

OIMB
QK
495
.P85
J38
1987

PREDATOR-PREY INTERRELATIONSHIPS AND THE INTRODUCED EELGRASS,

ZOSTERA JAPONICA (ASCHERS. AND GRAEBN.) IN THE SOUTH

SLOUGH OF COOS BAY, OREGON, U.S.A.

by

SONIA NICOLAS JAVIER

A THESIS

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
Master of Science

December 1987

OIMB LIBRARY

DEC 9 1987

APPROVED:

Dr. James T. Carlton

An Abstract of the Thesis of
Sonia Nicolas Javier for the degree of Master of Science
in the Department of Biology to be taken December 1987
Title: PREDATOR-PREY INTERRELATIONSHIPS AND THE INTRODUCED EELGRASS,
ZOSTERA JAPONICA (ASCHERS. AND GRAEBN.) IN THE SOUTH SLOUGH OF
COOS BAY, OREGON, U.S.A.

Approved: _____

Dr. James T. Carlton

The role of the introduced eelgrass Zostera japonica as a refuge from epibenthic predators was investigated. Caging experiments were employed inside and outside eelgrass beds, and density of the spionid polychaetes were determined. A 2-way analysis of variance showed that spionid density is dependent on several factors: site, season, caging treatment, and the presence or absence of Z. japonica. Four species were common: Pygospio elegans, Streblospio benedicti, Pseudopolydora kempi, and Boccardia truncata.

The Wilcoxon signed-ranks test was used to compare spionid densities inside and outside eelgrass beds, and to determine which species contribute to the significant effect in the three sites. Two sites showed significant effects. The four most common spionids showed significantly higher densities inside eelgrass beds. The exclusion of

epibenthic predators was correlated with the relative abundance patterns of spionids in the control and exclusion plots.

Zostera japonica, as a refuge for prey, contributed to the abundance of the spionid community. Other factors, beyond the scope of this study, may also be playing important roles in this community.

VITA

NAME OF AUTHOR: Sonia Nicolas Javier

PLACE OF BIRTH: Manila, Philippines

DATE OF BIRTH: July 1, 1957

GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon
University of Santo Tomas

DEGREES AWARDED:

Master of Science, 1987, University of Oregon
Bachelor of Science, 1979, University of Santo Tomas

PROFESSIONAL EXPERIENCE:

Research Assistant, University of the Philippines Publications
Office, College of Science, Diliman, Quezon City, Philippines,
1981-1984

AWARDS AND HONORS:

P.E.O. International Peace Scholarship Fund, 1985-1987
Sigma Xi, Grant-In-Aid of Research, 1986

ACKNOWLEDGEMENTS

I would like to express my deepest gratitude to the following: my adviser, Dr. James T. Carlton for sharing with me his invaluable suggestions and endless "exotic" ideas in the preparation of this manuscript; Dr. Peter Frank for his statistical input; Dr. Martin H. Posey for speaking his mind about the "soft-bottom" communities; and Dr. Paul P. Rudy for his help in various ways. Very special thanks are due to my best friend Gliss Pimentel who is always there for me through thick and thin; my parents, brothers and sisters for the moral and spiritual encouragement they have given me throughout the duration of my studies here in the U.S. I also thank the O.I.M.B. staff and graduate students for their support in many ways. This research was supported in part by the P.E.O. International Peace Scholarship Fund and by the Sigma Xi, The Scientific Research Organization.

TABLE OF CONTENTS

Chapter	Page
I. INTRODUCTION	1
II. MATERIALS AND METHODS	4
Study Area	4
Caging Experiments	4
Sediment Types	10
Statistical Analysis	10
III. RESULTS	12
Sediment Analysis	12
Faunal Community in the <u>Zostera japonica</u> beds ...	14
Seasonal Patterns	14
Comparison of Spionid Abundances Inside and Outside the Eelgrass Beds	23
Eelgrass and Predation	37
IV. DISCUSSION	42
V. SUMMARY AND RECOMMENDATIONS	52
BIBLIOGRAPHY	54

LIST OF TABLES

Table	Page
1. Mean and Cumulative Percentage Weight of the Sediment Fractions Inside and Outside the <u>Zostera japonica</u> Beds at Sites A, B, and C. Standard Errors are in Parenthesis	13
2. Average Densities (No. per 86.6 cm ²) in Control Plots of Each Spionid Species in Sites A, B, and C at All Sampling Dates Inside and Outside the <u>Zostera japonica</u> Bed	15
3. Proportion of <u>Pygospio elegans</u> and <u>Streblospio benedicti</u> Inside the Eelgrass in the Control Plots at Sites A, B, and C	22
4. Mean Densities (No. per 86.6 cm ²) of the Spionid Species in the Control Plots Inside and Outside the Eelgrass Beds at Sites A, B, and C	24
5. Mean Densities (No. per 86.6 cm ²) of the Spionid Species in the Exclusion Cage Inside and Outside the Eelgrass Beds at Sites A, B, and C	25
6. Total Spionid (N=8) Densities (No. per 86.6 cm ²) Per Cage Inside and Outside the Eelgrass Bed at Three Sites	26
7. Average Densities (No. per 86.6 cm ²) of Each Spionid Polychaetes Inside and Outside the <u>Zostera japonica</u> Beds at Site A	28
8. Average Densities (No. per 86.6 cm ²) of Each Spionid Species Inside and Outside the <u>Zostera japonica</u> Beds at Site B	31
9. The 2-way ANOVA Results on the Effects of Caging on the Densities of Spionid Species Inside the <u>Zostera japonica</u> Bed in the Different Sites in July and October 1986, and January and April 1987 ...	35

10.	The 2-way ANOVA Results on the Effects of Caging on the Densities of Spionid Species Outside the <u>Zostera japonica</u> Bed in the Different Sites in July and October 1986, and January and April 1987 ...	36
11.	Mean Densities (No. per 86.6 cm ²) of the Spionid Species in the Exclusion (exc) Cage and Control (con) Plots Inside the Eelgrass Beds at Sites A, B, and C	38
12.	Mean Densities (No. per 86.6 cm ²) of the Spionid Species in the Exclusion (exc) Cage and Control (con) Plots Outside the Eelgrass Beds at Sites A, B, and C	39
13.	Mean Densities (No. per 86.6 cm ²) of the Spionid Species in the Exclusion (exc) Cage Inside the Eelgrass Bed, and in the Control (con) Plots Outside the Eelgrass Bed in Sites A, B, and C	40
14.	Mean Densities (No. per 86.6 cm ²) of the Spionid Species in the Exclusion (exc) Cage Outside the Eelgrass Bed, and in the Control (con) Plots Inside the Eelgrass Bed at Sites A, B, and C	41

LIST OF FIGURES

Figure	Page
1. Sites of Study Area: Site A- Ferrie Marsh; Site B- Ferrie Marsh Levee; Site C- Ferrie Marsh Point	5
2. Flow Diagram of the Experimental Design Used in this Study	7
3. Types of Treatments Used in the Study: A- Roof-only Cage; B- Sides-only Cage; C- Exclusion Cage; D- Control Plot ...	8
4. Log-transformed Values of Densities (No. per 86.6 cm) Per Cage of <u>Pygospio elegans</u> Inside (in) and Outside (out) the <u>Zostera japonica</u> Bed Throughout the Study Period in Sites A, B, and C. Legend: E- Exclusion Cage; C- Control Plot; R- Roof-only Cage; S- Sides-only Cage	16
5. Log-transformed Values of Densities (No. per 86.6 cm) Per Cage of <u>Streblospio benedicti</u> Inside (in) and Outside (out) the <u>Zostera japonica</u> Bed Throughout the Study Period in Sites A, B, and C. Legend: E- Exclusion Cage; C- Control Plot; R- Roof-only Cage; S- Sides-only Cage	17
6. Log-transformed Values of Densities (No. per 86.6 cm) Per Cage of <u>Pseudopolydora kempfi</u> Inside (in) and Outside (out) the <u>Zostera japonica</u> Bed Throughout the Study Period in Sites A, B, and C. Legend: E- Exclusion Cage; C- Control Plot; R- Roof-only Cage; S- Sides-only Cage	18
7. Log-transformed Values of Densities (No. per 86.6 cm) Per Cage of <u>Boccardia truncata</u> Inside (in) and Outside (out) the <u>Zostera japonica</u> Bed Throughout the Study Period in Sites A, B, and C. Legend: E- Exclusion Cage; C- Control Plot; R- Roof-only Cage; S- Sides-only Cage	19
8. Log-transformed Values of Densities (Nos. per 86.6 cm) Per Cage of All Spionid Species (N=8) Inside (in) and Outside (out) the <u>Zostera japonica</u> Bed Throughout the Study Period in Sites A, B, and C. Legend: EX= Exclusion Cages; CO= Control Plots; RF= Roof-only Cages; SD= Sides-only Cages	20

CHAPTER I

INTRODUCTION

The low density of predators in seagrass beds may explain the extremely high densities of animals routinely recorded among masses of "drift algae" in beds (Tabb et al., 1962; Marsh, 1973; Orth, 1973; Thorhaug and Roessler, 1977; Gore et al., 1981; Heck and Thoman, 1981) and it is one of the major proposed explanations for the nursery role of seagrass habitats (Thayer and Phillips, 1977; Hanekom and Baird, 1984; Wilson et al., 1987). Wilson et al. (1987) showed that juvenile blue crabs inside an eelgrass bed were preyed on at lower rates than those on adjacent bare sand patches. Other investigations also show that areas of greater eelgrass and algal biomass have lower levels of predation intensity than areas of lesser plant biomass (Kikuchi, 1980; Lewis, 1984; Orth et al., 1984; Summerson and Peterson, 1984; Leber, 1985; Ryer, 1987).

These general patterns have shown that predation is an important determining factor in structuring communities within seagrass meadows (Young and Young, 1977, 1978; Young et al., 1976; Orth, 1977; Virnstein, 1978; Nelson, 1979, 1981; Kikuchi, 1980; Homziak et al., 1982; Virnstein et al., 1984; Main, 1987). These investigations have led to the hypothesis that the proximate cause of correlation between

prey abundances and structural complexity of seagrass is predation (Nelson, 1979; Heck and Orth, 1980; and, Stoner, 1983a).

The effects of epibenthic predators can be assessed experimentally using exclosure cages. The limitations of such manipulations in soft sediment environments (Virnstein, 1978) can be overcome with an experimental design that includes assessing the possible effects of exclosure artifacts. Based upon exclusion experiments in soft sediment communities (Reise, 1977, 1978, 1985; Schneider, 1978; Peterson, 1979; Quammen, 1984; Gee et al., 1985; and Posey, 1986a) invertebrates such as shrimps and crabs, and small vertebrates such as gobiid fishes, appear to have a much greater effect on the infaunal invertebrate populations than large fish and birds (Posey, 1986b; Main, 1987; Raffaelli and Milne, 1987).

Zostera japonica Aschers. & Graebn. is an Asian eelgrass that was first collected in North America in 1957 (Harrison, 1982a). It occurs in the mid- and upper-intertidal zones from southwestern British Columbia, Canada to Oregon and Washington, U.S.A., where it is often abundant on a variety of sediment types (Harrison, 1982b, 1982c).

Zostera japonica represents an excellent example of a recent biological invasion: it is a Japanese species believed to have been introduced to the Pacific Northwest with oysters (Harrison and Bigley, 1982). Posey and Rudy (1986) reported that records from the South Slough National Estuarine Research Reserve in Coos Bay, Oregon showed that Z. japonica has been in the Reserve for over 15 years. Surveys in the early 1970's showed that Z. japonica was present in patches in the upper reaches of

the Reserve. By the early 1980's it had covered 100% of some of the large mid-intertidal areas of the upper estuary, and had established in smaller patches near the mouth of Coos Bay.

The introduction of Zostera japonica into Coos Bay has provided an unusual opportunity to test some of the roles ascribed to predation in eelgrass communities in a system where the eelgrass is an ecologically new and major regulator of benthic patterns and processes. Little is known about the relative patterns of infauna inside and outside Z. japonica beds. Posey (unpublished) has shown that the densities of both native and introduced polychaetes are higher in Z. japonica beds than in adjacent unvegetated areas. Similar results are known for other eelgrass communities (e.g. Summerson and Peterson, 1984). The mechanisms that produced these polychaete patterns inside and outside Z. japonica beds in Coos Bay are not known.

The objectives of this study are as follows: (1) to determine the seasonal patterns of abundance of spionid polychaete worms inside and outside the Zostera japonica beds, and, (2) to investigate experimentally whether the exclusion of epibenthic predators can be correlated with these relative abundance patterns. The null hypothesis being tested is that predation does not regulate the abundance, density, or diversity patterns of spionid polychaetes inside or outside a bed of Zostera japonica.

CHAPTER II

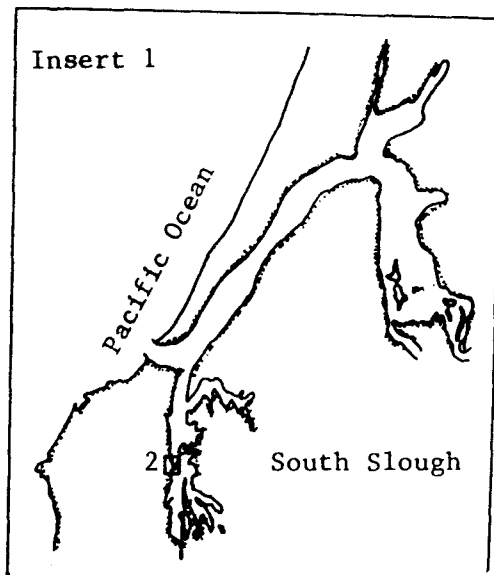
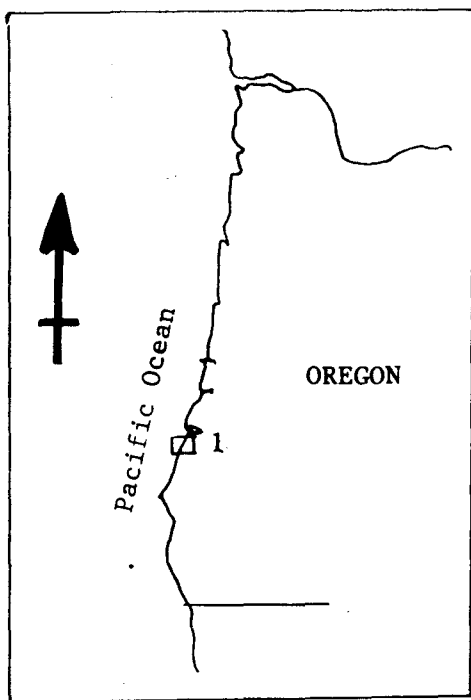
MATERIALS AND METHODS

Study Area

The study area is an intertidal muddy sandflat (0.9m above MLLW) of the South Slough in Coos Bay, Oregon (43.20°lat., 120°long.). Three sites, each with areas with and without Z. japonica beds, were selected: Ferrie Ranch Marsh (Site A); Ferrie Marsh levee (Site B); and Ferrie Marsh Point (Site C) (Fig. 1). Ferrie Ranch Marsh was a diked pasture that has developed into a marsh with sandy mud flats. Ferrie Marsh levee is 20m west of the channel entrance to Ferrie Ranch Marsh. The Ferrie Ranch Point site is 20m east of the Ferrie levee. Site C is an open site relative to sites A and B. These sites were chosen because they represent a range of sediment regimes, as well as having extensive Z. japonica patches.

Caging Experiments

Exclusion cages were employed to investigate the effect of predatory epifauna on spionids inside and outside the eelgrass beds. The experimental design consisted of randomly assigning various



Insert 2

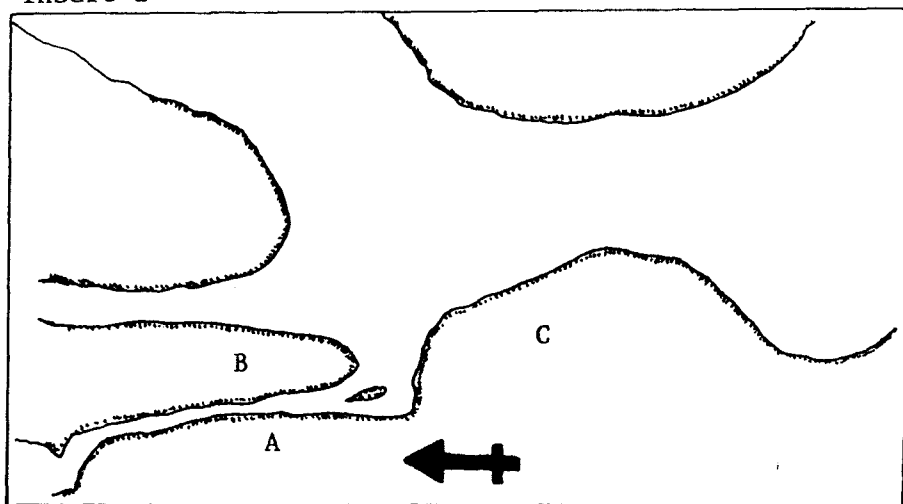


Figure 1. Sites of study area (insert 2): site A- Ferrie Ranch Marsh; site B- Ferrie Ranch levee; site C- Ferrie Marsh Point.

treatments to 1-m²/plots inside and outside of Zostera japonica beds (Fig. 2). Treatments included various caging combinations and a control, i.e., caged plots and uncaged plots respectively. Each site had four types of treatments: exclusion/full cage, "sides only" cage, "roof only" cage, and the control/no cage (Fig. 3). The cages with "sides-" or "roof only" were controls for cage effects in the environment under study. Cage effects result from the unnatural presence of a physical structure that can alter the physical nature and hydrodynamics of the caged area (Virnstein, 1978). The sides-only cages will control for slowing down of currents and increased sediment load within the cage. The roof-only cages control for these processes and shading as well.

Wood-framed, galvanized wire cages (1.0-m x 1.0-m, 1.27-cm mesh) were used. The cages were driven into the sediments up to 10-cm deep and extended approximately 15 cm above the mudflat surface for the exclusion and side-only cages, and approximately 25 cm for the roof-only cage. Between sampling dates, the meshes of all cages were cleaned of all detritus and algae. It was assumed that the cages in all three sites were equally effective in excluding predators (defined here as those animals that are too large to pass through the 1.27-cm wire mesh).

A 10.5-cm diameter core sampler was set to collect samples up to a depth of 30-cm for sites B and C, and 15-cm for site A. This was done for site A because the corer could not go any deeper than 15-cm because of the presence of marsh plant roots and stems in the

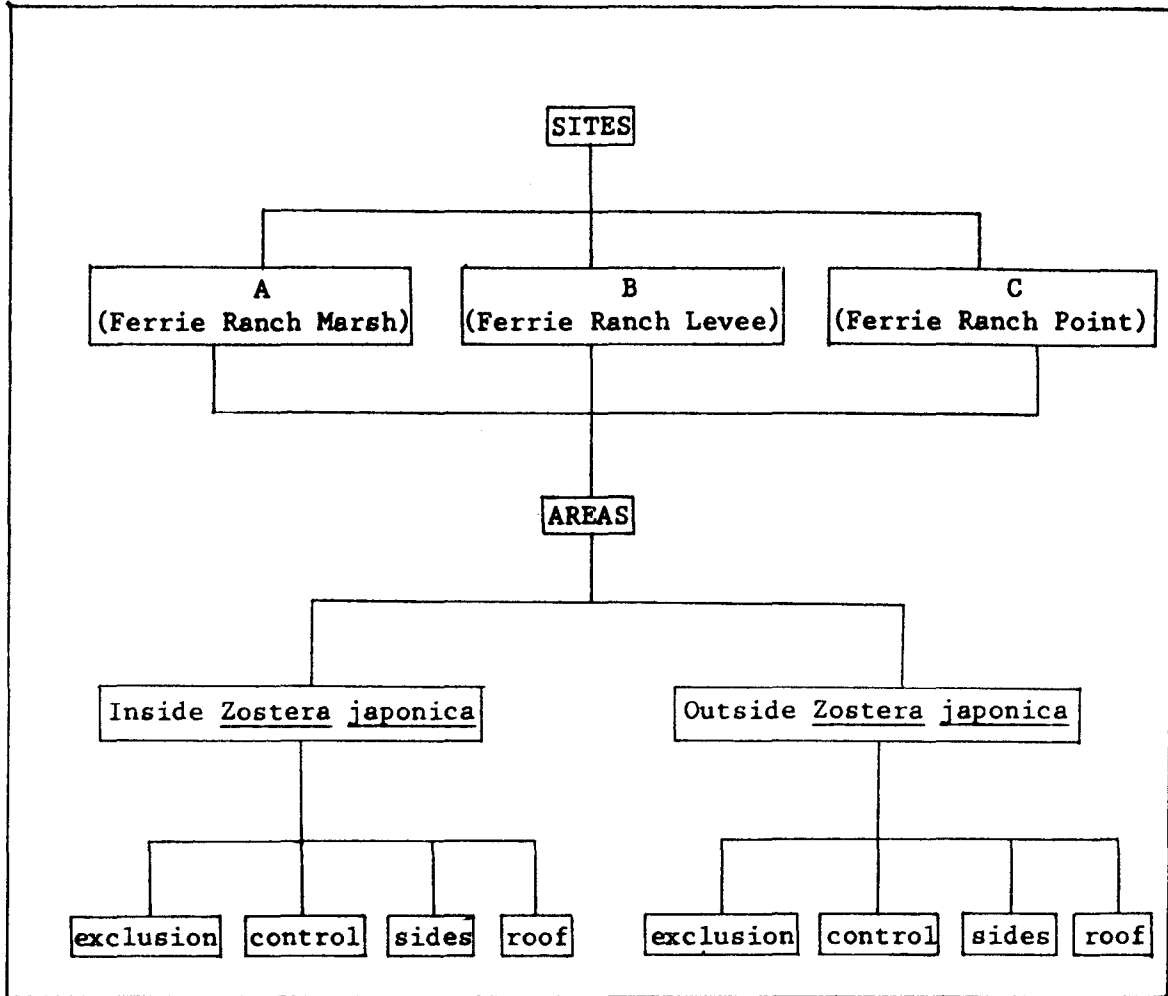


Figure 2. Flow diagram of the experimental design used in this study.

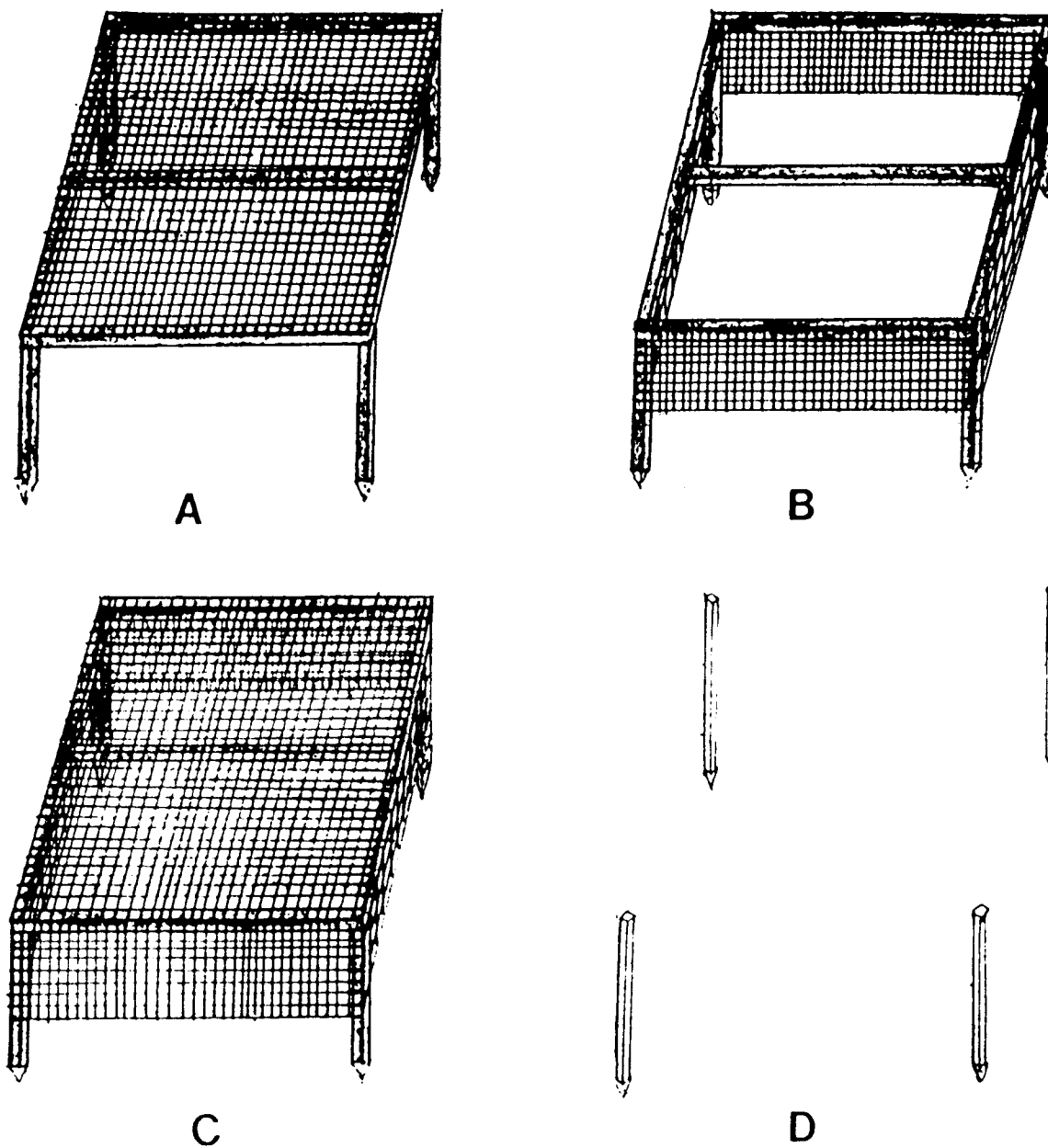


Figure 3. Types of caging treatments used: A- roof-only cage; B- sides-only cage; C- exclusion/full cage; D- control plot.

substratum. Each cage was sampled with three cores once every three months for one year resulting in 24 cores for each site. The sampling dates were July 27 and October 29, 1986, January 25 and April 17, 1987.

To sample a plot, the cage was carefully pulled out of the sediments and set aside. A grid was visually placed over the caged plot and three cores were taken per plot at positions determined by randomly pre-selected two-digit numbers. No cores were taken within 5-cm of the edge of the cage. Samples were brought to the laboratory, fixed in 10% buffered formaldehyde solution with rose-bengal for 24-hrs (Gonor and Kemp, 1978) and then passed through three metal sieves (1.27-cm, 1.0-mm, 0.5-mm) to separate the infauna from the eelgrass fragments and detritus. Large debris from the residue of the 1.27-cm sieve was discarded after large worms were removed and the rest was preserved in 70% isopropyl alcohol along with the residues retained in the two finest sieves. These samples were then examined under the dissecting microscope for spionid polychaetes, which were removed, counted and identified, recording only the number of whole individuals or the head or anterior portion of the whole organism. Polychaetes were initially identified by M.H. Posey. Additional identification sources were Berkeley and Berkeley (1952); Day (1967); Hartman (1969); Blake (1975); Light (1978); Fauchald (1977) and Rudy and Rudy (1983). Due to the large sample size, a subsample of one-half the whole sample was used for sorting and identification of spionid worms. This is based on the assumption that the population of

the spionid worms is homogeneously distributed.

Sediment Types

Sediment grain characteristics within the three study sites were determined. Sediment samples were taken using the same core sampler as in faunal sampling. In each site, three core samples were taken inside and outside the Z. japonica beds. The sediment samples were air dried and the clumped soil was separated into smaller particles. Plant parts and other non-sediment materials were removed prior to dry sieving of the sediment samples. Dry sieving was done by a portable mechanical sieve shaker model R-24. Seventy-gram subsamples were passed through a series of sieves (US Standard Sieve Mesh Nos. 4.0, 1.0, 0.25, 0.125 and 0.0625-mm) for 15 minutes. The sediment particles that passed through the smallest screen (0.0625-mm) were considered silt-clay and were not separated further. The residue in each sieve was weighed, and the data were analyzed for particle size according to the methods given by Folk (1961).

Statistical Analysis

The effects of predation and the role of eelgrass as a refuge, as reflected in the differences in densities of spionids in uncaged and caged plots inside and outside the Z. japonica beds, were analyzed by comparing paired spionid densities inside and outside the eelgrass by

the Wilcoxon signed-ranks test within sites. Within sites that showed statistically significant differences in density between inside and outside the eelgrass bed, species counts were also subjected to the Wilcoxon signed-ranks tests. The effects of the treatments (cages) and the sites on spionid densities were analyzed by a two-way analysis of variance (ANOVA).

All individual counts for ANOVA were $\log_{10}(x+1)$ transformed in order to normalize the effects of very dense samples over less dense ones (Sokal and Rolf, 1981). All statistical analyses were done using the Multivariate General Linear Hypothesis and the Non-parametric modules of the statistical package, SYSTAT by Wilkinson (1986).

CHAPTER III

RESULTS

Sediment Analysis

Sediments in all sites varied from fine sand (2.0 phi) to very fine sand (4.0 phi) to silt and/or clay (above 4.0 phi). At site A, there is a high cumulative percentage value of -2.0 and 0.0 phi of the sediment size outside the eelgrass bed compared to the inside (Table 1). Visual inspection of the first top 10.0 cm. of the substrata showed a sediment sample consisting mostly of marsh plant roots and stems. This is one of the reasons why the volume of the samples in this site is reduced from 30-cm. deep to 15 cm. deep. The corer could not penetrate any deeper than 15 cm. In general, the high values obtained at the -2.0 phi and 0.0 phi consisted mostly of clumps of sand in between the eelgrass and marsh plant roots and other plant parts.

At site B, the gravel fraction consisted entirely of some pieces of wood, metal, shell fragments and some plant parts despite the thorough mixing and pounding done before dry-sieving. These accounted for the high cumulative percentage values at the -2.0 phi and 0.0 phi obtained outside the eelgrass bed as compared to the inside (Table 1).

At site C, the sediments are generally well-sorted and well

Table 1. Mean and cumulative percentage weight of the sediment fractions inside and outside the *Zostera japonica* beds at sites A, B, and C. Standard errors are in parentheses.

Site A				
Phi values	Inside		Outside	
	Mean weight	Cumulative percentage	Mean weight	Cumulative percentage
-2.0	0.37 (0.08)	0.54	3.95 (0.47)	5.71
0.0	1.59 (0.16)	2.84	5.60 (0.22)	13.80
2.0	44.48 (2.02)	64.21	36.58 (3.44)	66.67
3.0	15.20 (1.61)	61.64	13.32 (1.65)	85.92
4.0	4.91 (1.81)	96.30	7.96 (0.22)	97.43
4.0 up	2.52 (0.05)	100.00	1.78 (1.42)	100.0

Site B				
Phi values	Inside		Outside	
	Mean weight	Cumulative percentage	Mean weight	Cumulative percentage
-2.0	1.23 (0.72)	1.80	6.29 (1.42)	9.08
0.0	3.49 (0.29)	6.79	6.18 (0.72)	18.00
2.0	30.72 (2.18)	50.92	26.60 (0.85)	56.40
3.0	18.75 (2.00)	77.92	13.33 (1.37)	75.65
4.0	12.02 (0.71)	95.20	13.59 (1.02)	95.96
4.0 up	3.34 (0.91)	100.00	3.28 (0.74)	100.00

Site C				
Phi values	Inside		Outside	
	Mean weight	Cumulative percentage	Mean weight	Cumulative percentage
-2.0	1.06 (0.40)	1.52	0.47 (0.08)	0.68
0.0	3.70 (0.54)	6.83	2.68 (0.18)	4.55
2.0	31.56 (3.42)	36.32	26.04 (2.66)	42.19
3.0	27.21 (3.83)	91.11	22.53 (1.04)	74.76
4.0	3.51 (0.47)	96.18	11.63 (0.95)	91.63
4.0 up	2.66 (0.28)	100.00	5.79 (0.87)	100.00

distributed. This may be due to the relatively high wave and current energy here. The cumulative percentage values inside the eelgrass are higher than the outside (Table 1).

Faunal Community in the *Zostera japonica* Beds

Seasonal Patterns

A total of seven species of spionid polychaetes were collected and identified from control core samples inside and outside the *Zostera japonica* bed throughout the study period. Some of these species were relatively rare. An eighth species, *Spiophanes bombyx*, was collected in some experimental cages. Table 2 shows the respective mean densities of these species in the control plots inside and outside the eelgrass bed. Figures 4 to 7 give the log-transformed densities of the four most common spionid species in all treatments. Figure 8 summarizes the mean densities of all spionid species (n=8) inside and outside the *Z. japonica* bed at sites A, B, and C for all caging treatments in July and October 1986 to January and April 1987. The following discussion summarizes the seasonal density patterns for the four most common species at each site in all treatments.

Pygospio elegans showed highest densities in April for site A and January for sites B and C (Table 2; Fig. 4). *Streblospio benedicti* showed variable seasonal peaks in densities: July in site A, January in site B and April in site C (Table 2; Fig. 5). Similarly *Pseudopolydora*

Table 2. Average densities (no. per 86.6 cm²) in control plots of each spionid species in Sites A, B and C at all sampling dates inside and outside the Zostera japonica bed.

Species*	July 1986		October 1986		January 1987		April 1987	
	in	out	in	out	in	out	in	out
<u>Site A</u>								
<u>P. elegans</u>	15.0	3.0	19.3	18.0	52.0	65.7	89.3	21.3
<u>S. benedicti</u>	38.3	20.0	10.0	6.0	22.7	12.7	15.3	27.3
<u>P. kempfi</u>	0.0	1.0	0.0	0.0	0.7	1.3	0.0	0.0
<u>B. truncata</u>	0.0	0.0	0.7	0.7	18.0	18.0	2.7	8.7
<u>P. ligni</u>	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0
<u>S. filicornis</u>	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
<u>Site B</u>								
<u>P. elegans</u>	40.0	14.7	284.0	95.3	434.7	143.3	154.7	108.0
<u>S. benedicti</u>	35.7	17.7	30.0	50.0	52.0	64.7	22.0	25.3
<u>P. kempfi</u>	39.0	31.1	18.7	4.7	2.0	7.3	5.3	2.0
<u>B. truncata</u>	9.7	3.3	12.7	35.3	4.0	0.0	2.0	0.7
<u>P. ligni</u>	1.0	3.7	0.0	6.0	0.0	0.0	0.0	0.0
<u>P. californica</u>	0.0	0.0	0.0	0.0	1.0	2.0	0.0	0.0
<u>Site C</u>								
<u>P. elegans</u>	5.7	24.0	20.7	48.7	88.0	172.0	68.0	37.3
<u>S. benedicti</u>	57.0	1.0	59.3	0.0	40.0	0.0	71.3	2.0
<u>P. kempfi</u>	15.7	18.7	20.7	0.0	8.7	0.7	23.3	3.3
<u>B. truncata</u>	0.0	0.3	0.7	0.0	0.0	0.0	0.0	0.0
<u>P. ligni</u>	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
<u>P. californica</u>	0.0	1.3	0.0	0.0	1.3	7.3	0.0	0.0

*The spionid species are: Pygospio elegans, Streblospio benedicti, Pseudopolydora kempfi, Boccardia truncata, Polydora ligni, Spio filicornis, Pygospio californica.

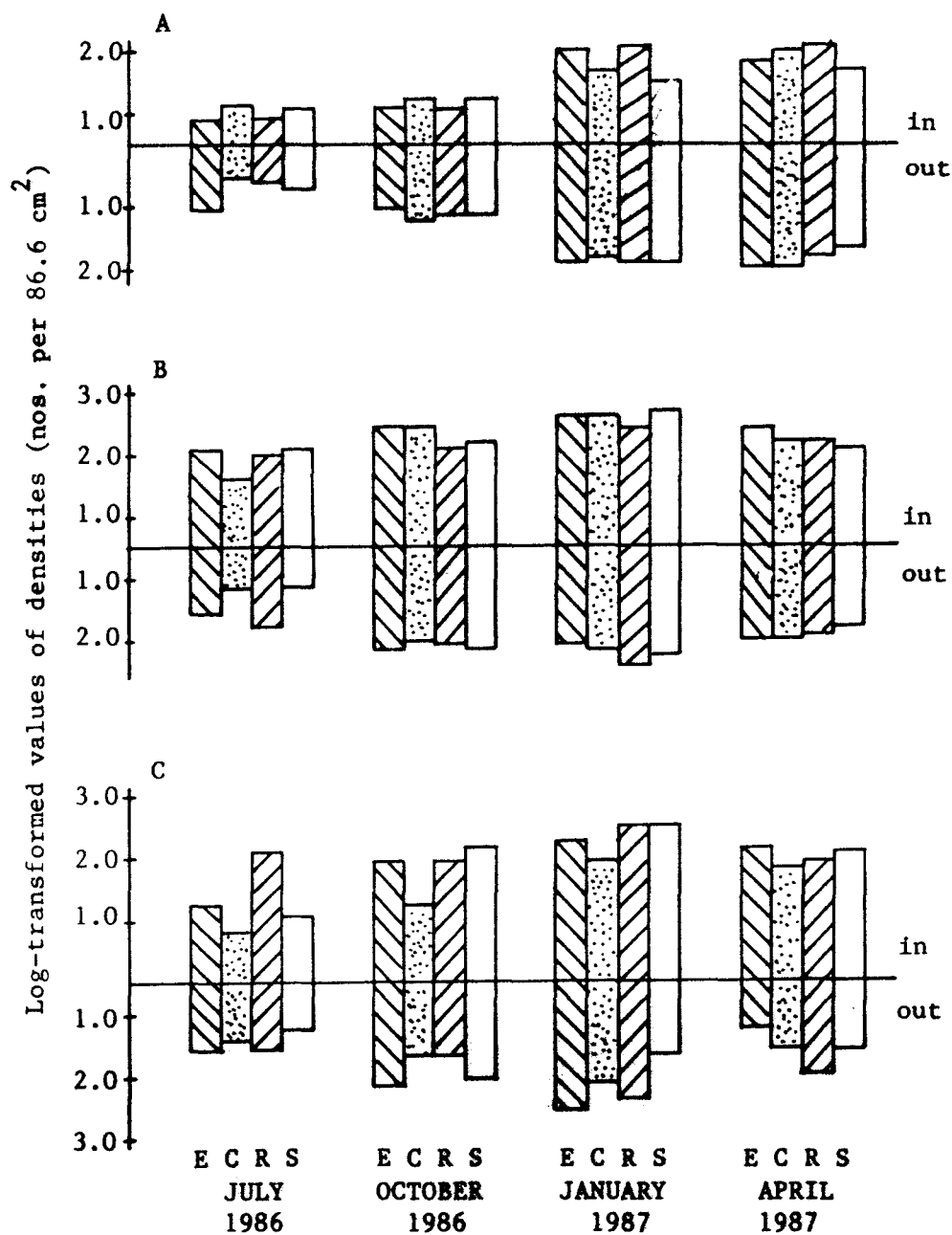


Figure 4. Log-transformed values of densities (nos. per 86.6 cm²) per cage of *Pygospio elegans* inside (in) and outside (out) the *Zostera japonica* bed throughout the study period in sites A, B, and C. Legend: E= exclusion cage; C= control plot; R= roof-only cage; S= sides-only cage.

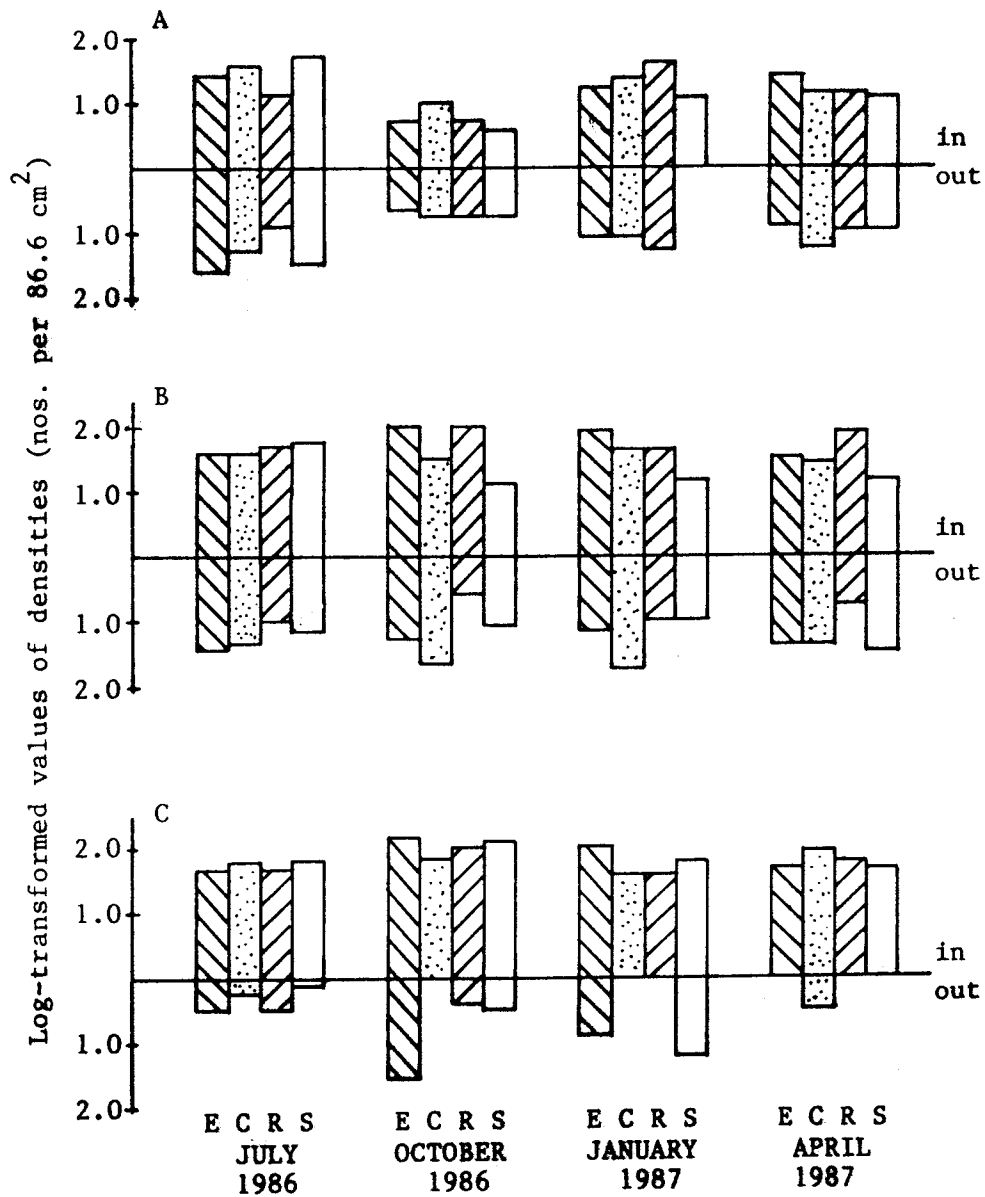


Figure 5. Log-transformed values of densities (nos. per 86.6 cm²) per cage of *Streblospio benedicti* inside (in) and outside (out) the *Zostera japonica* bed throughout the study period in sites A, B, and C. Legend: E= exclusion cage; C= control plot; R= roof-only cage; S= sides-only cage.

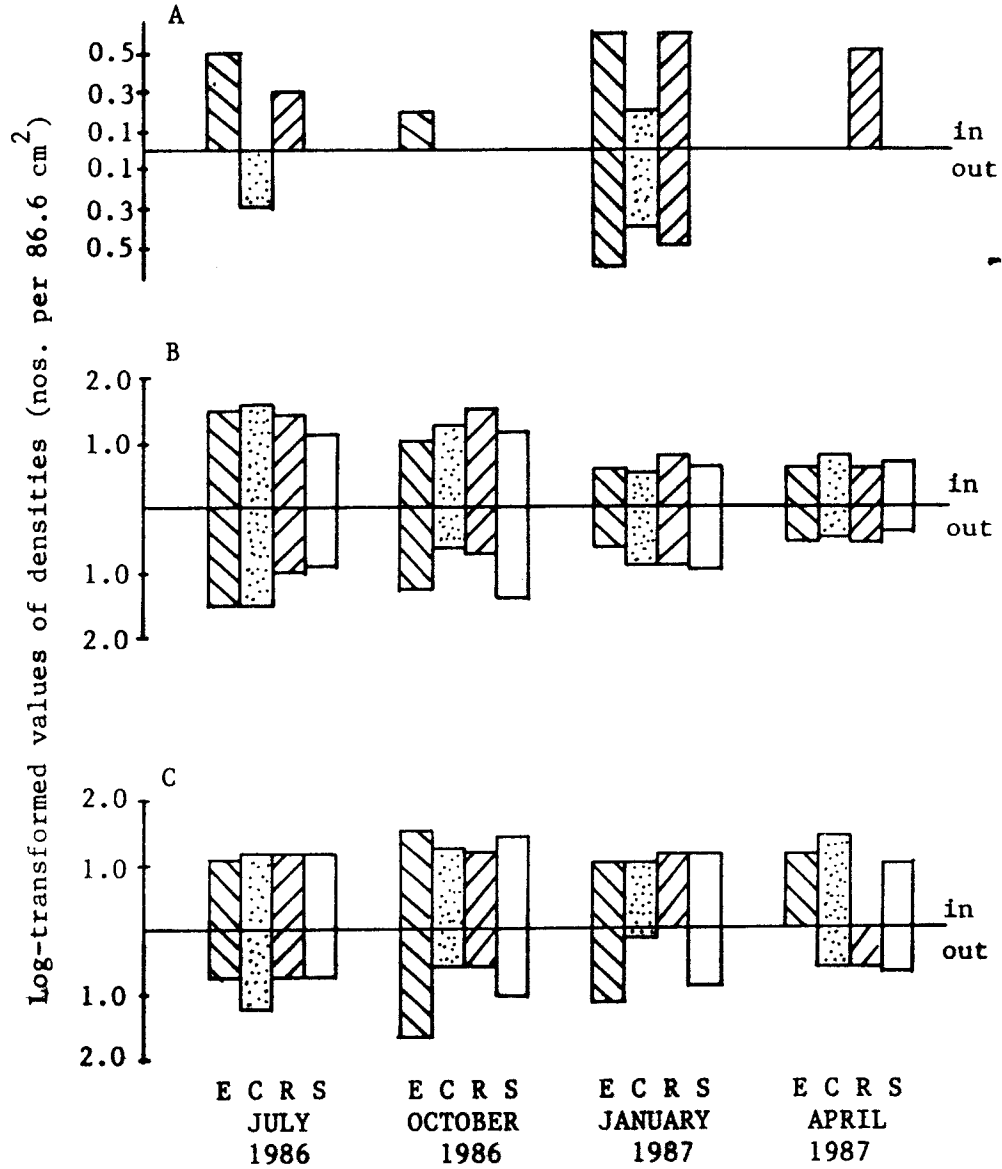


Figure 6. Log-transformed values of densities (nos. per 86.6 cm²) per cage of *Pseudopolydora kempfi* inside (in) and outside (out) the *Zostera japonica* bed throughout the study period in sites A, B, and C. Legend: E= exclusion cage; C= control plot; R= roof-only cage; S= sides-only cage.

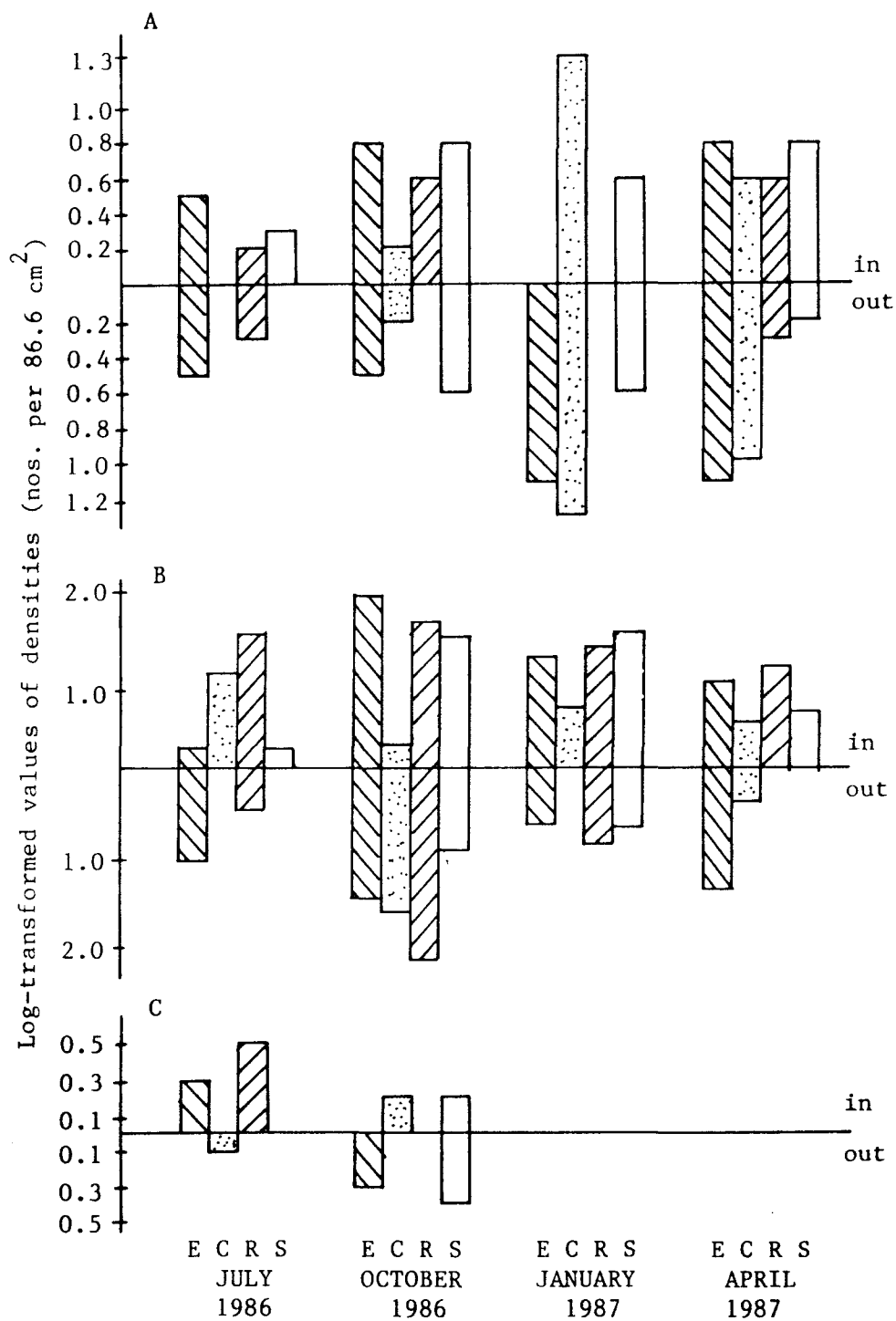


Figure 7. Log-transformed values of densities (nos. per 86.6 cm²) per cage of *Boccardia truncata* inside (in) and outside (out) the *Zostera japonica* bed throughout the study period in sites A, B, and C. Legend: E= exclusion cage; C= control plot; R= roof-only cage; S= sides-only cage.

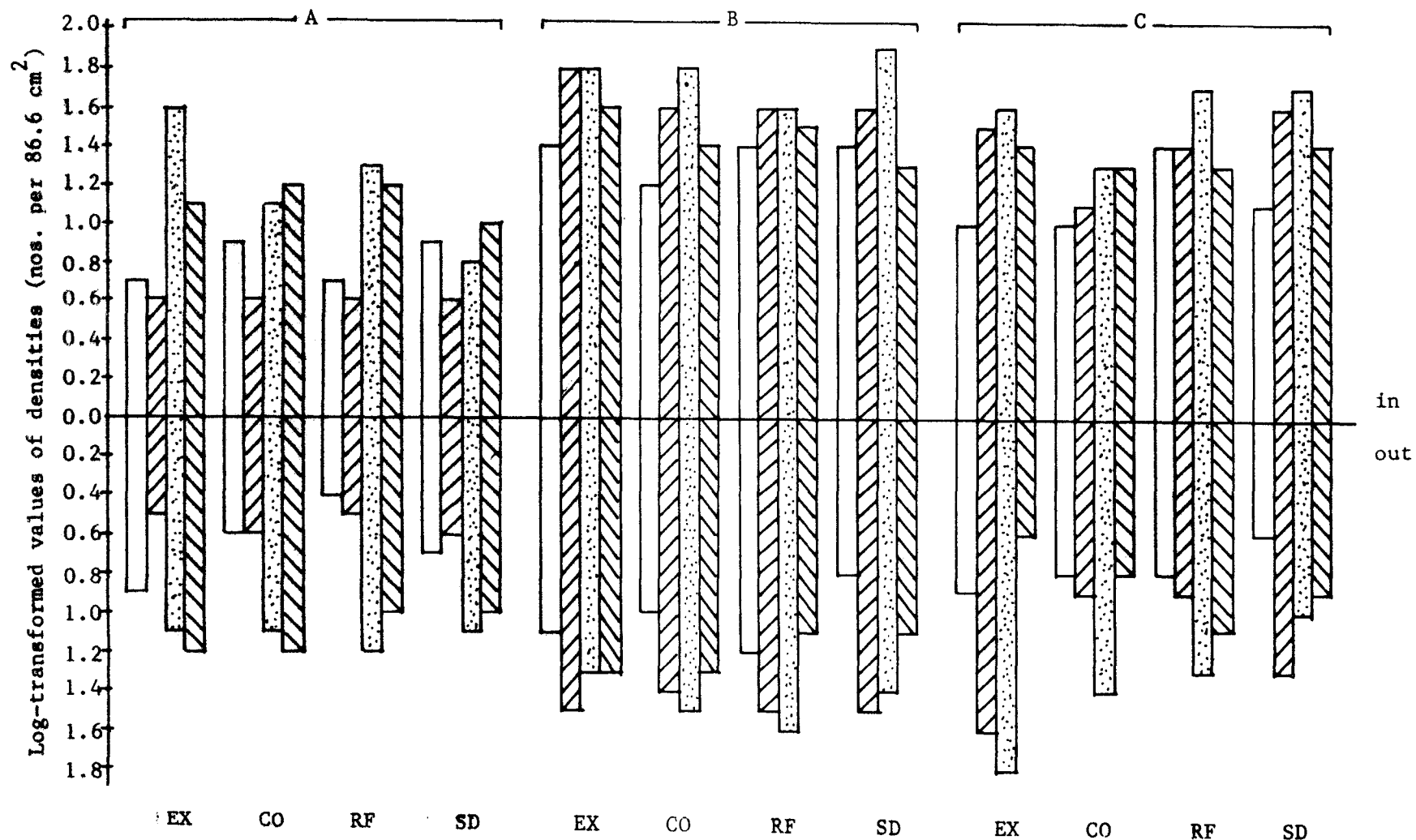


Figure 8. Log-transformed values of densities (nos. per 86.6 cm²) per cage of all sponid species (n=8) inside (in) and outside (out) the *Zostera japonica* bed throughout the study period in July (□), October (▨), January (▩), and April (▧) in sites A, B, and C. Legend: EX= exclusion cages; CO= control plots; RF= roof-only cages; SD= sides-only cages.

kempi showed highest density in the different sites at different sampling dates: January in site A (but rare), July in site B, and April in site C (Table 2; Fig. 6).

The rest of the spionids showed peaks in densities at different seasons. Boccardia truncata is present throughout the year in sites A and B, but not in site C (Fig. 7). This species did not show any preference in habitat with respect to the occurrence of eelgrass (Fig. 7). Polydora ligni is present throughout the year only in site B where it showed higher densities outside than inside the eelgrass bed (Table 2). Pygospio californica is absent in site A but present throughout the year in sites B and C. Generally it showed higher densities outside than inside the eelgrass beds (Table 2).

Pygospio elegans and S. benedicti were present at all sites throughout the four sampling dates. To determine the seasonality of these two most abundant species, their relative percentage abundances during the four sampling dates in the control plots were computed inside and outside the eelgrass beds (Table 3). Both species exhibited variable percentage abundances throughout the year at all sites. Pygospio elegans showed high abundance inside the eelgrass in July and April at site A; July, October and January in site B, and April in site C. Streblospio showed relatively the same percentage abundance for sites A and C throughout the year, except in April at site A where it dropped from 64.1% to 35.9% inside the eelgrass bed. At site B, there are variable seasonal peaks in abundances (Table 2; Fig. 5). In site B, there was an increase in relative abundance from October to April, but a

Table 3. Proportion of Pygospio elegans and Streblospio benedicti inside the eelgrass in the control plots at Sites A, B, and C.

	July 1986	October 1986	January 1987	April 1987
<u>Species</u>				
<u>Site A</u>				
<u>P. elegans</u>	83.3	51.7	44.2	80.7
<u>S. benedicti</u>	65.7	62.5	64.1	35.9
<u>Site B</u>				
<u>P. elegans</u>	73.1	74.9	75.2	58.9
<u>S. benedicti</u>	66.8	37.5	44.6	46.5
<u>Site C</u>				
<u>P. elegans</u>	18.9	29.8	33.8	64.6
<u>S. benedicti</u>	98.3	100.0	100.0	97.7

drop from July to October.

Comparison of Spionid Abundances Inside and Outside the Eelgrass Beds

To have a baseline data on the effects of eelgrass beds on species density, spionid mean densities in the control plots and the exclusion cages inside and outside the eelgrass bed were compared for each site (Table 4). Only the four most abundant species were included in the analysis because the rest of the spionids were in small numbers and were not present in the three sites consistently. In site A, throughout the study period, P. elegans showed higher densities inside than outside the eelgrass bed for half of the year. In site B, P. elegans densities were higher inside than outside throughout the year. In site C, P. elegans densities were higher outside than inside the eelgrass bed throughout the year except in April. The other three species, S. benedicti, P. kempfi and B. truncata showed generally higher densities inside than outside the eelgrass bed at all sites. The same trend of distribution of the different species is apparent in the exclusion cages inside and outside the eelgrass bed (Table 5). Pygospio elegans have the same density distribution in the different sites as in the control plots, while the other three species have generally higher densities inside than outside the eelgrass beds.

Table 6 shows the total spionid densities per cage inside and outside the eelgrass bed at the three sites. To determine whether spionid densities in the three sites were significantly different inside

Table 4. Mean densities (no. per 86.6 cm²) of the spionid species in the control plots inside and outside the eelgrass beds at sites A, B, and C.

Species*	Pe		St		Pk		Bt	
	in	out	in	out	in	out	in	out
Site A								
July 1986	15.0	3.0	38.3	20.0	0.0	1.0	0.0	0.0
October 1986	19.3	18.0	10.0	6.0	0.0	0.0	0.7	0.7
January 1987	52.0	65.7	12.7	12.7	0.7	1.3	18.0	18.0
April 1987	89.3	96.0	15.3	21.3	0.0	0.0	2.7	8.7
Site B								
July 1986	40.0	14.7	35.7	17.7	39.0	31.0	9.7	3.3
October 1986	284.0	95.3	30.0	50.0	18.7	4.7	12.7	35.3
January 1987	434.7	143.7	52.0	64.7	2.0	7.3	4.0	0.0
April 1987	154.7	108.0	22.0	25.3	5.3	2.0	2.0	0.7
Site C								
July 1986	5.7	24.0	57.0	1.0	15.7	18.7	0.0	0.3
October 1986	20.7	48.7	59.3	0.0	20.7	2.7	0.7	0.0
January 1987	88.0	172.0	40.0	0.0	8.7	0.7	0.0	0.0
April 1987	68.0	37.3	71.3	2.0	23.3	3.3	0.0	0.0

*The spionid species are Pygospio elegans (Pe), Streblospio benedicti (St), Pseudopolydora kemp (Pk), and Boccardia truncata (Bt).

Table 5. Mean densities (no. per 86.6 cm²) of the spionid species in the exclusion cage inside and outside the eelgrass beds at sites A, B, and C.

Species*	Pe		St		Ps		Bt	
	in	out	in	out	in	out	in	out
Site A								
July 1986	7.0	11.0	24.0	46.0	2.0	0.0	2.3	2.0
October 1986	12.0	12.7	4.7	4.0	0.7	0.0	5.3	2.0
January 1987	89.0	70.0	18.0	10.7	3.0	3.0	0.0	12.0
April 1987	57.7	94.0	24.0	7.3	0.0	0.0	6.0	11.3
Site B								
July 1986	116.3	36.3	38.7	24.0	32.7	28.0	12.7	8.3
October 1986	267.3	164.0	107.3	21.3	9.3	17.3	75.3	26.0
January 1987	389.0	139.3	72.7	15.3	3.3	4.0	16.7	4.0
April 1987	250.0	104.0	28.7	25.3	2.7	3.3	10.0	15.3
Site C								
July 1986	19.3	42.7	47.0	2.3	13.0	5.0	1.0	0.0
October 1986	87.0	170.0	157.0	37.0	33.0	53.0	0.0	1.0
January 1987	186.0	456.0	102.0	7.3	8.7	14.0	0.0	0.0
April 1987	142.3	21.3	52.3	0.0	14.0	0.0	0.0	0.0

*The spionid species are Pygospio elegans (Pe), Streblospio benedicti (St), Pseudopolydora ligni (Pk), and Boccardia truncata (Bt).

Table 6. Total spionid (n=8) densities (no. per 86.6 cm²) per cage inside and outside the eelgrass bed at three sites.

Sites	A		B		C	
	in	out	in	out	in	out
July 1986						
exclusion	4.4	7.4	26.4	12.8	10.1	6.7
control	6.7	3.0	15.9	28.8	9.8	5.7
side-only	7.9	4.1	26.2	14.5	10.8	2.9
roof-only	3.8	1.6	26.4	4.8	23.4	5.7
October 1986						
exclusion	2.8	2.3	57.4	28.7	32.2	36.6
control	2.9	3.1	43.2	23.9	12.7	6.4
side-only	3.2	3.2	40.2	27.2	38.5	18.4
roof-only	2.6	2.4	41.0	31.7	25.9	7.7
January 1987						
exclusion	37.4	12.2	61.4	20.6	37.3	60.8
control	11.7	12.2	62.8	27.2	17.2	22.5
side-only	5.7	12.1	71.8	25.5	54.8	9.6
roof-only	21.2	13.2	42.4	34.8	46.7	33.7
April 1987						
exclusion	11.0	14.1	36.4	18.6	26.1	2.7
control	13.5	15.8	23.0	17.0	20.3	5.3
side-only	8.3	8.1	18.5	12.4	21.8	6.1
roof-only	16.7	9.2	31.1	11.4	18.6	12.7
	n=16		n=16		n=16; P > 0.05	
	in > out; P < 0.05		in > out; P < 0.005		not significant	

and outside the eelgrass bed, a one-tailed test using the Wilcoxon-signed ranks method was done to test the hypothesis that spionid densities inside the eelgrass beds are greater than spionid densities outside the eelgrass for each site throughout the year. These tests resulted in significant effects for site A ($P < 0.05$) and site B ($P < 0.005$), but not at site C ($P > 0.05$). Therefore, spionid densities inside the eelgrass are greater than outside for sites A and B.

To determine further which species in sites A and B have significantly different densities inside vs. outside the eelgrass bed, Wilcoxon-signed ranks tests were done for the four most abundant species for sites A and B. Table 7 and 8 show mean densities of each spionid per cage inside and outside the eelgrass in sites A and B respectively. For site A, only S. benedicti showed a significant result ($P < 0.01$) for a one-tailed test; therefore the density of this species inside the eelgrass is greater than outside on a year-round basis. Thus, it is this species that contributed to the moderately significant ($P < 0.05$) result of a Wilcoxon test on the spionid density differences inside and outside the eelgrass in site A (Table 7). For site B, among the four numerically dominant species, three showed significantly higher densities inside than outside the eelgrass bed: P. elegans ($P < 0.005$), S. benedicti ($P < 0.025$), and B. truncata ($P < 0.05$). These significant tests contributed to the earlier highly significant result for site B ($P < 0.005$) that the spionid densities are greater inside than outside the eelgrass bed (Table 8).

To test the influence of the caging treatments, a two-way ANOVA was

Table 7. Average densities (no. per 86.6 cm²) of each spionid polychaetes inside and outside the Zostera japonica beds at site A.

I. <u>Pygospio elegans</u>		
	outside	inside
July 1986		
exclusion	11.0	7.0
control	3.0	15.0
sides-only	4.0	6.7
roof-only	5.0	11.0
October 1986		
exclusion	12.7	12.0
control	18.0	19.3
roof-only	14.0	12.7
sides-only	16.7	17.3
January 1987		
exclusion	70.0	109.0
control	65.7	52.0
roof-only	84.0	126.0
sides-only	72.0	30.0
April 1987		
exclusion	94.0	57.7
control	96.0	89.3
roof-only	62.0	114.0
sides-only	54.0	51.3
n=16 inside=outside; not significant		

II. Streblospio benedicti

	outside	inside
July 1986		
exclusion	46.0	24.0
control	20.0	38.3
roof-only	7.0	16.3
sides-only	28.0	51.0

	outside	inside
October 1986		
exclusion	4.0	4.7
control	6.0	10.0
roof-only	5.3	5.3
sides-only	5.3	2.7
January 1987		
exclusion	10.7	18.0
control	12.7	22.7
roof-only	19.3	40.0
sides-only	0.0	12.7
April 1987		
exclusion	7.3	24.0
control	21.3	15.3
roof-only	10.0	14.0
sides-only	10.0	10.7
	n=16	
	inside > outside; P < 0.01	

III. Pseudopolydora kempi

	outside	inside
July 1986		
exclusion	0.0	2.0
control	1.0	0.0
roof-only	0.0	1.0
sides-only	0.0	0.0
October 1986		
exclusion	0.0	0.7
January 1987		
exclusion	3.0	3.0
control	1.3	0.7
roof-only	2.0	3.3
April 1987		
roof-only	0.0	2.3
	n=9	
	inside = outside; not significant	

IV. Boccardia truncata

	outside	inside
<hr/>		
July 1986		
exclusion	2.0	2.3
roof-only	1.0	0.7
sides-only	0.0	1.0
October 1986		
exclusion	2.0	5.3
control	0.7	6.7
roof-only	0.0	2.7
sides-only	3.3	5.3
January 1987		
exclusion	12.0	0.0
control	18.0	18.0
sides-only	22.0	2.7
April 1987		
exclusion	11.3	6.0
control	8.7	2.7
roof-only	1.3	2.7
sides-only	0.7	4.7
	n=14	
	inside=outside;	
	not significant	
<hr/>		

Table 8. Average densities (no. per 86.6 cm²) of each spionid species inside and outside the Zostera japonica beds at site B.

I. Pygospio elegans

	outside	inside
July 1986		
exclusion	36.3	116.3
control	14.7	40.0
roof-only	71.0	89.7
sides-only	16.3	111.7
October 1986		
exclusion	164.4	267.3
control	95.3	284.0
roof-only	127.3	140.0
sides-only	143.3	255.3
January 1987		
exclusion	193.3	389.0
control	143.3	434.7
roof-only	255.3	259.3
sides-only	182.7	518.7
April 1987		
exclusion	104.0	250.0
control	108.0	154.7
roof-only	82.0	158.0
sides-only	65.2	128.0
	n=16	
	inside>outside; P<0.005	

II. Streblospio benedicti

	outside	inside
July 1986		
exclusion	24.0	38.7
control	17.7	35.7
roof-only	8.3	49.7
sides-only	14.0	68.3

	outside	inside
October 1986		
exclusion	21.3	107.3
control	50.0	30.0
roof-only	2.7	102.0
sides-only	39.3	16.0
January 1987		
exclusion	15.3	72.7
control	64.7	52.0
roof-only	10.0	52.0
sides-only	8.7	14.7
April 1987		
exclusion	25.3	28.7
control	25.3	22.0
roof-only	5.3	74.7
sides-only	32.7	13.3
	n=16	
	inside>outside; P<0.025	

III. Pseudopolydora kemp

	outside	inside
July 1986		
exclusion	28.0	32.7
control	31.0	39.0
roof-only	9.7	24.7
sides-only	7.7	15.0
October 1986		
exclusion	17.3	9.3
control	4.7	18.7
roof-only	5.3	32.7
sides-only	22.7	15.3
January 1987		
exclusion	4.0	3.3
control	7.3	2.0
roof-only	6.7	5.3
sides-only	8.0	3.3

	outside	inside
April 1987		
exclusion	3.3	2.7
control	2.0	5.3
roof-only	3.0	3.0
sides-only	1.3	4.0
	n=16	
	inside=outside;	
	not significant	

IV. Boccardia truncata

	outside	inside
July 1986		
exclusion	8.3	12.7
control	3.3	9.7
roof-only	22.0	42.0
sides-only	0.0	12.0
October 1986		
exclusion	26.0	75.3
control	35.3	12.7
roof-only	115.3	50.0
sides-only	12.0	34.0
January 1987		
exclusion	4.0	16.7
control	0.0	4.0
roof-only	6.7	20.0
sides-only	4.7	31.3
April 1987		
exclusion	15.3	10.0
control	0.7	2.0
roof-only	0.0	13.3
sides-only	0.0	2.7
	n=16	
	inside>outside; P<0.05	

done for the different spionid species using site and cage treatments as factors. Inside the eelgrass beds, caging had no significant effects on the density of three of the four common spionid species in July; significant in three out of four species in October; not significant in one out of four species in January; and significant effects in two out of four species in April (Table 9).

Outside the eelgrass beds, caging treatments showed a significant effect for all four common spionid species in July; a significant effect in two of the four species in October and April; and no significant effect in one species in January (Table 10).

Based on the mean density at each site for each season for each cage treatments, it appears that only sites B and C have higher mean density values in the exclusion cages relative to the control and the other partial cages for the four most common spionid species whether inside or outside the eelgrass bed. In site B, P. elegans and B. truncata have higher densities in the exclusion cage in October; January for S. benedicti and April for B. truncata. In site C, P. elegans, S. benedicti, and P. kempfi have high mean density values in October and January whether inside or outside the eelgrass bed.

Site had a statistically significant effect on the density of the different spionid species (Table 9 and 10). Except for S. benedicti (July; inside), all other species densities were significantly different at the different sites. This substantiates the results of the Wilcoxon-signed ranks test on the density differences inside and outside the eelgrass bed in each site. The highly significant effects of site

Table 9. The 2-way ANOVA results on the effects of caging on the densities of spionid species inside the Zostera japonica bed in the different sites in July and October 1986, and January and April 1987.

Species	Caging Treatment	Site	Site-Treatment Interaction
I. July 1986			
<u>P. elegans</u>	*	***	***
<u>S. benedicti</u>	n.s.	n.s.	n.s.
<u>P. kempfi</u>	n.s.	***	n.s.
<u>B. truncata</u>	n.s.	***	n.s.
II. October 1986			
<u>P. elegans</u>	**	***	***
<u>S. benedicti</u>	**	***	***
<u>P. kempfi</u>	n.s.	***	**
<u>B. truncata</u>	*	***	*
III. January 1987			
<u>P. elegans</u>	*	***	***
<u>S. benedicti</u>	***	***	***
<u>P. kempfi</u>	n.s.	***	n.s.
<u>B. truncata</u>	*	***	***
IV. April 1987			
<u>P. elegans</u>	n.s.	***	*
<u>S. benedicti</u>	*	***	*
<u>P. kempfi</u>	**	***	***
<u>B. truncata</u>	n.s.	***	n.s.

+Significance level: *=P<0.05, **=P<0.01, ***=P<0.001.

Table 10. The 2-way ANOVA results on the effects of caging on the densities of spionid species outside the Zostera japonica bed in the different sites in July and October 1986, and January and April 1987.

Species	Caging Treatment	Site	Site-Treatment Interaction
I. July 1986			
<u>P. elegans</u>	**	***	n.s.
<u>S. benedicti</u>	**	***	n.s.
<u>P. kempfi</u>	*	***	n.s.
<u>B. truncata</u>	**	***	*
II. October 1987			
<u>P. elegans</u>	n.s.	***	n.s.
<u>S. benedicti</u>	***	***	***
<u>P. kempfi</u>	***	***	***
<u>B. truncata</u>	n.s.	***	**
III. January 1987			
<u>P. elegans</u>	**	***	***
<u>S. benedicti</u>	***	***	***
<u>P. kempfi</u>	n.s.	***	n.s.
<u>B. truncata</u>	*	***	***
IV. April 1987			
<u>P. elegans</u>	n.s.	*	n.s.
<u>S. benedicti</u>	*	***	n.s.
<u>P. kempfi</u>	n.s.	***	*
<u>B. truncata</u>	***	***	**

*Significance level: *= $P < 0.05$, **= $P < 0.01$, ***= $P < 0.001$.

on the different spionid densities are also reflected in the significant results of site-treatment interactions for some species.

Eelgrass and Predation

To determine whether the exclusion of epibenthic predators can be correlated with the relative abundance patterns of spionids, densities of the four most abundant spionid species in the control plots and exclusion cages were compared. Tables 11 and 12 show a comparison of mean densities in the exclusion cage and control plots inside and outside the eelgrass bed, respectively. These tables show that at all sites, with some exceptions, the spionids have generally higher densities in the exclusion cages than in the control whether both cages are inside or outside the eelgrass bed. An even more dramatic comparison is between the mean densities of exclusion cages inside the eelgrass and the control outside the eelgrass (Table 13). The data substantiates the same conclusion that exclusion cages have higher spionid densities, but the differences between the means are greater due to the combined protective effects of the eelgrass and the exclusion cage. Furthermore, a comparison of spionid densities in the control plots inside the eelgrass beds and exclusion cages outside the eelgrass beds (Table 14) show a trend (with some exceptions) towards higher densities in the control plots inside the eelgrass bed. This again substantiates the earlier results that the eelgrass bed serves as a refuge from predators.

Table 11. Mean densities (no. per 86.6 cm²) of the spionid species in the exclusion (exc) cage and control (con) plots inside the eelgrass beds at sites A, B, and C.

Species*	Pe		St		Pk		Bt	
	exc	con	exc	con	exc	con	exc	con
Site A								
July 1986	7.0	15.0	24.0	38.3	2.0	0.0	2.3	0.0
October 1986	12.0	19.3	4.7	10.0	0.7	0.0	5.3	0.7
January 1987	89.0	52.0	18.0	22.7	3.0	0.7	0.0	18.0
April 1987	57.7	89.3	24.0	15.3	0.0	0.0	6.0	2.7
Site B								
July 1986	116.3	40.0	38.7	35.7	32.7	39.0	12.7	9.7
October 1986	267.3	284.0	107.3	30.0	9.3	18.7	75.3	12.7
January 1987	389.0	434.7	72.7	52.0	3.3	2.0	16.7	4.0
April 1987	250.0	154.7	28.7	22.0	2.7	5.3	10.0	2.0
Site C								
July 1986	19.7	5.7	47.0	57.0	13.0	15.3	1.0	0.0
October 1986	87.0	20.7	157.0	59.3	33.0	20.7	0.0	0.7
January 1987	186.0	88.0	107.0	40.0	8.7	8.7	0.0	0.0
April 1987	142.3	68.0	52.3	71.3	14.0	23.3	0.0	0.0

*The spionid species are Pygospio elegans (Pe), Streblospio benedicti (St), Pseudopolydora kempfi (Pk), and Boccardia truncata (Bt).

Table 12. Mean densities (no. per 86.6 cm²) of the spionid species in the exclusion (exc) cage and control (con) plots outside the eelgrass beds at sites A, B, and C.

Species*	Pe		St		Pk		Bt	
	exc	con	exc	con	exc	con	exc	con
Site A								
July 1986	11.0	3.0	46.0	20.0	0.0	1.0	2.0	0.0
October 1986	12.7	18.0	4.0	60.0	0.0	0.0	2.0	0.7
January 1987	70.0	65.7	10.7	12.7	3.0	1.3	12.0	18.0
April 1987	94.0	96.0	7.3	21.3	0.0	0.0	11.3	8.7
Site B								
July 1986	36.3	14.7	24.0	17.7	28.0	31.0	8.3	3.3
October 1986	164.0	95.3	21.3	50.0	17.3	4.7	26.0	35.3
January 1987	139.3	143.7	15.3	64.7	4.0	7.3	4.0	0.0
April 1987	104.0	108.0	25.3	25.3	3.3	2.0	15.3	0.7
Site C								
July 1986	42.7	24.0	2.3	1.0	5.0	18.7	0.0	0.3
October 1986	170.0	48.7	37.0	0.0	53.0	2.7	1.0	0.0
January 1987	456.0	172.0	7.3	0.0	14.0	0.7	0.0	0.0
April 1987	21.3	37.3	0.0	2.0	0.0	3.3	0.0	0.0

*The spionid species are Pygospio elegans (Pe), Streblospio benedicti (St), Pseudopolydora kempfi (Pk), and Boccardia truncata (Bt).

Table 13. Mean densities (no. per 86.6 cm) of the spionid species in the exclusion (exc) cage inside the eelgrass bed and the control (con) plots outside the eelgrass bed at sites A, B, and C.

Species*	Pe		St		Pk		Bt	
	exc	con	exc	con	exc	con	exc	con
Site A								
July 1986	7.0	3.0	24.0	20.0	2.0	1.0	2.3	0.0
October 1986	12.0	18.0	4.7	60.0	0.7	0.0	5.3	0.7
January 1987	109.0	65.7	18.0	12.7	3.0	1.3	0.0	18.0
April 1987	57.7	96.0	24.0	21.3	0.0	0.0	6.0	8.7
Site B								
July 1986	116.3	14.7	38.7	17.7	32.7	31.0	12.7	3.3
October 1986	267.3	95.3	107.3	50.0	9.3	4.7	75.3	35.3
January 1987	389.0	143.7	72.7	64.7	3.3	7.3	16.7	0.0
April 1987	250.0	108.0	28.7	25.3	2.7	2.0	10.0	0.7
Site C								
July 1986	19.7	24.0	47.0	1.0	13.0	18.7	1.0	0.3
October 1986	87.0	48.0	157.0	0.0	33.0	2.7	0.0	0.0
January 1987	186.0	172.0	102.0	0.0	8.7	0.7	0.0	0.0
April 1987	142.3	37.3	52.3	2.0	14.0	3.3	0.0	0.0

*The spionid species are Pygospio elegans (Pe), Streblospio benedicti (St), Pseudopolydora kempi (Pk), and Boccardia truncata (Bt).

Table 14. Mean densities (no. per 86.6 cm²) of the spionid species in the exclusion (exc) cage outside the eelgrass bed and in the control (con) plots inside the eelgrass bed at sites A, B, and C.

Species*	Pe		St		Pk		Bt	
	exc	con	exc	con	exc	con	exc	con
Site A								
July 1986	11.0	15.0	46.0	38.3	0.0	0.0	2.0	0.0
October 1986	12.7	19.3	4.0	10.0	0.0	0.0	2.0	0.7
January 1987	70.0	52.0	10.7	22.7	3.0	0.7	12.0	18.0
April 1987	94.0	89.3	7.3	15.3	0.0	0.0	11.3	2.7
Site B								
July 1986	36.3	40.0	24.0	35.7	28.0	39.0	8.3	9.7
October 1986	164.0	284.0	21.3	30.0	17.3	18.7	26.0	12.7
January 1987	139.3	434.7	15.3	52.0	4.0	2.0	4.0	4.0
April 1987	104.0	154.7	25.3	22.0	3.3	5.3	15.3	2.0
Site C								
July 1986	42.7	5.7	2.3	57.0	5.0	15.7	0.0	0.0
October 1986	170.0	20.7	37.0	59.3	53.0	20.7	1.0	0.7
January 1987	456.0	88.0	7.3	40.0	14.0	8.7	0.0	0.0
April 1987	21.3	68.0	0.0	71.3	0.0	23.3	0.0	0.0

*The spionid species are Pygospio elegans (Pe), Streblospio benedicti (St), Pseudopolydora kemp (Pk), and Boccardia truncata (Bt).

CHAPTER IV

DISCUSSION

A total of eight spionid species were identified and collected in the study area. Only two of the eight species were present at all sites throughout the year. The following discussion focuses on the spionid species that showed relatively distinct patterns of distribution throughout the study.

Pygospio elegans is a deposit and filter feeder that lives in clear, papery tubes in mud and sand flats. It can switch from deposit to suspension feeding when water flow velocity increases (Taghon et al., 1980). The high relative abundance of this spionid in the summer (July) at site A could be due to the fact that there is more eelgrass cover during this time (Harrison 1982a and 1982b), which protects them from predators that are also known to be more abundant in the summer. The decline in winter (January) at site A could be due to the reduced or absent eelgrass cover during the winter, therefore making them more prone to predation. There thus may be a direct relationship between the abundance of Zostera and P. elegans at site A. Another factor that could have contributed to the abundance of Pygospio in July is that it may have been reproducing and recruitment may thus have exceeded predation. The increase in abundance observed from January to April at

site A may have been due to the sediment build-up in that area caused by the winter storm in December 1986. The sediment imported into the area could have carried with it a population of spionids thus resulting to an increase in abundances. Moreover, this sediment build-up could have provided more surface area for the survival and settlement of the polychaetes.

At sites B and C, there appeared to be an inverse relationship between P. elegans and the abundance of predators. When the abundance of predators declines from summer to winter (Le Mao, 1986; Wiltse et al., 1984), there is a slight increase in the percentage abundance of P. elegans from summer (July) to winter (January) inside the eelgrass bed. Some of the reasons for this increase could be the following: (1) the Zostera acts as a refuge against predation for this spionid, thereby generally producing an increase in abundance throughout the year at sites B and C (except in April for site B); (2) some reproduction could be taking place; and (3) the decay of the rhizomes, stems, and blades of the eelgrass cause organic nutrients to leach into the sediments, thereby enhancing the growth and survival of this spionid through the year. Moreover, P. elegans may be reproducing throughout the year, which may have contributed to the high January densities (Table 2). The decrease in abundance in April at site B could be due to the disturbance by a winter storm in late January. Half of the trail at site B was eroded by the storm. Although this site is protected from strong tides and waves by the channel, it is not however protected from landward erosion.

In the April samples many individuals of this species were observed to have regenerating parts of their anterior or posterior body segments. This was not observed in January samples. This would suggest an increase in predation from January to April, which may be caused by browsing predators. Many predators known to feed on polychaete tentacles and tails are visual feeders, like dab, plaice, and juvenile flatfish (Groot, 1971; Muus, 1976). Posey (1986a) reported that the known polychaete predators in my study sites are the staghorn sculpin Leptocottus armatus, the shiner perch Cymatogaster aggregata, and the Dungeness crab Cancer magister.

Streblospio benedicti is believed to be introduced with the importation of adult and seed oysters, Crassostrea virginica, from the Atlantic coast (Carlton, 1979). This spionid species is a deposit feeder, living in a membranous tube in the sediment and feeding at the surface by means of long grooved palps (Young and Young, 1978). The mean density of this organism at all sites is generally higher inside the eelgrass bed than outside the bed. Jones (1961:234 in Light, 1978) reported that the period of greatest abundance of S. benedicti extends from January to April and from July to November in San Francisco Bay. In my study, S. benedicti had highest relative abundances at different seasons depending on the site: July in sites A and B and almost throughout the year at site C (Table 3). The slight decrease in abundance at site A from July to October could be due to the presence of predators in a less dense eelgrass bed which may have persisted throughout the early part of the winter. However, the increase in

abundance from October to January may be due to the fact that the presumed absence of predators in the winter enabled them to survive despite the absence of Zostera. The drop in abundance inside the bed from January to April may have been caused by the winter storms of December 1986 and January 1987. A high relative abundance of S. benedicti is observed in July in site B, and throughout the year at site C. Moreover, the presumed decrease in predator abundance in the winter enabled the worms to increase in abundance from October to April at site B. This decrease in predator intensity could explain the large number of individuals of this species observed to have regenerating palps and tentacles in the October samples. These tissue (tentacles and tails) losses affect the growth rate (Trevallion et al., 1970; De Vlas, 1979) and reproductive output (Gibbs, 1968) of infauna because energy is expended for regeneration rather than reproduction. Described as an opportunistic species by some authors (Grassle and Grassle, 1974; McCall, 1977), this spionid species is observed to have a higher overall density inside than outside eelgrass beds in Chesapeake Bay (Virnstein, 1977). This is also true of the S. benedicti population in South Slough.

Another exotic species believed to be imported with the Japanese oyster Crassostrea gigas (Carlton, 1979) is Pseudopolydora kempi. It is a spionid that inhabits mucoid tubes in sandy mud environments. It is primarily a deposit-feeder and without exposing the anterior end out of its tube, it holds its tentacles on the sediment surface to feed (Taghon et al., 1980; Woodin, 1982). Pseudopolydora kempi is absent at site A

except in January when it appears in low densities. Processes that could have accounted for this phenomenon are: (1) failure of the larvae to reach site A but no such failure for sites B and C; (2) it has a preferred habitat for survival of the larvae; and (3) the presence of other aggressive competitive species in the community competing for food resources. At sites B and C, they show variable abundances.

Generally, P. kemp had higher densities inside than outside the eelgrass bed at all sites except in site B in January (Table 2).

Boccardia truncata is a deposit feeder and like S. benedicti and P. kemp has a tendency to suspension feed (Taghon et al., 1980).

Boccardia truncata does not show any preference in habitat with regard to the presence or absence of Z. japonica beds at the three sites. The highest peak in abundance of Boccardia was in January in site A, but in October at sites B and C (Table 2). It was in October however that a significant number of individuals were found to brood their young or larvae in their leathery tubes. Boccardia appears to brood in relatively open sandy-muddy intertidal areas (sites B and C) and the young consequently migrate to other areas (site A). This could explain the difference in time of peak abundance between sites B and C and site A.

Polydora ligni is a sedentary spionid that lives in a fragile U-shaped tube and feeds at the sediment surface. Two palps are extended that carry food particles to the mouth (Young and Young, 1978; Dauer et al., 1981). It introduced with the Atlantic oyster. Rare in site A, P. ligni generally showed higher densities outside than inside the eelgrass

beds in Sites B and C.

The other species found in the study showed variable occurrences and low densities (cumulative, 1.6%) and will not be discussed further.

All of these spionids were either deposit or suspension-feeders, and therefore the differences in their distribution among the three sites appear to be a function of the sediment characteristics of the three sites. Moreover, the temporal differences in abundance of these organisms could be due to differences in time of reproduction, recruitment and growth of these organisms (Virnstein, 1978, 1980; Peterson, 1979) and the presence or absence of the Z. japonica beds.

The exclusion of epibenthic predators from seagrass beds has given variable results. Virnstein (1978) did not find consistent significant effects at two eelgrass sites in his study in Florida, and suggested that predation may not play the major role in community structure of seagrass beds. In my study, I found that exclusion cages result in higher densities of worms for abundant species at some but not all sites. Therefore the observed structure of seagrass communities may also be explained by other physical and/or biological phenomena: habitat preference (Orth, 1977; Stoner, 1980; Bell and Westoby, 1986; Main 1987), nutrient and food availability (Whitlatch, 1980; Kitting, 1984; Wiltse et al., 1984), sediment stabilization and current disruption (Coull, 1970; Young and Rhoads, 1971; Orth, 1977), intraspecific competition (Peterson, 1979) and differences in passive settlement (Woodin, 1974). For example, Main (1987) showed that prey survival increased within seagrass that had a better cover suggesting that

preference for the habitat would be selected.

The effects of predatory infauna, like nemerteans, amphipods and nereid polychaetes, although not accounted for in this study, should also be considered. A significant number of these predators were observed in my samples. Nevertheless, their effects in the regulation of the structure of soft-bottom communities have not been extensively studied and are poorly understood (Trevallion et al., 1970; Witte and de Wilde, 1979; Wilson, 1979, 1984; Woodin, 1984; Comito and Ambrose, 1985).

The presence of more species at site B both inside and outside the Zostera, compared to sites A and C, could be due to the presence of shell fragments, and pieces of metal, wood and rocks in the sediments here, creating a more spatially heterogeneous habitat. Objects in the sediments such as wood stakes and rocks, other than supporting an attachment for epifaunal community, also appear to attract a rich infaunal community close to them (Orth, 1977). Moreover, Posey and Rudy (1986) reported that the Ferrie Ranch marsh (site B) had the longest history of Z. japonica colonization. At sites A and B, there were more spionid polychaetes inside than outside the eelgrass. This could be due to the fact that these two sites are more protected from the energy of the waves and tides as they come into the estuary. This protection therefore may enhance the settlement of the organisms due to the relatively lower movement of the substratum and the stabilizing effect of the rhizomes and other physical structures of the Zostera (Orth et al., 1984). As previously stated, the presence of objects in site B and

the presence of plant marsh roots and stems in the substratum of site A, in the presence of Zostera, could have contributed to the observed higher density of spionid polychaetes inside than outside the eelgrass bed. Moreover, site A is more protected than site B.

At site C, the area is relatively unprotected subjecting it to high wave and tide energy. This high energy would cause drastic shifts in the sediments, thereby not enabling some organisms to survive and settle, despite the presence of Zostera.

The one-time occurrence of Spio filicornis at site A in the April sampling could be due to the sediment importation brought about by the winter storms in late December 1986 and late January 1987. Sediments were piled in the area down to approximately 2.5 cm of the top sediment layer. This suggests that site A is a low energy area which permitted sedimentation. Therefore, the physical environment of site A is different from sites B and C which may also explain the difference in seagrass community structure observed. This sediment build-up at site A could be responsible for the development of patches of Z. japonica here. The expansion of Zostera could be due to habitat modification (Peterson, 1979; Harrison and Bigley, 1982 ; Bertness, 1984). On the other hand, the establishment of Zostera at site A could have also contributed to the sedimentation at this site.

The physical presence of the cages had a significant effect on the density of spionids inside or outside the Z. japonica beds. This could be due to the development of a thick mat of the alga Ulva sp. on some of the cages during these sampling dates. It was observed at site A that

there were more Ulva sp. entangled on some cages, and less at sites B and C. This is again an evidence of the low energy present at site A. Hodder (1985) showed that densities of Ulva sp. were highest during the summer and fall seasons in the South Slough Estuary. Cages with algal mats exerted more effects outside of eelgrass than inside because vegetation was a "new" occurrence outside of the Z. japonica beds resulting in significant cage effects, while algal mats inside the Zostera beds may be equivalent to the effect of more Zostera growth. The accumulation of detritus and algae inside the cages could have an effect on the animals that are inside or outside the eelgrass bed, due to the nutrients leached out by the detritus and algae. This could be one of the reasons why there were some cage effects outside the eelgrass.

The results of this study have demonstrated that predation is one of the primary processes controlling the differential abundance of spionids inside versus outside the eelgrass beds, although there were important exceptions. This result is supported by the experimental data obtained from predator exclusion cages. Zostera japonica affects the benthic community by several mechanisms, some of which are evident in South Slough: (1) the nursery function of submerged vegetation (Hanekom and Baird, 1984; Wilson et al., 1987); (2) the ability to provide cover for and enhance survival of eelgrass inhabitants (Heck and Thoman, 1981; Main, 1987); and, (3) the positive correlation of eelgrass with sedentary species (Posey and Rudy, 1986). These factors could explain the generally higher densities of spionids inside than outside the

eelgrass beds. Other than the added protection of the spionid tube, the stabilizing effect of the Zostera on the substrate and the physical structures of the eelgrass (e.g. roots-rhizome mat and plant canopy) also contribute to the protection of the spionids.

CHAPTER V

CONCLUSION AND RECOMMENDATIONS

The density and abundance of the spionid worms in the South Slough of Coos Bay is evidently influenced by the presence of the introduced eelgrass Zostera japonica. Inside the Zostera bed there are a high abundance and density of spionid worms as compared to adjacent unvegetated areas. Changes in faunal abundances are also affected by species, site, and season.

The results of this study demonstrate the potential importance of Zostera, as an introduced species, in structuring part of the benthic community. The role of Z. japonica as a refuge from predation is only one of the factors that contribute to the abundance of the spionid polychaete community. Other factors such as larval recruitment, passive transport, nutrient availability, disturbance and reproduction may also be playing important roles in this community.

However, the predictions made in this study should be taken with caution since they represent only a year of observation. Measurement of eelgrass cover, in particular, is subject to yearly variations. Correlation of the eelgrass cover with abundance and diversity of the spionid community for two or three consecutive years is therefore recommended. This will also determine more effectively the role of Z.

japonica in providing protection and refuge from predation.

It is also recommended that monthly sampling of epifaunal predators should be done to better assess the amount of predation. Furthermore, infaunal predators must also be considered.

To minimize cage effects a larger cage dimension should be employed, but the problem here is its management in the field (i.e., bringing it to the study site, etc.). Moreover, cages should be rotated to control for the alteration of hydrodynamic characteristics around the cage.

BIBLIOGRAPHY

- Adams, S.M. 1976. Feeding ecology of eelgrass fish communities. *Trans. Am. Fish. Soc.* 105(4):514-519.
- Bell, J.D., and M. Westoby. 1986. Abundance of macrofauna dense seagrass is due to habitat preference, not predation. *Oecologia* 68:205-209.
- Berkeley, E., and C. Berkeley. 1952. Canadian Pacific fauna. Pt.9 Annelida 9b(2). Polychaeta Sedentaria.
- Bertness, M.D. 1984. Habitat and community modification by an introduced herbivorous snail. *Ecology* 65(2):370-381.
- Blake, J. 1975. Polychaeta, p.151-243. In Smith, W. and J.T. Carlton (eds.), *Light's Manual: intertidal invertebrates of the Central California Coast*. University of California Press, Berkeley, California, U.S.A.
- Carlton, J.T. 1979. History, bibliography, and ecology of the introduced marine and estuarine invertebrates of the Pacific Coast of North America. Ph.D. Dissertation, University of California, Davis.
- Carr, W.E.S., and C.A. Adams. 1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. *Trans. Am. Fish. Soc.* 102(3):511-540.
- Commuto, J.A., and W.G. Ambrose, Jr. 1985. Predatory infauna and trophic complexity in soft-bottom communities, p.323-333. In P.E. Gibbs (ed.), *Proceedings of the Nineteenth European Marine Biology Symposium*, Cambridge University Press, Cambridge, England.
- Coull, B.C., and J.B.J. Wells. 1983. Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. *Ecology* 64:1599-1609.
- Day, J.H. 1967. A monograph on the Polychaeta of South Africa. Pt.2. Sedentaria. Eyre and Spottiswoode, Lmtd., Portsmouth.
- Dauer, D.M., C.A. Maybury, and R. Michael Ewing. 1981. Feeding behavior and general ecology of several spionid polychaetes from the Chesapeake Bay. *J. Exp. Mar. Biol. Ecol.* 54:21-38.

- De Groot, S.J. 1971. On the interrelationships between morphology of the alimentary tract, food and feeding behaviour in flatfishes (Pisces: Pleuronectiformes). *Neth. J. Sea Res.* 5:121-196.
- De Vlas, J. 1979. Secondary production by tail regeneration in a tidal flat population of lugworm (Arenicola marina), cropped by flatfish. *Neth. J. Sea Res.* 13:362-393.
- Fauchald, K. 1977. The polychaete worms. Definitions and keys to orders, families and genera. *Sci. Ser. Nat. Hist. Mus. Los Angeles Cty.* Vol. 28, p.1-190.
- Folk, R.L. 1961. Petrology of sedimentary rocks. Hemphill's, Austin, Texas.
- Frankenberg, D., and A.S. Leiper. 1977. Seasonal cycles in benthic communities of the Georgia continental shelf, p.383-397. In B.C. Coull (ed.), *Ecology of Marine Benthos*. Univ. of South Carolina Press, Columbia, South Carolina.
- Gambi, M.C., and H. Giangrande. 1986. Distribution of soft-bottom polychaetes in two coastal areas of the Tyrrhenian Sea (Italy): structural analysis. *Est. Coastal Shelf Sci.* 23:847-862.
- Gee, J.M., R.M. Warwick, J.T. Davey, and C.L. George. 1985. Field experiments on the role of epibenthic predation in determining prey density in an estuarine mudflat. *Est. Coastal Shelf Sci.* 21:429-448.
- Gonor, J.J., and P.F. Kemp. 1978. Procedures for quantitative ecological assessments in intertidal environment. Grant No. R805018-01. E.V. Environmental Protection Agency, Corvallis, Oregon.
- Gore, R.H., L.E. Scotto, K.A. Wilson, and E.E. Gallagher. 1981. Studies on decapod crustacea from the Indian River region of Florida. XI. Species composition, structure, biomass and species-area relationships of seagrass and drift-algae associated macrocrustaceans. *Est. Coastal Mar. Sci.*
- Grassle, J.F., and J.P. Grassle. 1976. Sibling species in the marine pollution indicator Capitella (Polychaeta). *Science* 192: 567-569.
- Gray, J.S. 1974. Animal-sediment relationships. *Oceanogr. Mar. Biol. Ann. Rev.* 12:223-261.
- Grosberg, R.K. 1981. Competitive ability influences habitat choice in marine invertebrates. *Nature* 290(3008):100-102.

- Hanekom, N., and D. Baird. 1984. Fish community structures in Zostera and non-Zostera regions of the Kromme estuary, St. Francis Bay. S. Afr. J. Zool. 19:295-301.
- Harper, J.L. 1969. The role of predation in vegetational diversity, Brookhaven Symp. Biol. 22:48-62.
- Harrison, P.G. 1979. Reproductive strategies in intertidal populations of two co-occurring seagrasses (Zostera spp.) Can. J. Bot. 57: 2635-2638.
- Harrison, P.G. 1982a. Spatial and temporal patterns in abundance of two intertidal seagrasses Zostera americana den Hartog and Zostera marina L. Aquat. Bot. 12:305-320.
- Harrison, P.G. 1982b. Comparative growth of Zostera japonica Aschers & Graebn. and Z. marina L. under simulated intertidal conditions. Aquat. Bot. 14:373-379.
- Harrison, P.G. 1982c. Seasonal and year-to-year variations in mixed intertidal populations of Zostera japonica Aschers. & Graebn. and Ruppia maritima L.S.l. Aquat. Bot. 14:357-371.
- Harrison, P.G., and R.E. Bigley. 1982. The recent introduction of seagrass, Zostera japonica Aschers. and Graebn. to the Pacific Coast of North America. Can. J. Fish. Aquat. Sci. 39:1642-1648.
- Hartman, O. 1969. Atlas of sedentariate polychaetous annelids from California. Allan Hancock Foundation, Los Angeles, 828 pp.
- Hayne, D.W., and R.C. Ball. 1956. Benthic productivity as influenced by fish predation. Limnol. Oceanogr. 1:162-175.
- Heck, K.L. Jr., and R.J. Orth. 1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblage, p.449-464. In V.S. Kennedy (ed.), Estuarine Perspectives. Academic Press, N.Y.
- Heck, K.L. Jr., and T.A. Thoman. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. J. Exp. Mar. Biol. Ecol. 53:125-134.
- Hodder, J. 1986. Production biology of an estuarine population of the green algae, Ulva spp. in Coos Bay. Univ. of Oregon Ph. D. Dissertation, 106 p.

- Honziak, J., M.S. Fonseca, and W.J. Kenworthy. 1982. Macrobenthic community structure in a transplanted eelgrass (Zostera marina) meadow. *Mar. Ecol. Prog. Ser.* 9:211-221.
- Johnson, R.G. 1967. The vertical distribution of the infauna of a sand flat. *Ecology* 48:571-578.
- Kikuchi, T. 1974. Japanese contributions on consumer ecology in eelgrass (Z. marina L.) beds, with special reference to trophic relationships and resources in inshore fisheries *Aquaculture* 4:145-160.
- Kikuchi, T. 1980. Faunal relationships in temperate seagrass beds, p.153-172. *In* R.C. Phillips and C.P. McRoy (eds.), *Handbook of Seagrass Biology*. Garland STPM Press, N.Y.
- Kikuchi, T., and J.M. Peres. 1977. Consumer ecology of seagrass beds, p.147-193. *In* C.P. McRoy and C. Helfferich (eds.), *Seagrass Ecosystems: a scientific perspective*.
- Kitting, C.L. 1984. Selectivity by dense populations of small invertebrates foraging among seagrass blade surfaces. *Estuaries* 7(4A):276-288.
- Knox, G.A. 1977. The role of polychaetes in benthic soft-bottom communities, p.547-604. *In* D.J. Reish and K. Fauchald (eds.), *Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman*. Allan Hancock Foundation, Inc.
- Lappalainen, A., G. Hallfors, and P. Kangas. 1977. Dynamics of macrobenthos in a sandy bottom Zostera marina community in Tvarminne Finland. *Int. Rev. ges. Hydrobiol.* 62(4):465-504.
- Leber, K.M. 1985. The influence of predatory decapod crustaceans, refuge, and microhabitat selection on seagrass communities. *Ecology* 66:1951-1964.
- Le Mao, P. 1986. Feeding relationships between the benthic infauna and the dominant benthic fish of the Rance Estuary (France). *J. Mar. Biol. Ass. U.K.* 66:391-401.
- Lewis, F.G. III. 1984. Distribution of macrobenthic crustaceans associated with Thalassia, Halodule and bare sand substrata. *Mar. Ecol. Prog. Ser.* 19:101-113.
- Light, W. J. 1978. *Spionidae: Polychaeta Annelida*. The Boxwood Press, Pacific Grove, California, U.S.A. 211p.

- Main, K.L. 1987. Predator avoidance in seagrass meadows: prey behavior, microhabitat selection and cryptic coloration. *Ecology* 68(1):170-180.
- Marsh, G.A. 1973. The *Zostera* epifaunal community in the York River, Virginia. *Chesapeake Sci.* 14:87-97.
- McCall, P.L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. *J. Mar. Res.* 35: 221-266.
- McRoy, C.P., and C. Helfferich. 1977. *Seagrass ecosystems: a scientific perspective.* Marcel Dekker, Inc. New York.
- Muus, B.J. 1967. The fauna of Danish estuaries and lagoons. Distributions and ecology of dominating species in the shallow reaches of the mesohaline zone. *Medd. Dan. Fisk. Havunders.* 5: 1-316.
- Nelson, W.G. 1979. Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. *J. Exp. Mar. Biol. Ecol.* 38:225-245.
- Nelson, W.G. 1981. Experimental studies of decapod and fish predation on seagrass macrobenthos. *Mar. Ecol. Prog. Ser.* 5: 141-149.
- Nixon, S.W., and C.A. Oviatt. 1972. Preliminary measurements of midsummer metabolism in beds of eelgrass, *Zostera marina*. *Ecology* 53(1):150-153.
- Orth, R.J. 1973. Benthic infauna of eelgrass, *Zostera marina*, beds. *Ches. Sci.* 14(4):258-269.
- Orth, R.J. 1977. The importance of sediment stability in seagrass communities, p.281-300. In B.C. Coull (ed.), *Ecology of Marine Benthos.* Univ. of South Carolina Press, Columbia.
- Orth, R.J., J.L. Heck, Jr., and J. van Montfrans. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* 7(4A):339-350.
- Peterson, C.H. 1979. Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons, p.233-261. In R.J. Livingston (ed.), *Ecological Processes in Coastal and Marine Systems.* Plenum Publ. Corp.

- Posey, M.H. 1985. The effects upon the macrofaunal community of a dominant burrowing deposit feeder, Callianassa californiensis, and the role of predation in determining its intertidal distribution. Univ. of Oregon, Ph. D. Dissertation, 119 p.
- Posey, M.H. 1986a. Predation on a burrowing shrimp: distribution and community consequences. J. Exp. Mar. Biol. Ecol. 103: 143-161.
- Posey, M.H. 1986b. Changes in a benthic community associate with dense beds of a burrowing deposit feeder, Calliannassa californiensis. Mar. Ecol. Prog. Ser. 31:15-22.
- Posey, M.H., and P.P. Rudy. 1986. The effects of an introduced seagrass, Zostera japonica on benthic communities in the South Slough National Estuarine Sanctuary. Draft Report, U.S. Dept. of Commerce, NOAA Grant # NA855AA-D-CZ036.
- Quammen, M.L. 1984. Predation by shorebirds, fish, and crabs on invertebrates in intertidal mudflats: an experimental test. Ecol. 65(2):529-537.
- Raffaelli, D., and H. Milne. 1987. An experimental investigation of the effects of shorebirds and flatfish predation on estuarine invertebrates. Est. Coastal Shelf Sci. 24:1-13.
- Reise, K. 1977. Predation pressure and community structure of an intertidal soft-bottom fauna, p.513-520. In B.F. Keegan, P.O'Ceidigh and P.J.S. Boaden (eds.), Biology of Benthic Organism. 11th European Symposium on Marine Biology, Galway, Ireland, 1976. Oxford, Pergamon Press.
- Reise, K. 1978. Experiments on epibenthic predation in the Wadden Sea. Helgolander wissenschaftliche Meeresuntersuchungen. 3: 55-101.
- Reise, K. 1985. Tidal Flat Ecology: an experimental approach to species interactions. Springer-Verlag, Berlin. 191p.
- Rhoads, D.C., and D.K. Young. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. J. Mar. Res. 28:150-178.
- Rudy, P. Jr., and L.H. Rudy. 1983. Oregon Estuarine Invertebrates: an illustrated guide to the common and important invertebrate animals. Fish and Wildlife Service. FWS 10B5-83/16. Charleston, Oregon, U.S.A.

- Ryer, C.H. 1987. Temporal patterns of feeding by blue crabs (*Callinectes sapidus*) in a tidal-marsh creek and adjacent seagrass meadow in the lower Chesapeake Bay. *Estuaries* 10(2): 136-140.
- Sanders, H.L. 1968. Marine benthic diversity: a comparative study. *Amer. Nat.* 102:243-282.
- Santos, S.L., and J. L. Simon. 1974. Distribution and abundance of the polychaetous annelids in a South Florida estuary. *Bull. Mar. Sci.* 24(3):669-689.
- Schneider, P. 1978. Equalisation of prey numbers by migratory shorebirds. *Nature* 271:353-354.
- Sokal, R.R., and F.J. Rohlf. 1981. *Biometry*. Second edition. W.H. Freeman, San Francisco, California, U.S.A.
- Stoner, A.W. 1980. Abundance, reproductive seasonality and habitat preferences of amphipod crustaceans in seagrass meadows of Apalachee Bay, Florida. *Mar. Sci.* 23:63-77.
- Stoner, A.W. 1983a. Distributional ecology of amphipods and tanaidaceans with three sea grass species. *J. Crus. Biol.* 49: 505-518.
- Stoner, A.W., and H.S. Greening. 1983b. Comparison of macrobenthos collected with cores and suction sampler in vegetated and unvegetated marine habitats. *Estuaries* 6(1):76-82
- Summerson, H.C., and C.H. Peterson. 1984. Role of predation in organizing benthic communities of a temperate-zone seagrass bed. *Mar. Ecol. Prog. Ser.* 15:63-77.
- Tabb, D.C., D. Dubrow, and R. Manning. 1962. The ecology of northern Florida Bay and adjacent estuaries. *Tech. Ser. Fla. St. Bd. Conserv.* 39:1-79.
- Taghon, G.L., A.M. Nowell, and P.A. Jumars. 1980. Induction of suspension feeding in spionid polychaetes by high particulate fluxes. *Science* 210(4469):562-564.
- Tenore, K.R., L. Cammen, S.E.G. Findlay, and N. Phillips. 1982. Perspective of research on detritus: do factors controlling the availability of detritus to macroconsumers depend on its source? *J. Mar. Res.* 40:473-490.

- Thayer, G.W., S.M. Adams, and M.W. La Croix. 1975a. Structural and functional aspects of a recently established Zostera marina community, p.518-540. In Estuarine Research. Vol. I. Academic Press, New York.
- Thayer, G.W., and R.C. Phillips. 1977. Importance of eelgrass beds in Puget Sound. Mar. Fish. Res. 39:18-22.
- Thorhaug, A., and M.A. Roessler. 1977. Seagrass community dynamics in subtropical estuarine lagoon. Aquaculture 12:253-277
- Trevallion, A.R., R.C. Edwards, and J.H. Steele. 1970. Dynamics of a benthic bivalve, p.285-295. In J.H. Steele (ed.): Marine Food Chains. Berkeley, University of California Press.
- 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, p.261-273. In V. S. Kennedy (ed.), Estuarine Interactions. Academic Press, Inc.
- Virnstein, R.W. 1980. Measuring effects of predation on benthic communities in soft sediments, p.281-290. In V.S. Kennedy (ed.), Estuarine Perspective. Academic Press, New York.
- Virnstein, R.W., W.G. Nelson, F.G. Lewis, III, and R.K. Howard. 1984. Latitudinal patterns in seagrass epifauna: do patterns exist, and can they be explained? Estuaries 7:310-330.
- Wilkinson, R.P. 1984. Systems Statistics. Ill.
- Wilson, J.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, J.H. Jr. 1984. An experimental analysis of spatial competition in a dense infaunal community: the importance of relative effects. Est. Coastal Shelf Sci. 18:673-684.
- Wilson, K.A., K.L. Heck, Jr., and K.W. Able. 1987. Juvenile blue crab, Callinectes sapidus, survival: an evaluation of eelgrass, Zostera marina, as refuge. Fish. Bull. 85(1):53-58.
- Wiltse, W.I., K.H. Foreman, J.M. Teal, and I. Valiela. 1984. Effects of predators and food resources on the macrobenthos of salt marsh creeks. J. Mar. Res. 42:923-942.

- Witte, F., and P.A.W.J. de Wilde. 1979. On the ecological relation between Nereis diversicolor and juvenile Arenicola marina. Neth. J. Sea Res. 13:394-405.
- Whitlatch, R.B. 1980. Patterns of resource utilization and coexistence in marine intertidal deposit-feeding communities. J. Mar. Res. 38:743-765.
- Woodin, S.A. 1974. Polychaete abundance patterns in a marine soft-sediment environment: the importance of biological interactions. Ecol. Monog. 44:171-187.
- Woodin, S.A. 1982. Browsing: important in marine sedimentary environments? Spionid polychaete examples. J. Exp. Mar. Biol. Ecol. 60:35-45.
- Woodin, S.A. 1984. Effects of browsing predators: activity changes in infauna following tissue loss. Biol. Bull. Mar. Biol. Lab., Woods Hole, Mass. 166:558-573.
- Woodwick, K.H. 1977. Lecithotrophic larval development in Boccardia proboscidea Hartman, p.347-372. In D.J. Reish and K. Fauchald (eds.): Essays on Polychaetous Anneclids in Memory of Dr. Olga Hartman. Allan Hancock Foundation, U.S.A.
- Young, D.K., and D.C. Rhoads. 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. I. A transect study. Mar. Biol. 11: 242-254.
- Young, D.K., M.A. Buzas, and M.W. Young. 1976. Species densities of macrobenthos associated with seagrass: a field experimental study of predation. J. Mar. Res. 34:577-592.
- Young, D.K., and M.W. Young. 1977. Community structure of the benthos associated with seagrass of the Indian River Estuary, Florida, p.359-382. In B.C. Coull (ed.), Ecology of Marine Benthos. Univ. of South Carolina Press, Columbia.
- Young, D.K., and M.W. Young. 1978. Regulation of species densities of seagrass-associated macrobenthos: evidence from field experiments in the Indian River estuary, Florida. J. Mar. Res. 36(4):569-593