April contained the fewest _Leptocottus_. The Empire site showed a similar pattern with sculpin abundances rising from a winter low to a peak during summer (Figure IV-4). In general, during the summer months the staghorn sculpin was one of the most common fish in areas of moderate to low wave action, comprising up to 30% of the fish caught in a sampling period.

Catches from the fish traps placed at Battle Flats (Table IV-1) indicate that sculpins forage in the areas occupied by dense shrimp beds. Aside from _Leptocottus_, the only fish taken in the traps were two shiner surfperch (_Cymatogaster aggregata_). However, sculpins appeared to forage preferentially below the shrimp bed ($G=20.96$; 2 d.f.; $p<.005$), with almost four times as many fish caught during the same time interval

Figure IV-3. Seasonal abundance of staghorn sculpins in Joe Ney Slough, Coos Bay. Bars represent catches from first beach seine haul taken on that date.

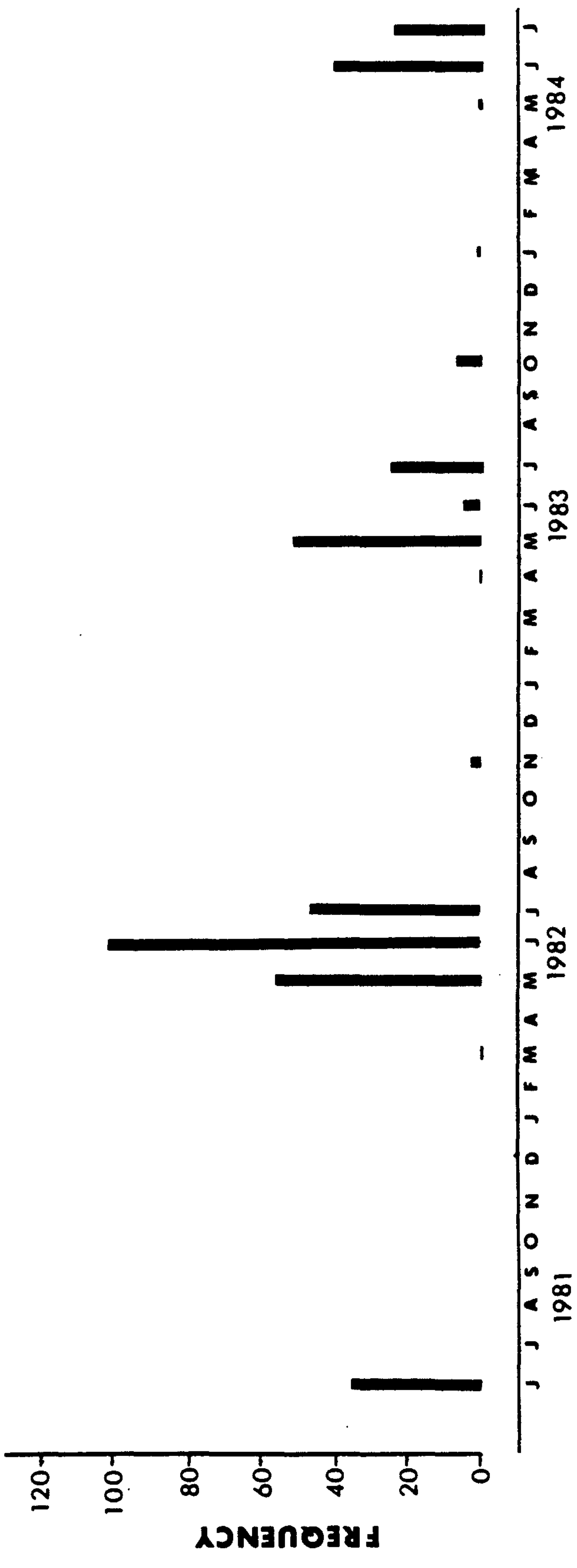
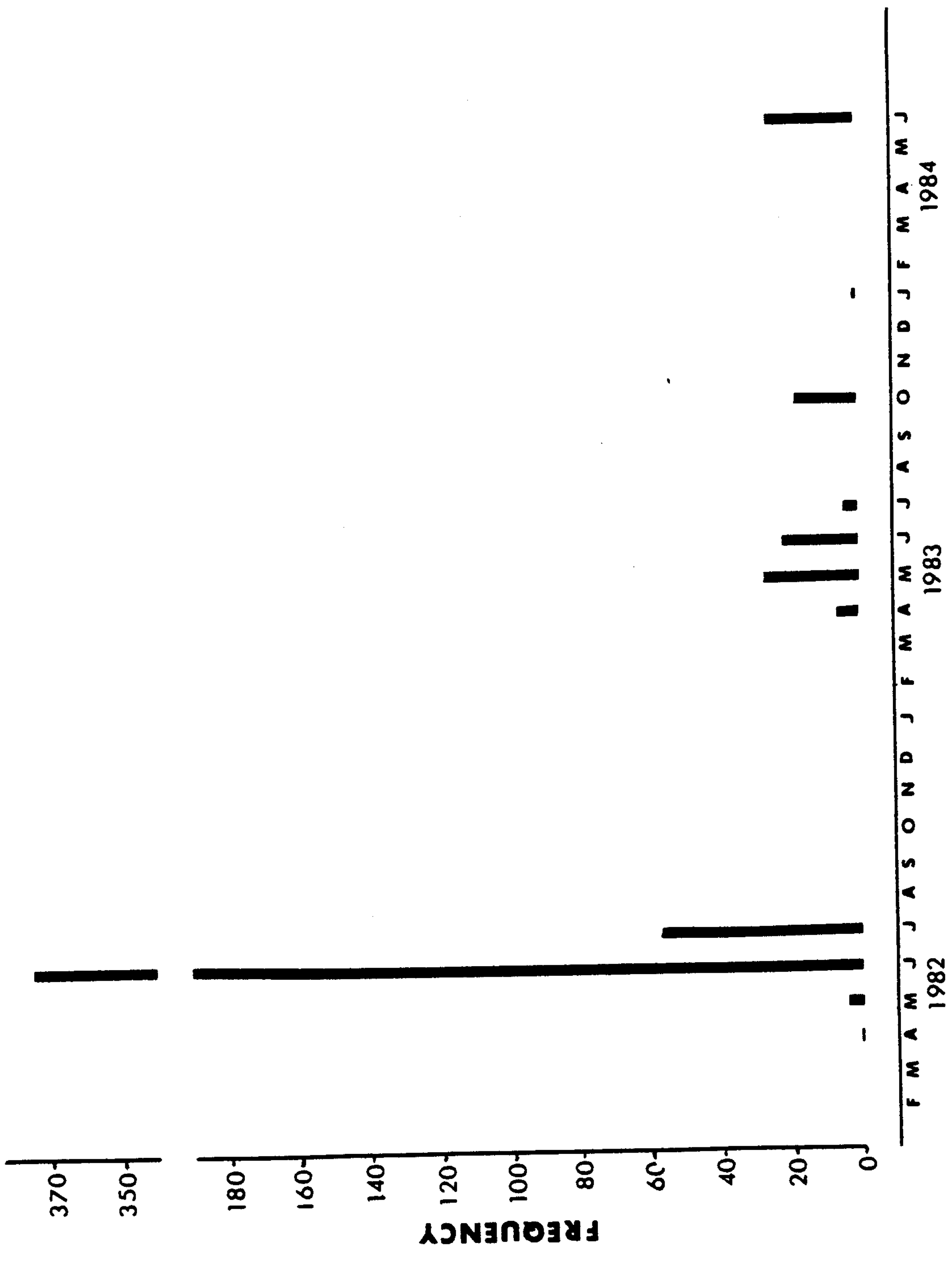

FREQUENCY
0
20
40
60
80
100
120
J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
1981
1982
1983
1984

Figure IV-4. Seasonal abundance of staghorn sculpins at Empire, Coos Bay. Bars represent catches from first beach seine haul taken on that date.


FREQUENCY
0
20
40
60
80
100
120
140
160
180
350
370
F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
1982
1983
1984

in the lower area as over a dense bed. Intermediate numbers of fish were taken along the transition zone from high to low shrimp density.

As discussed earlier, the Battle Flats site had a dense shrimp bed restricted primarily to the mid intertidal, as seen in most areas within Coos Bay, whereas the causeway bed extended throughout the intertidal. A total of 44 fish were caught in traps at Battle Flats on the first day while only 7 fish were taken from the causeway during the same period. On the following day, catches from Battle Flats and the causeway were 23 and 20 sculpins respectively. Although the total catches for the two days indicate a significantly higher number of sculpins at Battle Flats (G=15.05; 3 d.f.; $p<.005$), the minimal difference in catches on the second day leads to uncertainty about whether a decrease in predator abundances can explain the lower extension of a dense bed at the causeway.

Discussion

Stomach analysis of Leptocottus armatus suggests that this fish is an important predator on Callianassa in Coos Bay. Since most studies of fish diets do not identify stomach contents to species, information on the importance of staghorn sculpin predation to Callianassa in other embayments is limited. 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. Jones (1962) observed Callianassa longimanus in the diets of a small number of sculpins from San Francisco Bay. Millicent Quammen (University of California, Santa Barbara; written communication) found that 10-20% of the staghorn sculpins she examined in Mugu Lagoon, California, had eaten ghost shrimp.

Within the vicinity of the shrimp beds, the abundance of adult *Leptocottus* varied seasonally over the two years of sampling. In 1979, the Oregon Department of Fish and Wildlife used beach seines to survey fish distributions at the Charleston boat basin, approximately .5 km north (downstream) of the Joe Ney site (R. Bender, unpublished data). During January, only two adult sculpins were caught at this site and only six adults were taken during a May 2 seine. However, samples taken on May 29, June 15, and August 13 had 250, 200, and 197 adult sculpins respectively. A somewhat lower total abundance of staghorn sculpins was also observed during winter in Yaquina Bay (Bayer, 1981), but no distinction was made between juveniles and adults. Horn (1980) noted primarily small juveniles during winter and larger sculpins during summer in Morro Bay, California. Bell (1978) found that *Leptocottus* left an Alaska estuary during winter, perhaps in response to freezing temperatures. Migration of larger staghorn sculpins out of Oregon estuaries during winter may be related to the requirement for breeding fish to remain in areas of higher salinity (Jones, 1962).

Although *Leptocottus armatus* was the only major predator on *Callianassa* implicated in this study, several other predators may be important in Coos Bay or other embayments. As mentioned, bottom feeding rays and sharks may be expected to prey upon *Callianassa* in some areas (Russo, 1975). Even though Dungeness crabs, *Cancer magister*, were not seen feeding on *Callianassa* in sediment-filled tanks, these crabs apparently do eat ghost shrimp under certain conditions (Stevens et al., 1982). Juvenile *Cancer* have been observed to attack exposed ghost shrimp at Valino Island and large numbers of these smaller crabs foraged in the low intertidal of Coos Bay sandflats during spring (personal observation). Additionally, several species of fish present in Coos Bay, such as the starry flounder, *Platichthys stellatus*, were not sampled with the beach seines but may prey on the ghost shrimp subtidally.

CHAPTER V

EFFECT OF PREDATION IN LIMITING THE LOWER DISTRIBUTION OF *CALLIANASSA CALIFORNIENSIS* BEDS

Introduction

Although the analysis of predator diets shows that infauna are eaten, the effect of predation on infaunal distributions is difficult to determine directly. The distribution of infauna must often be inferred indirectly from burrow openings or tubes (Aller and Dodge, 1974; Ronan, 1975; Swinbanks and Murray, 1981; Suchanek, 1983) or observed through destructive, and usually time consuming, core samples. Tests of predation effects have usually involved field or laboratory manipulations or monitoring of natural experiments, all three methods posing inherent drawbacks (Virnstein, 1978; Peterson, 1979). Yet, despite these problems, manipulations of predator densities, and especially field exclusion studies, have provided important information on the role of predation in soft-sediment communities (Virnstein, 1977; Woodin, 1978; Peterson, 1979; Quammen, 1984).

Two field predator exclusion experiments and one natural experiment examined the effect of predation in limiting the lower distribution of *C. californiensis* in Coos Bay, Oregon. The predator exclusion studies involve two distinct but related aspects of the zonation pattern: 1) does the ghost shrimp bed extend downwards when predator abundance is reduced; and 2) do aggregations of adult *Callianassa* placed below a dense bed survive significantly better with reduced predation. The natural experiment involves monitoring a cohort of juvenile _C. californiensis_ that settled in the low-intertidal zone during early fall 1983.

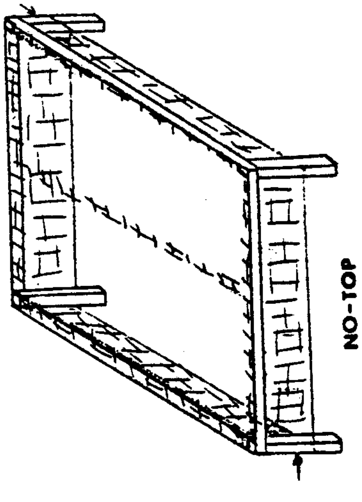
Methods

Migration Studies

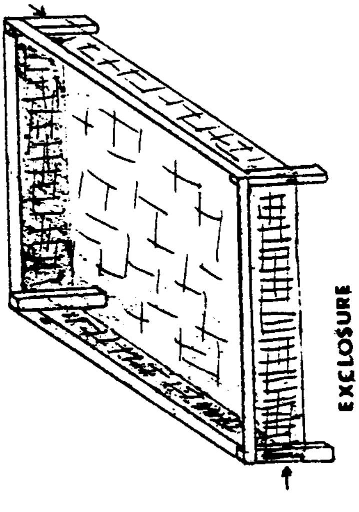
The relatively abrupt lower edge common to many _Callianassa californiensis_ beds allowed an experimental approach analogous to Paine's (1974) study of sea star predation on mussels in the rocky intertidal. Predator exclosures and controls were placed immediately below several dense ghost shrimp beds at Valino Island and Long Island Point, Coos Bay. The upper edge of these treatments bordered the lower edge of the bed (Figure V-1), and change in number of shrimp burrow holes within these treatments was assumed to be caused by migration of adult shrimp from the adjacent dense bed. A direct test of this assumption is discussed later. If pressure for downward expansion of the bed exists and if predation is important in limiting this expansion, then a higher density of shrimp (and shrimp holes) would be expected within the exclosures relative to the other plots.

There were three control treatments: 1) a no-top cage with sides but only a partial roof; 2) a sideless cage; and, 3) an unmanipulated control plot lacking any cage structure. The no-top treatment was designed to control for potential effects of current disruption by a cage while the sideless treatment simulated some of the shading

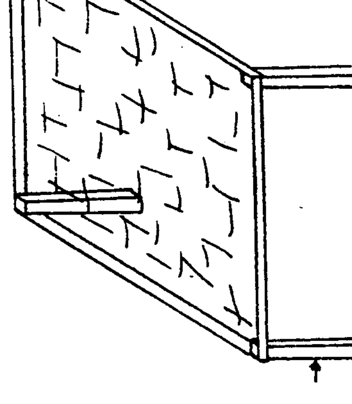
Figure V-1. Exclosure cage and controls used in migration studies. Inset shows placement of cage immediately below the lower edge of a dense shrimp bed.



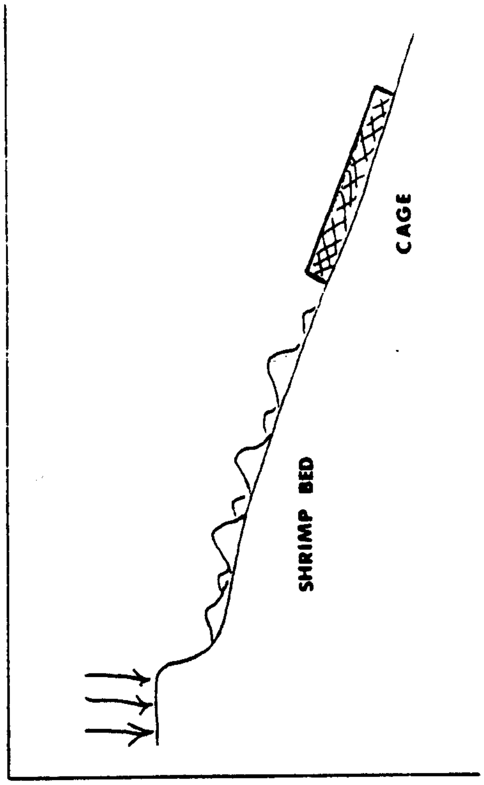
NO-TOP



EXCLOSURE



ROOF



properties. The three cage structures were made of 12.5 mm mesh galvanized hardware cloth placed over a light wooden frame. This mesh size was small enough to exclude most predators capable of preying on adult ghost shrimp (Chapter IV) yet large enough to allow the passage of most Callianassa individuals. Behavior and survivorship of ghost shrimp were not noticeably affected after several weeks of exposure to cage materials in laboratory aquaria. Exclosure and no-top treatments extended approximately 12.5 cm above the tideflat surface, with 5 cm buried into the sediment. The sideless cage control was 21-24 cm high. The increased height of this control was needed to give predators access to the underlying substrate. All four treatments, full cage and three controls, were 1 m on each side.

Replicate sets of these four treatments (Table V-1) were placed seasonally at Long Island Point and Valino Island (Figure V-2). Physical conditions at these sites varied from strong tidal currents, direct wave action, and sand ripples near the channel to low currents and fine sediments near the salt marsh. Experiments were begun during the summer of 1982 and repeated each season through the summer of 1984, although sideless controls were not added until spring 1983. Exact location of a treatment within a site was chosen haphazardly with the toss of a shell. Because of potential seasonal variations in ghost shrimp activity and predator abundance and the possibility of significant cage artifacts with increasing duration of caging experiments, experimental sets were left in place for 40 to 60 days and then removed. Monitoring during the course of the experiments suggested that density responses, if present, became noticeable within 14-28 days.

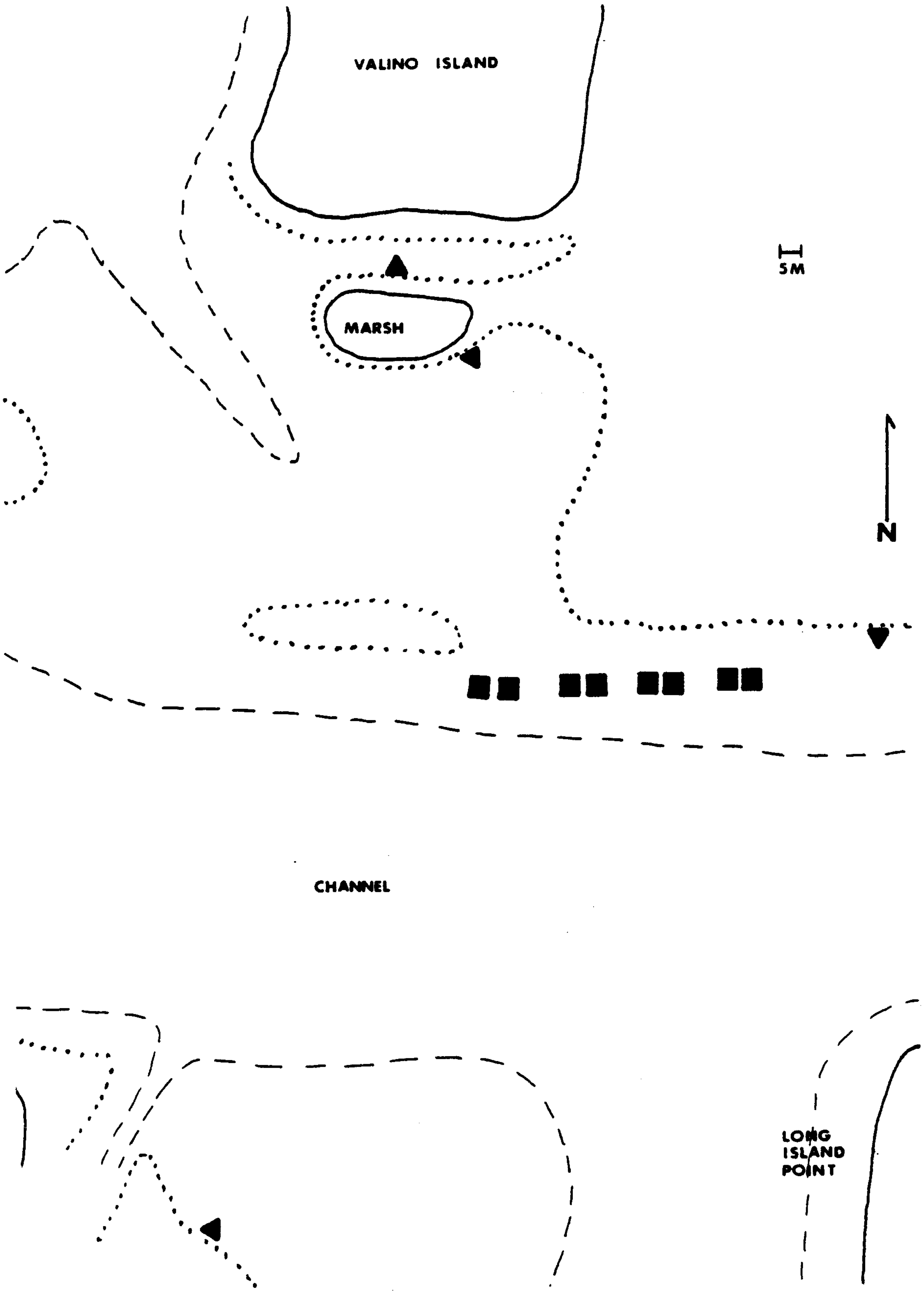
TABLE V-1. Results of migration experiments. Values for a row represent a single set of treatments. Different rows represent different areas or years. Standard errors are calculated by taking the square root of the ANOVA error mean square.

		Change in Number of Holes		
Season	Exclosure	Unmanipulated	Sideless	No-top
Fall	3	7	-	5
	-16	-16	-	-23
	1	-11	-	-3
	-10	-12	-	-6
	53	16	-	-34
	13	47	7	20
	-2	15	-1	8
	-20	-12	-	-42
	S.E.=16.86	F=1.59	p>.2	
Winter	19	0	-	2
	29	19	-	6
	26	12	13	26
	10	-1	12	8
	-22	1	21	-44
	-8	37	20	-1
	S.E.=15.14	F=1.41	p>.3	
Spring	-3	-2	2	3
	8	4	18	18
	31	-10	18	8
	6	1	-	-22
	26	11	12	-6
	72	4	-12	6
	12	25	-12	20
	-1	-7	-9	-11
	S.E.=16.35	F=2.13	p>.1	
Summer	46	25	-	-
	69	8	-	10
	10	-14	-	-25
	84	30	-	-1
	29	-5	11	11
	3	-13	0	32
	21	2	11	10
	77*(A)	21	21	-1
	9*(B)	7	18	8
	71*(C)	31	15	10
	S.E.=17.83†	F=5.57	p>.01	

*Sets used for sediment grain analysis.

†From untransformed data.

Figure V-2. Location of migration (triangles) and transplant (squares) experiments. Dashed lines show approximate level of mean lower low water and dotted lines indicate position of shrimp beds during the summer of 1984.


VALINO ISLAND
5M
MARSH
N
CHANNEL
LONG ISLAND POINT

Treatment cages were cleaned of drift algae at least biweekly.

The number of C. californiensis holes was recorded from each of the replicates at the beginning and end of an experiment, counts for all sets being made on the same day. Some counts were independently repeated by students from the Oregon Institute of Marine Biology; the relative number of holes among the four treatments recorded by these students was consistent with that observed here.

Sediment characteristics within exclosure cages and in the surrounding areas were determined from samples taken with a 50 cm long by 12.5 diameter corer. The core was halved lengthwise, and grain size and sorting properties of one half were analyzed separately for the top and bottom 25 cm, using dry seiving techniques (Ingram, 1971).

Settlement Studies

During fall of 1983, dense aggregations of ghost shrimp burrows were noticed at several locations in the low intertidal of Coos Bay sandflats, often equalling or exceeding the densities observed in well established beds. Excavation of some of these areas indicated that they were inhabited almost entirely by newly settled (11-13 mm length) C. californiensis. At Long Island Point, a 25 m^2 area containing one such bed of newly settled shrimp, approximately at MLLW, was monitored several times by counting the number of burrow holes in haphazardly placed 0.25 m^2 quadrats.

Transplant Studies

During the summer of 1984, four pairs of transplant plots on Valino

Island were placed at approximately 0.6 m above MLLW (Figure V-2). The lower edge of the main shrimp bed was about 10 m away and 0.9 m above MLLW. Each pair of transplants included a 1 m^2 full cage (exclosure) and a 1 m^2 uncaged treatment. Fifty shrimp were transplanted into each treatment of three experimental pairs and 40 ghost shrimp were placed into the two plots of the fourth. Callianassa were collected from a sandflat near the Oregon Institute of Marine Biology and transplanted into the experimental plots within two days of collection. Reburrowing was aided by putting the shrimp into 8 cm deep, water-filled starter holes. Most individuals immediately began enlarging these initial burrows. Since large shrimp had difficulty in excavating new burrows, only individuals between 10 and 70 mm length were used.

Both exclosure and control treatments were covered with a cage for 3-5 days after transplanting to allow shrimp to begin constructing their burrow systems. (In the laboratory the initial stages of burrow construction, formation of a Y-shaped burrow with two openings and a turn-around chamber, usually occurred within a few days.) After 3-5 days, the cage was removed from the control plot. Holes were counted at this time and again after 35-50 days. Both treatments within an experimental pair were counted on the same day. Partial cage structures were not used to control for cage effects since the exclusion cages were identical to those in the migration experiments, for which partial cages were included, and the work involved in transplanting an additional 100 shrimp per set was prohibitive.

Statistical Analysis

In both migration and transplant studies, changes between the initial and final number of holes were used as an indicator of treatment effects on shrimp density. Treatments for the migration experiment were compared separately for each season using a one-way analysis of variance (ANOVA), blocking for differences between experimental sets (Sokal and Rohlf, 1981). A square root transformation ($\pm\sqrt{|\text{change} + .5|}$) was applied where an F-max test indicated heteroscedasticity (this occurred only for the summer experiments; application of the transform resulted in a slight decline in significance levels). Similar analysis also tested treatment effects in the transplant studies.

Sediment grain size and sorting coefficients were calculated using moment statistics as described in McBride (1971).

Results

Migration Studies

The effect of excluding predators on Callianassa californiensis abundance immediately below a bed varied seasonally (Table V-1). Experiments during the three summers demonstrated a highly significant effect. No significant difference between treatments was observed during the fall, winter and spring experiments. The results for spring, however, appear intermediate to those of winter and summer.

Although the presence of unequal sample sizes prevented an analysis of single degrees of freedom, much of the difference between treatments during summers can be attributed to the great increase in the number of holes within the exclosure cages. Their average was over three times that in the controls, with exclosure cages exhibiting the greatest increases in eight of the ten experimental sets (Table V-1). Excavation of a limited number of treatment sets indicated that the great majority of individuals within both exclosure and control plots were more than 1 year old (40 mm or longer), few individuals coming from that year's size class.

An interesting result of these experiments was the variability in response to a particular treatment between different experimental sets, especially during fall and winter. This is demonstrated by the fall no-top treatment, which varied from the lowest decline in hole numbers to an anomalously large decline (Table V-1). There was also fluctuation within a treatment over time. Fluctuations in hole number were especially noticeable between weekly summer visits. Such variations, both between areas and within a treatment, suggest that the edge of the bed is not static but rather represents a dynamic front with contraction and expansion.

Cage Artifacts

A major problem in the interpretation of caging experiments in soft sediments is the potential for cage artifacts. Cage structures may disrupt currents possibly leading to increased larval settlement (Virnstein, 1978; Eckman, 1983; Hannan, 1984) or siltation (McCall, 1977; Hulberg and Oliver, 1980), shade the substrate surface affecting growth of microalgae (Peterson, 1979), become fouled increasing local food concentrations for some species and decreasing food for others (Peterson, 1979), or provide refuges for secondary predators or juveniles of larger predators (Arntz, 1977; Young et al., 1976; Lee II, 1978). Even straws partially inserted into the sediment may lead to significant local effects on species composition and abundance (Eckman, 1983).

The relatively short duration of my caging experiments should minimize cage artifacts, as suggested by the lack of significant cage effects during spring, winter, and fall periods. However, in order to determine if the summer increases within the exclosure cages may be due to physical effects associated with the presence of a cage, two types of potential cage artifacts will be examined further: 1) that the hole numbers may increase in response to changing hole-to-shrimp ratios rather than to increases in shrimp number; and, 2) that shrimp density may increase in response to physical changes associated with the cage structure rather than to predator exclusion.

Because a cage structure may disrupt currents, holes may persist longer within an exclosure treatment, leading to an increase in hole numbers without a corresponding increase in shrimp density (the reverse hypothesis, that increased turbulence may lead to decreased persistence of holes, is also possible, but would not contribute to the significantly higher number of holes seen in summer exclosures). The relationship between shrimp numbers and shrimp holes was measured within summer exclosure cages using the procedure described in Chapter III. There is a strong correlation between holes and number of shrimp within these treatments (Figure V-3; $r=.93$; $p<.001$); however, the slope of the least squares regression line is significantly higher than that measured outside the cages during the same time period ($F=31.96$; $p<.0001$). This

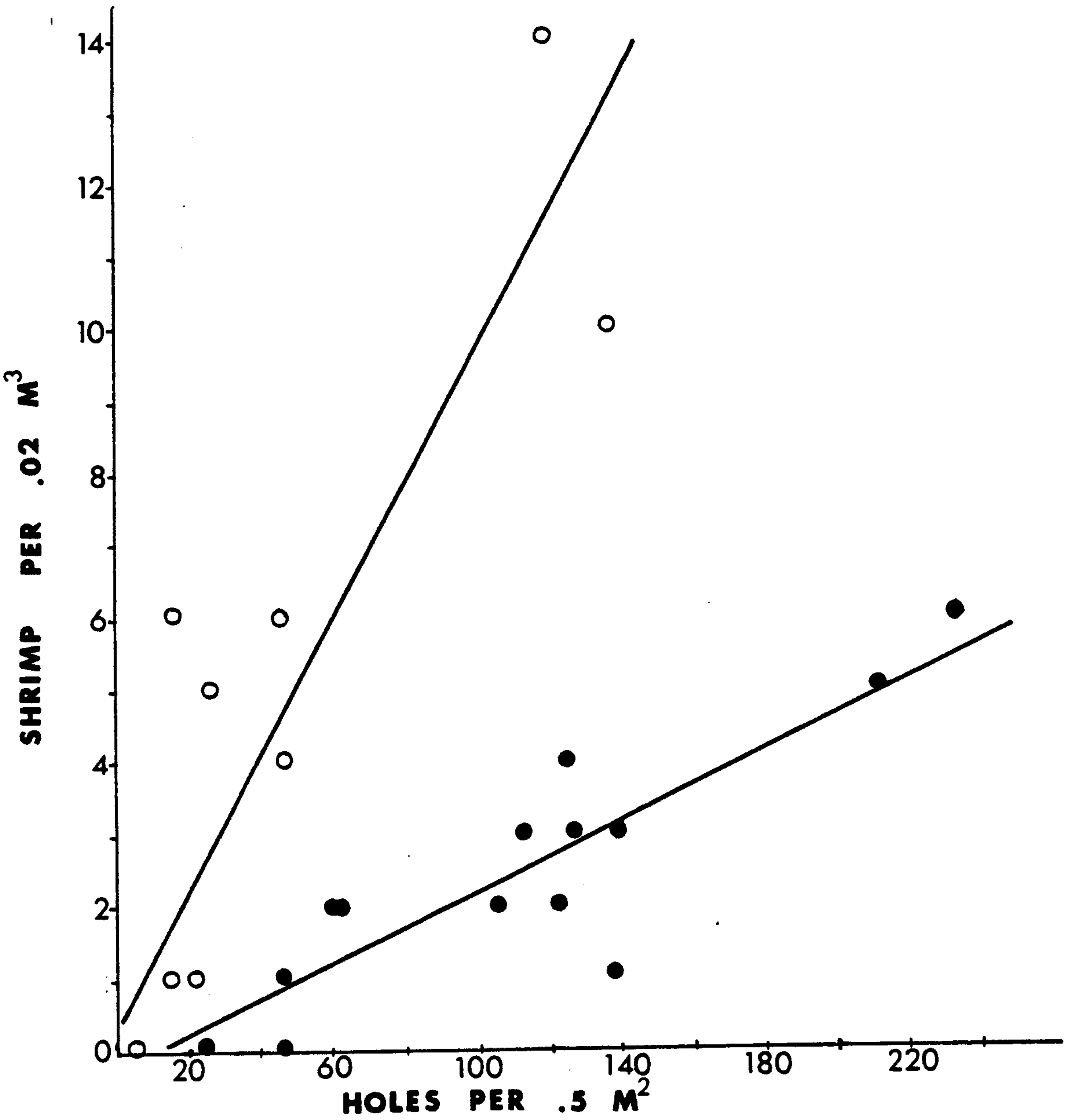


Figure V-3. Comparison of the relationship between hole density and shrimp abundance within exclosure cages (open circles) and outside of cages (filled circles) during the summer 1982. r for cages = .92; r for outside = .88. p for both >.001.

suggests that holes provide a conservative estimate of shrimp density in exclosures as compared to uncaged areas, possibly even underestimating the density of ghost shrimp in caged plots. The decline of hole-to-shrimp ratios within exclosures is not readily explained. The pattern is similar to the difference between summer and winter measurements, which may be attributable to reduced winter activity. A similar mechanism may operate here. Because of the initially low numbers of *Callianassa*, the exclosure areas may represent a richer food source (Bird, 1982) and more difficult burrowing conditions (Brenchley, 1978) than a dense bed. Both the greater accessibility of detrital food and increased effort needed to burrow may contribute to reduced burrowing activity.

Whether the increase in shrimp numbers within exclosures is due to a cage artifact or to treatment effects represents a second problem with interpreting the results of these experiments. If cage artifacts are important, cage controls that allow access to predators while mimicking some of the physical disturbances associated with a complete cage should show intermediate results. There is little difference between the two cage controls and the unmanipulated plot during summer experiments. Sediment grain size analysis from cores taken within exclosure and unmanipulated plots also suggests that exclosure cages do not cause major changes in the underlying substrate (Table V-2). Comparisons between cores taken in cages and their unmanipulated controls within the same experimental set showed similar mean particle sizes and sorting coefficients between these treatments. Sediment characteristics were similar even when treatments were several meters from each other and hence subject to local variability in current patterns. Another

TABLE V-2. Mean and standard deviation (sorting) of particle size in sediment samples taken in exclosure (E) and unmanipulated (O) treatments. Letter identifications of experimental sets refer to notations in Table V-1.

Experimental Set	Treatment	Depth Range (cm)	Mean Grain Size (ϕ)	Standard Deviation
A	E	0-25	2.4	.783
	0	0-25	2.4	.738
	E	25-50	2.4	.798
	0	25-50	2.3	.748
B	E	0-25	2.4	.777
	0	0-25	2.4	.838
	E	25-50	2.4	.757
	0	25-50	2.4	.829
C	E	0-25	-	-
	0	0-25	2.6	.759
	E	25-50	2.3	.853
	0	25-50	2.5	.756

potential artifact may arise from increased settlement around a cage. As mentioned previously, excavation of exclosures showed that the majority of the shrimp in these plots were adults. Callianassa settlement in Coos Bay was highest during late August (Johnson and Gonor, 1979; personal observation) while increases in hole number within summer exclosures usually were evident by mid July. Also, in summer 1982 the cages contained only 4.5% newly settled ghost shrimp by late August while an adjacent bed at the same time contained 8.8% juveniles. The lack of increases in number of holes within summer cage controls, no differences in sediment grain size and sorting between caged and uncaged areas, and no increase of shrimp settlement within complete cages all suggest that cage artifact effects are small relative to treatment effects and that the increases in number of holes are real and resulted from reduced predation.

Transplant Studies

All four exclosure cages had significantly higher numbers of holes relative to initial counts than their paired control plots (Table V-3; $F=40.09$; $p<.008$). Since the exclosure cages for the transplant studies were identical to those in the migration experiments, since the transplant plots were not near any dense aggregations of ghost shrimp, and because these experiments were conducted before most settlement occurred, most of the differences between caged and uncaged plots are explained by differential mortality or emigration. At the start of these experiments the density of *Callianassa* holes immediately surrounding the transplants was low, $1\text{-}2/m^2$; it did not increase significantly during the course of the summer. The lack of an increase in hole numbers in the area around the transplant plots and the negligible cage artifacts observed among the cage controls of the migration experiments suggest that decreased mortality (resulting from decreased predation) is the major cause of the difference between caged and uncaged treatments.

Settlement Studies

Callianassa californiensis collected near the low-intertidal settlement area in October were 11-13 mm in length, indicating that they settled during the previous two to three months (Johnson and Gonor, 1979;

TABLE V-3. Change in the number of holes within transplant plots. Values for a row represent a single treatment pair. Different rows represent different areas.

Exclosure	Unmanipulated
8	-4
15	-5
33	7
38	12

Bird, 1982). Collections of ghost shrimp from higher in the intertidal indicated that Callianassa larval settlement had occurred throughout a tidal range from at least 1.5 m above (within an established bed) to -0.2 m below MLLW. However, hole density declined in the study area (at approximately 0 m above MLLW) from October to July (Figure V-4). Collecting shrimp from an adjacent area in October and again in June also suggested a decline in Callianassa abundance over the nine month period. The single October observation of 67 holes/0.25 m^2 was close to the 57 holes/0.25 m^2 observed in a dense bed at Valino Island during this same period, while the late July estimate of 8 holes/0.25 m^2 approximates the 5-6 holes/0.25 m^2 at the same tidal height on Valino Island in early August of the preceding year (before most settlement had occurred).

Discussion

Several authors have suggested mechanisms to account for the

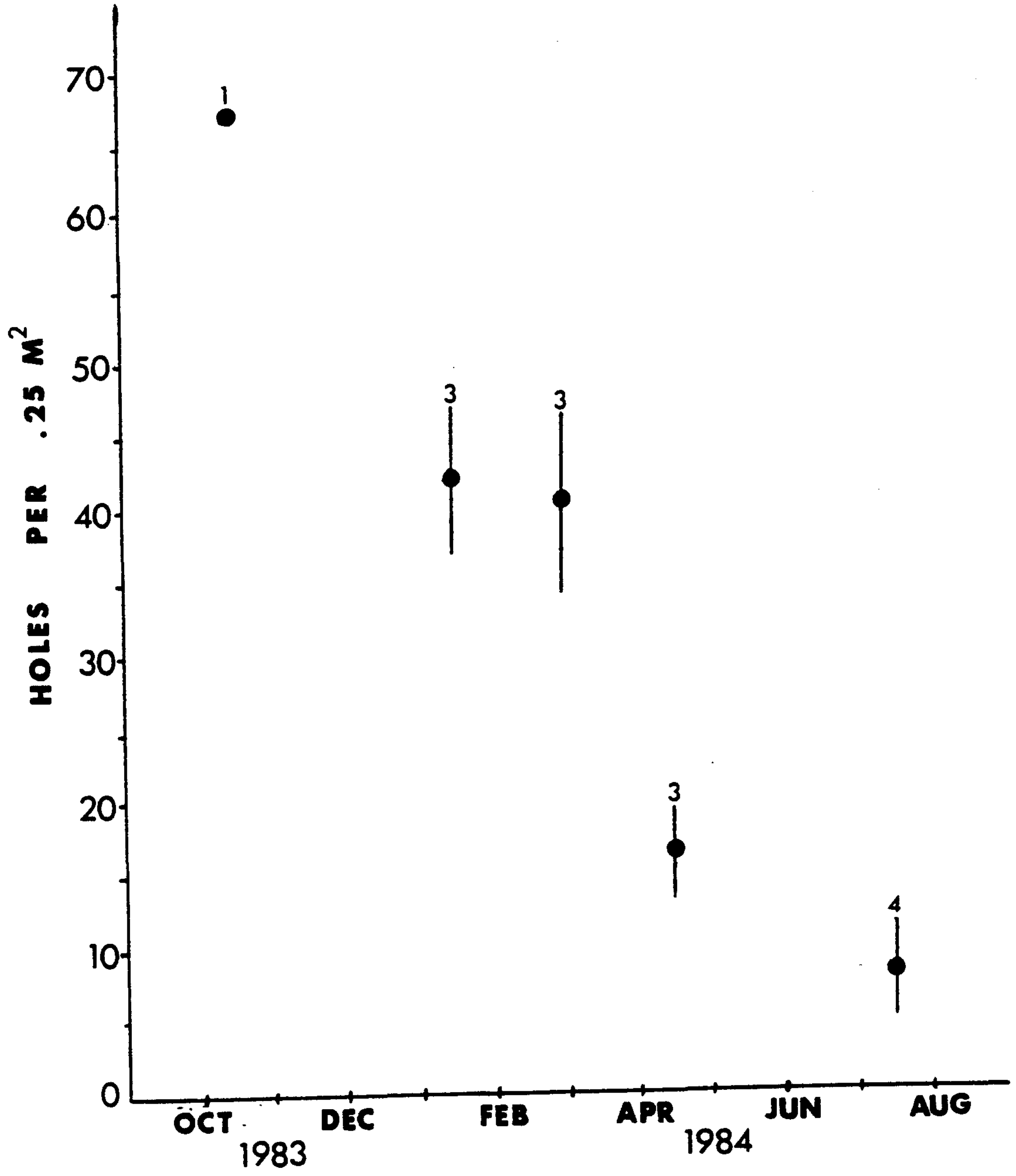


FIGURE V-4. Hole densities within low intertidal settlement area. Bars indicate ± 1 standard deviation and numbers above bars give the sample size.

intertidal zonation of *Callianassa californiensis*. However, these explanations have seldom been tested and their appropriateness to the Valino Island community is questionable.

Thompson and Pritchard (1969) suggested that occupation of higher tidal levels may provide *Callianassa* with protection "from lower interstitial salinities at times of overflowing brackish water." In river dominated systems, one might expect channel salinities to drop at low tide and salinities to increase from the influx of ocean water on flood tides. While low-tide surface water salinities at Valino Island (Table V-4) may drop below the 8 ^{o}/oo salinity tolerance of *C. californiensis* (Thompson and Pritchard, 1969) for short periods, such a hypothesis does not appear adequate to explain the zonation pattern in this area. First, interstitial salinities, measured from pooled water using a refractometer, did not differ greatly between a dense bed and an area 3 m away that had few ghost shrimp (Table V-4). Secondly, the presence of ghost shrimp in the lower intertidal and subtidally, although at lower densities, indicates that they can survive in these areas. Also, zonation is evident near the mouths of many Oregon Bays where tidal variations in salinity would be reduced. Finally a salinity hypothesis cannot explain the downward migration of adult ghost shrimp observed in exclosure cages.

McCrow (1971) suggested that the lower limit of *C. californiensis* in Oregon may be determined through competition with the burrowing shrimp *Upogebia pugettensis*. Although *Upogebia* beds are commonly found along the lower edge of *Callianassa* beds in some Oregon estuaries, this pattern is not prevalent in Coos Bay (personal observation). At both

TABLE V-4. Comparisons of low-tide salinities ($^{o}/oo$) from three locations at Valino Island, Coos Bay.

Date	Channel	Shrimp Burrows in a Dense Bed	Interstitial 3m Below Bed
1983			
19 February	4	18	17
4 March	11	22	22
19 March	12	20	-
4 April	6	14	-
4 May	16	20	20
21 July	17	30	-
31 July	27	31	-
28 November	7	-	16
13 December	9	16	16
1984			
11 January	14	19	18
25 February	9	17	19
5 May	4	24	24

Long Island Point and Valino Island, dense beds of these two burrowing shrimps are widely separated.

Although not proposed specifically to explain zonation patterns, MacGinitie (1935) suggested a cyclic pattern for the establishment of ghost shrimp beds that may lead to the occurrence of dense aggregations at higher tidal levels. He suggested that as sandy bottoms are built up through deposition, benthic algae, such as Enteromorpha spp., may occupy the substrate. These algae would greatly increase the sedimentation rate, causing the sandflat to be rapidly built up above the low-intertidal zone and the original growth of algae to be buried. As the algae begin to decay, Callianassa invade the area with its abundant detrital food source. The activities of the ghost shrimp further build up the substrate surface and prevent the establishment of additional algae. When the organic matter has been depleted, the ghost shrimp leave, the remaining clean, sifted sand is eroded away, and the level of the substrate is lowered so that the cycle may begin anew. Although such a cycle may occur under certain circumstances, it does not appear to be widespread. Bird (1982) saw no evidence for a cyclic pattern in a northern Oregon shrimp bed and Peterson (1979) implied a relatively stable position for ghost shrimp beds in Mugu Lagoon, California. Except for seasonal variations in hole number (Chapter III), cycles were not observed at Valino Island and comparisons with surveys conducted during the early 1970s (P. Rudy, Oregon Institute of Marine Biology, unpublished data) suggests that the position of the bed is similar to that of a decade ago. Additionally, the beds in South Slough are above the area of greatest algal growth (Pregnall and Rudy, 1985).

Sediment grain size and sorting have been suggested as important factors to the distribution of several deposit feeders, including Callianassa major from the Atlantic coast of North America (Pearse et al., 1942; Pohl, 1946). Because bioturbation by C. californiensis may change both mean grain size and sorting (Bird, 1982), direct comparisons between Callianassa beds and adjacent low density areas are not very useful. However, ghost shrimp beds in northern Oregon occur under a wide variety of grain sizes (1.5-2.7 mean grain size) and sorting coefficients (0.4-1.2 standard deviations) (Bird, 1982). The below-bed controls used in the migration studies (Table V-3) fall well within this range.

Devine (1966) found that *Callianassa filholi* had a predominately intertidal distribution and suggested this was in response to the intertidal distribution of one of its major food items, the diatom *Chaetoceras*. Feeding ecology varies among species of *Callianassa* and it is not likely that a similar explanation could explain the sharp zonation of *C. californiensis*. Powell (1974) mentions that the diet of *C. californiensis* included both planktonic and detrital components while MacGinitie (1934) found mainly detrital material and bacteria. Stomach content analysis of ghost shrimp collected from Valino Island and near the Oregon Institute of Marine Biology in Charleston revealed predominately detrital material, with a small percentage of diatoms. Under laboratory conditions, ghost shrimp readily feed upon commercially sold shrimp pellets (dried shrimp sold as fish food). A sharp zonation pattern would be difficult to explain on the basis of the availability of detrital food, especially without a significant difference in sediment grain characteristics and the observation that dense shrimp beds are often lower in organic content than adjacent low density areas.

The migration and transplant studies discussed here suggest that during the summer months predation may play an important role in limiting the distribution of *Callianassa californiensis*. The migration studies further indicate that this effect is highly seasonal, there being virtually no difference between exclosures and controls by the end of fall or winter. As discussed in Chapter IV, abundances of the major predator of C. californiensis, adult staghorn sculpins (Leptocottus armatus), also peak in the early summer and decline in the fall. However, although predation may limit the distribution of Callianassa beds during late spring and summer, another mechanism must be involved in the maintenance of zonation during the winter months.

The use of holes to estimate the density of the fall 1983 cohort of ghost shrimp at Long Island Point requires that care be taken in the interpretation of these results. Monitoring of hole densities within established beds and determination of hole-to-shrimp ratios (Chapter III) suggests a decline in the number of holes observed per shrimp during the winter months. Within a shrimp bed, hole densities may decline by 60% between September and February with a corresponding increase, gradual at first, between April and June. Thus the 40% decline in hole densities in the low-intertidal settlement area between October and March may be explained by natural fluctuations in hole-to-shrimp ratios. Actual reductions in shrimp numbers are probably reflected by the decline of hole densities between March and late April (censuses were taken during the last week of April) and between April and late June. These periods are well past the time of harshest salinity and wave conditions, but do coincide with the appearance of several predators in the shallow waters of Coos Bay. Adult Leptocottus began increasing in numbers in April and May. An unusually large settlement of juvenile Cancer magister also occurred from late March 1983 to April 1983 (personal observation). These crabs attacked exposed adult Callianassa under field conditions (although usually unsuccessfully) and killed and consumed juvenile ghost shrimp in the laboratory. During April low tides, juvenile *Cancer* were found buried in the sand of the low-intertidal area, where *Callianassa* settled, at densities between 120-200/m^2. A third group of predators, juvenile *Leptocottus*, was present from mid-winter into early spring, but the few fish examined did not have *Callianassa* in their stomachs. Although it is difficult to determine which predators are most important, the appearance of these predators at about the same time at which juvenile shrimp densities began to decline in the low intertidal strongly suggests that they control the number of juveniles surviving in this zone.

CHAPTER VI

CONCLUSION

The studies discussed in the preceding chapters lead to a number of conclusions:

1. Dense aggregations of Callianassa californiensis in most Oregon embayments are limited primarily to the mid intertidal.

2. High densities of Callianassa are correlated with changes in the abundance of other tideflat organisms. In particular, sedentary polychaetes and amphipods displayed lower abundances within shrimp beds. These effects appear to depend upon the ghost shrimps' disruption of the sediment.

3. During summer, the lower limit of dense shrimp beds within Coos Bay, Oregon, appears to be determined largely by predation.

4. Predation has little effect in maintaining zonation during winter. However, the lack of a strong downward expansion in this season seems related to lower winter activity of the shrimp.

These results suggest a general model for the zonation of Callianassa in Coos Bay. One of the major factors preventing the establishment of dense beds in the low intertidal and subtidally is seasonal predation. Although predation is reduced during winter, there is also less movement of adult shrimp, and hence little expansion of existing beds. Aggregations of shrimp that do occupy the low intertidal during the winter, such as periodic settlements of juvenile shrimp, appear to be cropped during the following year. It should be emphasized that this model would explain only the present lower limit to dense beds. The genus Callianassa is generally restricted to shallow water (Pickett et al., 1971) and predation is not a likely explanation for its rarity in greater depths.

As mentioned above, the two most important mechanisms for the expansion of dense ghost shrimp beds into the low intertidal and subtidal involve the summer migration of adult Callianassa and larval settlement. Larval settlement is sporadic (Bird, 1982; Chapter V) and juvenile shrimp may be susceptible to several predator species. However, only one major predator of adult ghost shrimp, the staghorn sculpin Leptocottus armatus, was observed in Coos Bay. Since information on diet and abundance is available for this species, it is possible to assess whether predation by the staghorn sculpin is sufficient to prevent downward expansion of the bed through migration of adult shrimp. Since fish diets and abundances, as well as shrimp migration, vary seasonally, the following discussion will be limited to data from June and July.

Between 6% and 38% of the staghorn sculpins caught in beach seines during June and July had Callianassa in their stomachs (Chapter IV). In virtually all cases, only a single shrimp was eaten. An average summer rate of 0.2 shrimp/sculpin is consistent with other estimates from diet studies (Tasto, 1975; M. Quammen, University of California, Santa Barbara, written communication) and will be assumed here. Since several hours are needed to digest an item as large as a ghost shrimp, this estimate will be taken as an approximation of predation rates over a tidal cycle.

Determining the density of Leptocottus immediately below a shrimp bed is more difficult. Information on staghorn sculpin abundances in Coos Bay comes from beach seines and fish traps. Seines cover a relatively large area, not sampling specifically in the mid-intertidal zone beneath a shrimp bed, and they often have a low catch efficiency owing to fish avoidance of the net. Avoidance or attraction may also occur with fish traps, but traps have the advantage of sampling a specific area. The total catch in the 24 traps placed immediately beneath the Callianassa bed at Battle Flats was 110 sculpins (Chapter IV). Although the exact area fished by a trap is uncertain, each covered a section 1 m wide and an area of 1 m^2 will be used as a conservative estimate. All traps were left in place for a single high tide. These figures suggest a maximum density of 4.6 sculpins/m^2 per tidal cycle. This estimate assumes that sculpins forage over a limited area and that adjacent 1 m^2 quadrats have similar densities. At the other extreme, a small number of fish could forage along the entire length of the shrimp bed and the sculpins caught in the traps may represent the entire population foraging beneath the Battle Flats bed. Since the Battle Flats bed was approximately 50 m long, this suggests a lower estimate of 0.09 sculpins/m^2 per tidal cycle. Using these densities and the 0.2 Callianassa/m^2 per tidal cycle rate discussed previously, Leptocottus may consume between 0.02 and 0.92 ghost shrimp/m^2 per tidal cycle, or 0.04 to 1.84 shrimp/m^2 per day, at Battle Flats during June and July.

Comparing summer exclosures and unmanipulated controls in the migration experiments provides a rough estimate of downward migration for adult Callianassa (Chapter V). Using an estimate of 4 holes/shrimp (Chapter III), there was an average summer difference of 8.2 shrimp/m^2 between these treatments and the maximum difference between an exclosure and its paired control was 15 shrimp/m^2. Since these experiments were continued for approximately 60 days, this gives an average migration rate of 0.14 shrimp $m^{-2}day^{-1}$ and a maximum rate within cages of 0.25 shrimp $m^{-2}day^{-1}$. Because of partial predation on burrows near the edge of a cage, these values may underestimate the actual downward migration. Summer Callianassa densities at both the Valino Island and Battle Flats beds were approximately 70 shrimp/m^2 (Chapter III). The final density in the 1 m wide band beneath the shrimp bed would not be expected to exceed this value, indicating a maximum immigration rate of 1.17 shrimp $m^{-2}day^{-1}$ during the 60 day period.

The figures given above represent only rough estimates of predation rates along the lower edge of a shrimp bed. However, estimates of predation rates between 0.04 and 1.84 shrimp $m^{-2}day^{-1}$ and migration rates ranging from 0.14 to 1.17 shrimp $m^{-2}day^{-1}$ suggest that Leptocottus predation could be sufficient to prevent downward expansion of the bed resulting from adult Callianassa movement.

Although zonation of shrimp beds is common in Coos Bay, the sharpness of this lower boundary varies between areas and over time. The lower edge of many beds was less defined during winter when predation decreased (Chapter III). Observations of beds then suggest that the lower boundary is more distinct on steeper slopes. Another factor that may contribute to sharp boundaries around moderately dense beds is intraspecific facilitation of burrowing (Brenchley, 1981). As noted earlier, dense aggregations of *Callianassa* disrupt the sediment, often giving it a soft, quicksand quality. Burrowing in such an area would require less energy than in packed sands. However, at higher densities, the negative intraspecific effects of food depletion and aggressive interactions may counteract burrowing facilitation.

As discussed in Chapter I, much of the previous work on intertidal communities in soft sediments has indicated that sediment grain size and current characteristics are the major factors that affect zonation of most deep-burrowing organisms. Competition is not generally important in causing zonation of soft-sediment fauna (Peterson, 1979), and predation appears to affect primarily epifauna and shallow infauna (Birkeland and Chia, 1971; Reise, 1978; Van Dolah, 1978; Race, 1982). *Callianassa californiensis* often forms burrow systems more than 50 cm deep (MacGinitie, 1934) and the lower distribution of shrimp beds appears to be determined to a large extent by summer predation. Adult *C. californiensis* apparently become susceptible to predation because they spend time near the burrow entrances and may leave the burrow on some occasions. These results emphasize the need to understand behavioral patterns of individual species in determining the relative importance of physical and biological factors to their distribution.

Predation on *Callianassa californiensis* in Coos Bay may also affect the abundance of other tideflat organisms in a manner analogous to the effect of sea star predation on mussels in the rocky intertidal (Paine, 1974). Due to the shrimps' strong bioturbating activity, the presence of a dense *Callianassa* bed is correlated with decreases in the abundances of certain sedentary organisms, such as spionid polychaetes and tubicolous amphipods, and increased numbers of some mobile forms (free burrowing amphipods in this study). If dense *Callianassa* beds existed throughout the intertidal, the relative abundance of many species would be quite different from that observed. The zonation of *C. californiensis* beds indicates that predation may be important in determining the relative abundances of intertidal organisms in soft sediments as well as on hard substrates.

Although *Callianassa californiensis* may represent an extreme example, other organisms have been reported to influence the relative abundance of soft-sediment fauna. Dense aggregations of the burrowing polychaete *Abarenicola pacifica* are associated with lower numbers of some tube-dwelling animals (Wilson, 1981) and *Arenicola marina* appears to have a significant effect on meiofaunal composition (Reise, 1983). Changes in the abundance of soft-sediment organisms have also been reported from dense assemblages of tube-building polychaetes (Wilson, 1979). If predation limits the distribution of these dominant animals under certain conditions, it could affect the composition of the intertidal community similarly to the zonation of *C. californiensis* beds.

APPENDIX

OCCURRENCE OF ANIMALS TAKEN IN BENTHIC CORES

A complete listing of animals taken in benthic cores (See Chapter II) is given below. Per cent abundance is calculated based on the total number caught during the two years of sampling. Less than 0.1% is shown by an asterisk (*). The data come from 8 sampling periods (seasonally from spring 1982 to fall 1984; see Chapter II)

Taxa	Per Cent Abundance	# of Sampling Periods Found
Crustacea		
Tanaidacea		
Leptochelia dubia	63.5	8
Amphipoda		
Eobrolgus spinosus	6.6	8
Corophium spp.	2.8	8
Grandidierella japonica	1.2	8
Ampithoe valida	0.3	2
Eohaustorius sp.	*	4
Ostracoda	7.1	8
Isopoda	*	3
Cumacea	2.1	8
Decapoda		
Callianassa californiensis (juveniles)	*	3
Hemigrapsis sp.	*	2
Insecta	*	7
Arachnida (spiders)	*	8

Taxa	Per Cent Abundance	# of Sampling Periods Found
Oligochaeta	11.1	8
Polychaeta		
Spionidae		
Pygospio elegans	1.5	8
Pseudopolydora kempi	1.5	8
Polydora ligni	*	5
Boccardia sp.	*	1
Streblospio benedicti	.8	8
Spio filicornis	*	2
Spiophanes bombyx	*	7
Rhynchospio arenicola	*	1
Spionid sp.	*	1
Capitellidae		
Mediomastus californiensis	0.3	8
Capitella sp.	0.3	8
Glyceridae		
Hemipodus californiensis	*	1
Paraonidae		
Paraonella platybranchia	*	6
Phyllodocidae		
Eteone californica	0.5	7
Eteone dilatae	*	1
Eteone sp.	*	1
Opheliidae		
Armandia brevis	*	3
Goniadidae		
Glycinde armigera	*	7
Glycinde polygnatha	*	1
Glycinde sp.	*	1
Orbiniidae		
Haploscoloplos elongatus	*	3
Syllidae sp.	*	1
Arenicolidae		
Abarenicola pacifica	*	1

Taxa	Per Cent Abundance	# of Sampling Periods Found
Oweniidae		
Owenia fusiformis	*	1
Bivalvia		
Macoma nasuta	*	8
Macoma balthica	*	5
Cryptomya californica	*	7
Transenella sp.	*	3
Mytilus sp. (Juvenile)	*	1
Saxidomus sp.	*	1
Protothaca sp.	*	1
Bivalve sp.	*	8
Gastropoda sp.	*	2
Nemertea spp.	*	8

BIBLIOGRAPHY

Allen, E. J. (1899). On the fauna and bottom-deposits near the thirty fathom line from the Eddystone Grounds to Start Point. J. Mar. Biol. Ass. U. K. 5: 365-540

Aller, R. C., Dodge, R. E. (1974). Animal-sediment relations in a tropical lagoon, Discovery Bay, Jamaica. J. Mar. Res. 32: 209-232

Arntz, W. E. (1977). Results and problems of an "unsuccessful" benthos cage predation experiment (western Baltic). In: Keegan, B. F., Ceidegh, P. O., Boaden, P. J. S. (eds.) Biology of benthic organisms. Pergamon Press, New York, p. 31-44

Barnard, J. L., Barnard, C. M. (1981). The amphipod genera *Eobrolgus* and *Eyakia* (Crustacea: Phoxocephalidae) in the Pacific Ocean. Proc. Biol. Soc. Wash. 94: 295-313

Barnes, R. D. (1980). Invertebrate zoology. Saunders College, Philadelphia

Bayer, R. D. (1981). Shallow-water intertidal ichthyofauna of the Yaquina Estuary, Oregon. Northwest Science 55: 182-193

Bell, M. A. (1978). Fishes of the Santa Clara river system, southern California. Nat. Hist. Mus. Los. Ang. Cty. Contrib. Sci. 295: 1-20

Biffar, T. A. (1971). The genus *Callianassa* (Crustacea, Decapoda, Thallassinidea) in south Florida, with keys to the western Atlantic species. Bull. Mar. Sci. 21: 637-715.

Bird, E. W. (1982). Population dynamics of the Thalassinidean shrimps and their community effects through sediment modification. Ph.D. Dissertation. University of Maryland, College Park

Birkeland, C., Chia, F.-S. (1971). Recruitment risk, growth, age, and predation in two populations of sand dollars, *Dendraster excentricus* (Eschscholtz). J. Exp. Mar. Biol. Ecol. 6: 265-278

Bloom, S. A., Simon, J. L., Hunter, V. D. (1972). Animal sediment relations and community analysis of a Florida estuary. Mar. Biol. 13: 43-56

Boesch, D. F. (1972). Species diversity of marine macrobenthos in the Virginia area. Ches. Sci. 13: 206-211

Boesch, D. F. (1973). Classification and community structure of macrobenthos in the Hampton Roads area, Virginia. Mar. Biol. 21: 226-244

Brenchley, G. A. (1978). On the regulation of marine infaunal assemblages at the morphological level: a study of the interactions between sediment stabilizers, destabilizers, and their sedimentary environment. Ph.D. Dissertation. The Johns Hopkins University, Baltimore

Brenchley, G. A. (1981). Disturbance and community structure: an experimental study of bioturbation in marine soft-bottom environments. J. Mar. Res. 39: 767-790

Brenchley, G. A. (1982a). Mechanisms of spatial competition in marine soft-bottom communities. J. Exp. Mar. Biol. Ecol. 60: 17-33

Brenchley, G. A. (1982b). Predation on encapsulated larvae by adults: effects of introduced species on the gastropod Ilyanassa obsoleta. Mar. Ecol. Prog. Ser. 9: 255-262

Bybee, J. R. (1969). Effects of hydraulic pumping operations on the fauna of Tijuana Slough. Calif. Fish and Game 55: 213-220

Carson, R. (1955). The edge of the sea. Houghton Mifflin, Boston

Chester, A. J., Ferguson, R. L., Thayer, G. W. (1983). Environmental gradients and benthic macroinvertebrate distributions in a shallow North Carolina estuary. Bull. Mar. Sci. 33: 282-295

Coe, W. (1953). Resurgent populations of littoral marine invertebrates and their dependence on ocean currents and tidal currents. Ecology 34: 225-229

Connell, J. H. (1961). The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. Ecology 42: 410-723

Darnell, R. M. (1958). Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. Publ. Mar. Sci. Univ. Texas 5: 353-416

Dauer, D. M. (1984). High resilience to disturbance of an estuarine polychaete community. Bull. Mar. Sci. 34: 170-174

Dayton, P. K. (1971). Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41: 351-389

Dayton, P. K. (1984). Processes structuring some marine communities: are they general? In: Strong, D. R. Jr., Simberloff, D., Abele, L. G., Thistle, A. B. (eds.) Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, New Jersey, p. 181-200

Devine, C. E. (1966). Ecology of Callianassa filholi Milne-Edwards 1878 (Crustacea, Thalassinidea). Trans. Roy. Soc. New Zeal. Zoology 8: 93-110

DeWindt, J. T. (1974). Callianassid burrows as indicators of subsurface beach trend, Mississippi River delta plain. J. Sedim. Petrol. 44: 1136-1139

Dorsey, J. H., Synnot, R. N. (1980). Marine soft-sediment benthic community offshore from the Black Rock sewage outfall, Connewaire, Victoria, Australia. Aust. J. Mar. Freshw. Res. 31: 155-162

Driscoll, E. G., Brandon, D. E. (1973). Mollusc-sediment relationships in northwest Buzzards Bay, Mass. Malacologia 12: 13-46

Eckman, J. E. (1983). Hydrodynamic processes affecting benthic recruitment. Limnol. Oceanogr. 28: 241-257

Fauchald, K. (1976). The polychaete worms: definitions and keys to the orders, families and genera. Nat. Hist. Mus. Los. Ang. Cty. Sci. Ser. 28

Fauchald, K., Jumars, P. A. (1979). The diet of worms: polychaete feeding guilds. Oceanogr. Mar. Biol. Ann. Rev. 17: 193-284

Featherstone, R. P., Risk, M. J. (1977). Effect of tube-building polychaetes on intertidal sediments of the Minos Basin, Bay of Fundy. J. Sedim. Petrol. 27: 446-450

Fenchel, T. (1975). Factors determining the distribution patterns of mud snails (Hydrobiidae). Oecologia 20: 1-7

Fenchel, T. (1977). Competition, coexistence and character displacement in mud snails (Hydrobiidae). In: Coull, B. C. (ed.) Ecology of marine benthos. University of South Carolina Press, Columbia, South Carolina

Frankenberg, D., Coles, S. L., Johannes, R. E. (1967). The potential trophic significance of Callianassa major fecal pellets. Limnol. Oceanogr. 12: 113-120

Gerrodette, J., Fleshig, A. O. (1979). Sediment-induced reduction in the pumping rate of the tropical sponge Verongia lacunosa. Mar. Biol. 55: 103-110

Gonor, J. J., Kemp, P. F. (1978). Procedures for quantitative ecological assessments in intertidal environments. EPA-600/3-78-087

Grant, J. (1981). Sediment transport and disturbance in an intertidal sandflat: infaunal distribution and recolonization. Mar. Ecol. Prog. Ser. 6: 249-255

Grant, W. D., Boyer, L. F., Sanford, L. P. (1982). The effects of bioturbation on the initiation of motion of intertidal sands. J. Mar. Res. 40: 659-677

Grassle, J. F., Grassle, J. P. (1974). Opportunistic life histories and genetic systems in marine benthic polychaetes. J. Mar. Res. 32: 253-284

Green, R. H., Hobson, K. D. (1970). Spatial and temporal variation in a temperate intertidal community, with special emphasis on *Gemma gemma* (Pelecypoda: Mollusca). Ecology 51: 999-1011

Hailstone, T. S., Stephenson, W. (1961). The biology of *Callianassa (Trypaea) australiensis* Dana 1852 (Crustacea Thalassinidea). Univ. Queensl. Pap., Dep. Zool. 1: 259-285

Hannan, C. A. (1984). Initial settlement of marine invertebrate larvae: the role of passive sinking in a near-bottom turbulent flow environment. Ph.D. Dissertation. Woods Hole Oceanographic Institution and Massachusetts Institute of Technology, Woods Hole, Massachusetts

Hartman, O. (1968a). Atlas of the errantiate polychaetous annelids from California. University of Southern California Press, Los Angeles

Hartman, O. (1968b). Atlas of the sedentariate polychaetous annelids from California. University of Southern California Press, Los Angeles

Heck, K. L. Jr., Thoman, T. A. (1981). Experiments on predator-prey interactions in vegetated aquatic habitats. J. Exp. Mar. Biol. Ecol. 53: 125-134

Hedgepeth, J. W. (ed.) (1952). Between Pacific tides. Stanford University Press, Stanford, California

Highsmith, R. C. (1982). Induced settlement and metamorphosis of sand dollar (*Dendraster excentricus*) larvae in predator-free sites: adult sand dollar beds. Ecology 63: 329-337

Hoffman, C. J. (1981). Associations between the arrow goby *Clevelandia ios* (Jordan and Gilbert) and the ghost shrimp *Callianassa californiensis* Dana in natural and artificial burrows. Pacific Science 35: 211-216

Holland, A. F., Dean, J. M. (1977). The biology of the stout razor clam Tagelus plebeius: I. Animal-sediment relationships, feeding mechanisms, and community biology. Ches. Sci. 18: 58-66

Horn, M. H. (1980). Diel and seasonal variations in abundance and diversity of shallow water fish populations in Morro Bay, California, USA. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 78: 759-770

Hulberg, L. W., Oliver, J. S. (1980). Caging manipulations in marine soft-bottom communities: importance of animal interactions or sedimentary habitat modifications. Can. J. Fish. Aquat. Sci. 37: 1130-1139

Ingram, R. L. (1971). Seive analysis. In: Carver, R. E. (ed.) Procedures in sedimentary petrology. Wiley-Interscience, New York, p. 49-68

Johnson, G. E., Gonor, J. J. (1982). The tidal exchange of Callianassa californiensis (Crustacea, Decapoda) larvae between the ocean and the Salmon River estuary, Oregon. Estuar. Coast. Shelf Sci. 14: 501-516

Johnson, R. G. (1970). Variations in diversity within benthic marine communities. Am. Nat. 104: 285-300

Jones, A. C. (1962). The biology of the euryhaline fish Leptocottus armatus Girard (Cottidae). Univ. Calif. Publ. Zool. 67: 321-367

Jones, N. S. (1950). Marine bottom communities. Biol. Rev. 25: 283-313

Kneib, R. J., Stiven, A. E. (1982). Benthic invertebrate responses to size and density manipulations of the common mummichog, Fundulus heteroclitus, in an intertidal salt marsh. Ecology 63: 1518-1532

Krebs, C. J. (1978). Ecology: the experimental analysis of distribution. Harper and Row, New York

Lawrence, J. M., Murdoch, J. (1977). The effect of particle-size frequency distribution of the substratum on the burrowing ability of Chiridota rigida (Semper.) (Echinodermata: Holothuroidea). Mar. Behav. Physiol. 4: 305-311

Lee II, H. (1978). Seasonality, predation and opportunism in high diversity soft-bottom communities in the Gulf of Panama. Ph.D. Dissertation. Chapel Hill, North Carolina

Levin, L. A. (1981). Dispersion, feeding behavior and competition in two spionid polychaetes. J. Mar. Res. 39: 99-117

Levin, L. A. (1982). Interference interactions among tube-dwelling polychaetes in a dense infaunal assemblage. J. Exp. Mar. Biol. Ecol. 65: 107-119

Levinton, J. S. (1972). Stability and trophic structure in deposit-feeding and suspension-feeding communities. Am. Nat. 106: 472-486

Levinton, J. S. (1977). Ecology of shallow water deposit-feeding communities Quisset Harbor, Massachusetts. In: Coull, B. C. (ed.) Ecology of the marine benthos. University of South Carolina Press, Columbia, South Carolina

Longbottom, M. R. (1970). The distribution of *Arenicola marina* (L.) with particular reference to the effects of particle size and organic matter of the sediments. J. Exp. Mar. Biol. Ecol. 5: 138-157

Lubchenco, J., Menge, B. A. (1978). Community development and persistence in a low rocky intertidal zone. Ecol. Monogr. 48: 67-94

MacGinitie, G. E. (1934). The natural history of *Callianassa californiensis* Dana. Amer. Midl. Natur. 15: 155-177

MacGinitie, G. E. (1935). Ecological aspects of a California marine estuary. Amer. Midl. Natur. 16: 630-763

McBride, E. F. (1971). Mathematical treatment of size distribution data. In: Carver, R. E. (ed.) Procedures in sedimentary petrology. Wiley-Interscience, New York, p. 109-128

McCall, P. L. (1977). Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. J. Mar. Res. 35: 221-226

McCrow, L. T. (1972). The ghost shrimp, *Callianassa californiensis*, in Yaquina Bay, Oregon. M. S. Thesis, Oregon State University, Corvallis, Oregon

Meadows, P. S., Campbell, J. I. (1972). Habitat selection by aquatic invertebrates. Adv. Mar. Biol. 10: 271-382

Mendoza, J. A. (1982). Some aspects of the autecology of *Leptochelia dubia* (Kroyer, 1842) (Tanaidacea). Crustaceana 43: 225-240

Miller, D. C. (1984). Mechanical post-capture particle selection by suspension- and deposit-feeding *Corophium*. J. Exp. Mor. Biol. Ecol. 82: 59-76

Moreno, E. C., Curros, P. V. (1979). The paleontology of the Cretaceous of Los Condemios, Guadalajara Province, Spaine. Bol. R. Soc. Esp. His. Nart. Secc. Geol. 77: 67-90

Morgan, E. (1970). The effect of environmental factors on the distribution of the amphipod *Pectenogammarus planicurus* with particular reference to grain size. J. Mar. Biol. Ass. U.K. 50: 769-785

Mountford, N. K., Holland, A. F., Mihursky, J. A. (1977). Identification and description of macrobenthic communities in the Calvert Cliffs region of Chesapeake Bay. Ches. Sci. 18: 360-369

Murphy, R. C. (1983). The introduced bivalve, Mercenaria mercenaria, in a shallow coastal ecosystem: 1) factors affecting its distribution; 2) contribution to benthic community metabolism. Ph.D. Dissertation. University of Southern California, Los Angeles

Myers, A. C. (1977). Sediment processing in a marine subtidal sandy bottom community: II. Biological consequences. J. Mar. Res. 35: 633-647

Naqui, S. M. Z. (1968). Effect of predation on infaunal invertebrates of Alligator Harbor, Florida. Gulf Res. Rep. 2: 313-321

Nelson, W. G. (1981). Experimental studies of decapod and fish predation on seagrass macrobenthos. Mar. Ecol. Prog. Ser. 5: 141-149

Nichols, F. H. (1970). Benthic polychaete assemblages and their relationship to the sediment in Port Madison, Washington. Mar. Biol. 6: 48-57

Nowell, A. R. M., Jumars, P. A., Eckman, J. E. (1981). Effects of biological activity on the entrainment on marine sediments. Mar. Geol. 42: 133-154

Oliver, J. S., Slattery, P. N., Hulberg, L. W., Nybakken, J. W. (1980). Relationships between wave disturbance and zonation of benthic invertebrates along a subtidal high-energy beach in Monterey Bay, California. Fish. Bull. 78: 437-454

Ott, J. A., Fuchs, B., Fuchs, R., Malasek, A. (1976). Observations on the biology of Callianassa stebbingi Borrodaile and Upogebia littoralis Risso and their effect upon sediment. Senckenberg. Mar. 8: 61-79

Paine, R. T. (1966). Food web complexity and species diversity. Am. Nat. 100: 65-75

Paine, R. T. (1974). Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15: 93-120

Paine, R. T. (1984). Ecological determinism in the competition for space. Ecology 65: 1339-1348

Pearse, A. S., Humm, H. J., Wharton, G. W. (1942). Ecology of sand beaches at Beaufort, N. C. Ecol. Monogr. 12: 135-190

Peterson, C. G. J. (1918). The sea bottom and its production of fishfood. Rep. Danish Biol. Sta. 25: 1-62

Peterson, C. H. (1979). Predation, competitive exclusion and diversity in the soft-sediment benthic communities of estuaries and lagoons. In: Livingston, R. J. (ed.) Ecological processes in coastal and marine systems. Plenum Press, New York

Peterson, C. H. (1982). The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella*. Ecol. Monogr. 52: 437-478

Peterson, C. H., Andre, S. V. (1980). An experimental analysis of intraspecific competition among marine filter feeders in a soft-sediment environment. Ecology 61: 129-139

Peterson, C. H., Quammen, M. L. (1982). Siphon snipping: its importance to small fishes and its impact on growth of the bivalve *Protothaca staminea* (Conrad). J. Exp. Mar. Biol. Ecol. 63: 249-268

Pfitzenmeyer, H. T., Drobeck, K. G. (1967). Some factors influencing reburrowing activity of the soft-shell clam, *Mya arenaria*. Ches. Sci. 8: 193-199

Pickett, T. E., Kraft, J. C., Smith, K. (1971). Cretaceous burrows--Chesapeake and Delaware Canal, Delaware. Paleontology 45: 209-211

Pohl, M. E. (1946). Ecological observations on *Callianassa major* Say at Beaufort, North Carolina. Ecology 27: 71-80

Powell, R. R. (1974). The functional morphology of the fore-gut of the thalassinid crustaceans, *Callianassa californiensis* and *Upogebia pugettensis*. Univ. Calif. Publ. Zool. 102: 1-41

Pratt, D. M. (1953). Abundance and growth of *Venus mercenaria* and *Callocardia morrhuana* in relation to the character of bottom sediments. J. Mar. Res. 12: 60-74

Pregnall, A. M., Rudy, P. P. (1985). The contributions of green macroalgal mats (*Enteromorpha* spp.) to seasonal production in an estuary. Mar. Ecol. Prog. Ser. In Press

Quammen, M. L. (1984). Predation by shorebirds, fish, and crabs on invertebrates in intertidal mudflats: an experimental test. Ecology 65: 529-537

Race, M. S. (1982). Competitive displacement and predation between introduced and native mud snails. Oecologia 54: 337-347

Ray, A. A. (ed.) (1982). SAS user's guide, statistics, 1982 edition. SAS Institute, Cary, North Carolina

Reise, K. (1978). Experiments on epibenthic predation in the Wadden Sea. Helgolander wiss. Meeresunters 31: 55-101

Reise, K. (1983). Experimental removal of lugworms from marine sands affects small zoobenthos. Mar. Biol. 74: 327-332

Rhoads, D. C., Young, D. K. (1970). The influences of deposit-feeding organisms on sediment stability and community trophic structure. J. Mar. Res. 28: 150-178

Ronan, T. E. (1975). Structural and paleo-ecological aspects of a modern marine soft-sediment community: an experimental field study. Ph.D. Dissertation. University of California, Davis, California

Rudy, P., Rudy, L. H. (1983). Oregon estuarine invertebrates: an illustrated guide to the common and important invertebrate animals. Fish and Wildlife Service. FWS/OB5-83/16

Russo, R. A. (1975). Observations on the food habits of leopard sharks (Triokis semifasciata) and brown smoothhounds (Mustelus henlei). Calif. Fish Game 61: 95-103

Sanders, H. L. (1958). Benthic studies in Buzzards Bay. I. Animal-sediment relationships. Limnol. Oceanogr. 3: 245-258

Sanders, H. L., Goudsmit, E. M., Mills, E. L., Hampson, G. E. (1962). A study of the intertidal fauna of Barnstable Harbor, Mass. Limnol. Oceanogr. 7: 63-79

Shelford, V. E., Weese, A. O., Rice, L. A., Rasmussen, D. I., Maclean, A. (1935). Some marine biotic communities of the Pacific Coast of North America. Part I. General survey of the communities. Ecol. Monogr. 5: 251-332

Smith, R. I., Carlton, J. T. (eds.) (1975). Light's manual: intertidal invertebrates of the central California coast. University of California Press, Berkeley, California

Snedecor, G. W., Cochran, W. G. (1980). Statistical methods. The Iowa State University Press, Ames, Iowa

Sokal, R. R., Rohlf, E. F. (1981). Biometry. W. H. Freeman, San Francisco

Stevens, B. A. (1928). Callianassidae from the west coast of North America. Publ. Puget Sound Biol. Sta. 6: 315-369

Stevens, B. G., Armstrong, D. A., Cusimano, R. (1982). Feeding habits of the Dungeness crab Cancer magister as determined by the index of relative importance. Mar. Biol. 72: 135-145

Stone, R., Palmer, R. (1975). Effects of turbidity on the bay scallop, Argopecten iriradiaus. Amer. Zool. 15:816 (abstract)

Suchanek, T. H. (1979). The Mytilus californianus community: studies on the composition, structure, organization, and dynamics of a mussel bed. Ph.D. Dissertation. University of Washington, Seattle, Washington

Suchanek, T. H. (1983). Control of seagrass communities and sediment distribution by Callianassa (Crustacea, Thalassinidea) bioturbation. J. Mar. Res. 41: 281-298

Swinbanks, D. D. (1982). Intertidal exposure zones: a way to subdivide the shore. J. Exp. Mar. Biol. Ecol. 62: 69-86

Swinbanks, D. D., Murray, J. W. (1981). Biosedimentological zonation of Boundary Bay tidal flats, Fraser River delta, British Columbia. Sedimentology 28: 201-237

Taghon, G. L., Nowell, A. R. M., Jumars, P. A. (1980). Induction of suspension feeding in spionid polychaetes by high particulate fluxes. Science 31: 562-564

Tasto, R. N. (1975). Aspects of the biology of Pacific staghorn sculpin, Leptocottus armatus Girard, in Anaheim Bay. In: Lane, E. D., Hill, C. W. (eds.) The marine resources of Anaheim Bay. Calif. Dept. Fish Game, Fish. Bull. no. 165, p. 123-135

Thompson, L. D., Pritchard, A. W. (1969). Osmoregulatory capacities of Callianassa and Upogebia (Crustacea: Thalassinidea). Biol. Bull. 136: 114-129

Thompson, R. K. (1972). Functional morphology of the hindgut of Upogebia pugettensis (Crustacea, Thalassinidea) and its role in burrow construction. Ph. D. Dissertation. University of California, Berkeley, California

Torres, J. J., Gluck, D. L., Childress, J. J. (1977). Activity and physiological significance of the pleopods in the respiration of Callianassa californiensis (Dana) (Crustacea: Thalassinidea). Biol. Bull. 152: 134-146

Van Dolah, R. F. (1978). Factors regulating the distribution and population dynamics of the amphipod Gammarus palustris in an intertidal salt marsh community. Ecol. Monogr. 48: 191-217

Vassalo, M. T. (1971). The ecology of Macoma inconspicua (Broderip and Sowerby, 1829) in central San Francisco Bay. Part I. The vertical distribution of the Macoma community. The Veliger 11: 223-234

Virnstein, R. W. (1977). The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology 58: 1199-1217

Virnstein, R. W. (1978). Predator caging experiments in soft sediments: caution advised. In: Wiley, M. L. (ed.) Estuarine interactions. Academic Press, New York

Weiser, W. (1956). Factors influencing the choice of substratum in Cumella vulgaris Hart (Crustacea, Cumacea). Limnol. Oceanogr. 1: 274-285

Weiser, W. (1959). The effect of grain size on the distribution of small invertebrates inhabiting the beaches of Puget Sound. Limnol. Oceanogr. 4: 181-194

Whitlach, R. B. (1977). Seasonal changes in the community structure of the macrobenthos inhabiting the intertidal sand and mud flats of Barnstable Harbor, Massachusetts. Biol. Bull. 152: 275-294

Whitlach, R. B. (1981). Animal-sediment relationships in intertidal marine benthic habitats: some determinants of deposit-feeding species diversity. J. Exp. Mar. Biol. Ecol. 53: 31-45

Willason, S. W. (1981). Factors influencing the distribution and coexistence of Pachygrapsus crassipes and Hemigrapsus oregonensis (Decapoda: Grapsidae) in a California salt marsh. Mar. Biol. 64: 125-134

Wilson, W. H. Jr. (1979). Community structure and species diversity of the sedimentary reefs constructed by Petaloproctus socialis (Polychaeta: Maldanidae). J. Mar. Res. 37: 623-641

Wilson, W. H. Jr. (1981). Sediment-mediated interactions in a densely populated infaunal assemblage: the effects of the polychaete Abarenicola pacifica. J. Mar. Res. 39: 735-748

Woodin, S. A. (1974). Polychaete abundance patterns in a marine soft-sediment environment: the importance of biological interactions. Ecol. Monogr. 44: 171-187

Woodin, S. A. (1976). Adult-larval interactions in dense infaunal assemblages: patterns of abundance. J. Mar. Res. 34: 25-41

Woodin, S. A. (1978). Refuges, disturbance, and community structure: a marine soft-bottom example. Ecology 59: 274-284

Woodin, S. A., Jackson, J. B. C. (1979). Interphyletic competition among marine benthos. Amer. Zool. 19: 1029-1043

Young, D. K., Buzas, M. A., Young, M. W. (1976). Species densities of macrobenthos associated with seagrasses: a field study of predation. J. Mar. Res. 34: 577-592

Young, D. K., Rhoads, R. C. (1971). Animal-sediment relations in Cape Cod Bay, Massachusetts. I. A transect study. Mar. Biol. 11: 242-254

Young, D. K., Young, M. W. (1978). Regulation of species densities of seagrass-associated macrobenthos: evidence from field experiments in the Indian River estuary, Florida. J. Mar. Res. 36: 569-593