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THE DISTRIBUTIONAL ECOLOGY OF HEMILEUCON HINUMENSIS AND ITS
RELATIONSHIP WITH SOFT SEDIMENT TUBE BUILDING
SPECIES IN COOS BAY, OREGON

by

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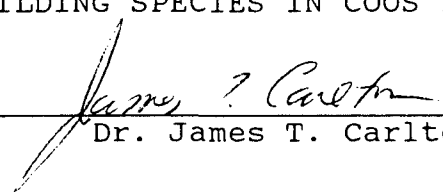
A THESIS

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AND ITS RELATIONSHIP WITH SOFT SEDIMENT TUBE
BUILDING SPECIES IN COOS BAY, OREGON

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Dr. James T. Carlton

Few studies have examined the role of introduced fauna in estuarine systems. Hemileucon hinumensis, a Japanese cumacean was introduced into Coos Bay in the mid 1970's. A survey of its distribution shows Hemileucon to be located specifically in the brackish regions of Coos Bay's upper estuary. It co-occurs with the cumacean Cumella vulgaris and the tube building species Streblospio benedicti (Spionidae) and Leptocheilia dubia (Tanidacea). Although its distribution is dependent upon several physical factors, interspecific interactions controlling small scale distributions occur. Weak negative relationships exist between Hemileucon with both Streblospio benedicti and Leptocheilia dubia. Experimental manipulations show the relationship with Leptocheilia to be density dependent. Moderate densities of Leptocheilia facilitate cumacean settlement in lab

experiments. High densities of Leptochelia inhibit cumacean settlement in both the laboratory and the field.

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To My Mother and Father

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CHAPTER I

INTRODUCTION

Increases in human activities around the world increase the possibility of species introductions (Carlton 1987, 1989) while questions concerning their role in today's environment remain unanswered. Non-native species abound in estuaries of the Pacific North American coast yet little is known about how these species interact with native communities. Do invading species have the capability of changing population dynamics or causing character displacement altering evolutionary processes (Connell and Slatyer 1977; Rummell and Roughgarden 1983)? What are the impacts of new species on community structure and diversity? To provide answers to these questions it is critical to understand the dynamics of species introduction.

In order to define how a community will be affected when a non-native species invades one must first determine if interactions occur between the species in question. Interactions inferred from observational data alone are commonly insufficient. Experimental methods allow more detailed examinations of species interactions (Underwood 1985). The use of both observational and experimental

methods provides the most reliable assessment of the relationships of introduced and native organisms (Schoener 1974).

The cumacean Hemileucon hinumensis (Gamo, 1967) is believed to have been introduced to Coos Bay, Oregon with ballast water in the 1960's or 1970's (Carlton, 1989a). Hemileucon has been identified in Coos Bay with increasing regularity over the last ten years (Jefferts 1977, Goner et. al. 1979, Posey 1986, Carlton 1986, OEIS 1988). It is now well established in Coos Bay.

Cumaceans are found world wide. While most are marine some, such as Hemileucon, are found in brackish waters and fresh water species are also known (Zimmer 1936; Jones 1976; Barnes 1980; Duncan 1984). Cumaceans range in size from five to 35 mm and occur in densities of up to 100,000/m² in benthic sediments. Little is known about the group and only a few studies have looked at the distributions of cumaceans and what environmental factors they respond to (Watkin 1942; Clark & Milne 1955; Weiser 1956; Bernard & Given 1961; Corey 1970).

Hemileucon forms dense populations in brackish regions of Coos Bay estuary. It co-occurs with the tanaid Leptochelia dubia and the native cumacean Cumella vulgaris. All three species are deposit feeders sifting fine sediments for organic materials. Leptochelia feeds from tubes it constructs in the sediments while Hemileucon and Cumella are free ranging.

The distribution and ecology of these species are poorly known. This study examines Hemileucon's distribution in relation to some of the physical and biological factors in the bay. I specifically examined the interactions between Hemileucon and Leptochelia.

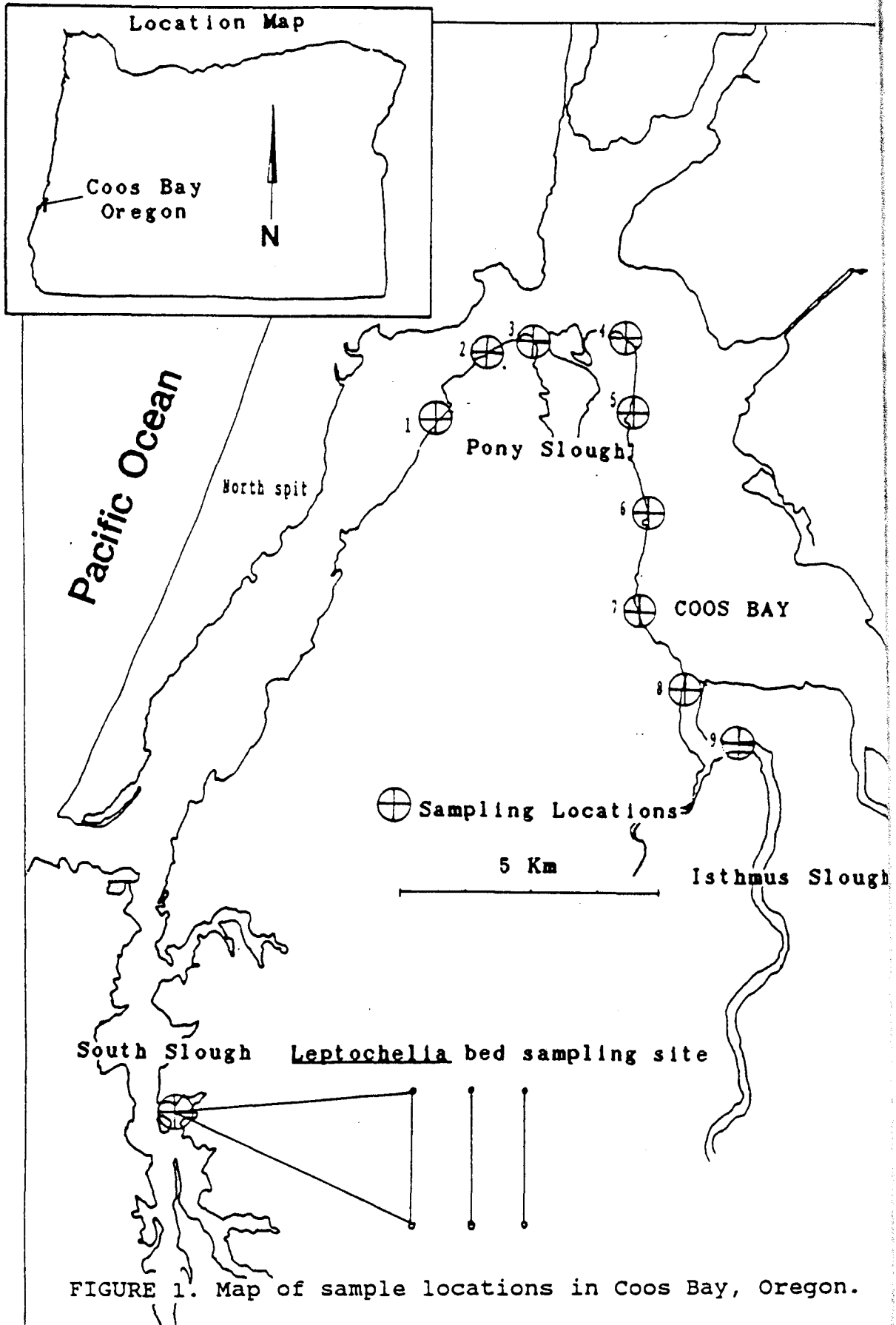
CHAPTER II

METHODS

Field Sampling

Hemileucon was sampled in the field from nine permanent sampling sites located at one mile (1.6 km) intervals from mile 7 (11.3 km) to mile 15 (24.1 km) along Coos Bay's main dredge channel (figure 1). These sites are referred to below as sites 7 through 15. A one meter length of iron rebar was fixed above the high tide line as a reference marker at each site. The distance and compass bearing from the reference marker to the sampling location at the zero tide line were recorded where a one meter long wooden stake was embedded.

A 10 m nylon line marked at 1 m intervals was extended from the zero tide stake toward the upper bay parallel to the water line. Five numbers between 0 and 9 from a random numbers table were chosen to determine the positions along the line to be sampled. One sample was removed from each position. The nylon line commonly touched the sediment below it. Therefore cores were removed 0.5 m from the line toward the water perpendicular to the transect to ensure that undisturbed sediment was collected. Samples were collected using a 6 cm diameter by 3 cm length of PVC pipe that was



pressed into the mud until it was flush with the surface. The sample could then be removed cleanly by inserting a spatula underneath and lifting.

Each location was sampled on a bimonthly basis from November 1988 until May 1989. Salinity, temperature, volatile solids and species abundances were measured for each site. Temperature was recorded by a thermometer inserted into the mud surface. Water samples were analyzed for salinity using a YSI meter. Extra sediment samples were collected to determine the volatile solids content. All invertebrate core samples were collected on night time low tides and sieved through an 0.5 mm screen within 48 hours of removal. Large stones or wood chips were removed from these samples by first sieving them through a 2 cm screen. The sieved samples were then preserved in 10% buffered formalin for 48 h before being transferred to 70% ETOH. All macrobenthic organisms were sorted out of these samples using a dissecting microscope and the most abundant organisms were identified to species.

The volatile solids content was determined from five 1 cm diameter by 3 cm deep core samples collected randomly from each location. These samples were combined, air dried at 50 °C and weighed. The samples were fired in a kiln at 500 °C for 10 h each then weighed again. The difference in weight before and after firing was used as the percent volatile solids.

Variation in the densities of Hemileucon were compared

with average numbers of other abundant species and variations in salinities, temperature, and percent volatile solids at all sites.

Leptochelia Bed Field Sampling

Sampling of a dense population of Leptochelia was conducted in South Slough reserve (figure 1). The area consists of a broad mudflat of 67 to 250 mu diameter sediments. Predominant species included Zostera marina, several species of bivalves and Callianassa californiensis. A ten by ten meter quadrat was established in a level area (figure 2) with three parallel transects five meters apart and perpendicular to the water line. A nylon line between transect stakes marked at 0.5 m intervals was used to designate the sampling locations along each transect. Surface samples, 3 cm deep, were removed using a 4 cm inner diameter corer. Since the line commonly contacted the mud surface, cores were removed 10 cm to the left of each line. Sixty samples were removed in all. Samples were immediately returned to the lab and washed on an 0.5 mm sieve. All cumaceans and Leptochelia remaining in the samples were counted using a 10X dissecting scope.

Response to Leptochelia Presence (laboratory)

The settlement response of Hemileucon and Cumella to established Leptochelia beds and open sediment was examined by laboratory and field experiments. In the laboratory a

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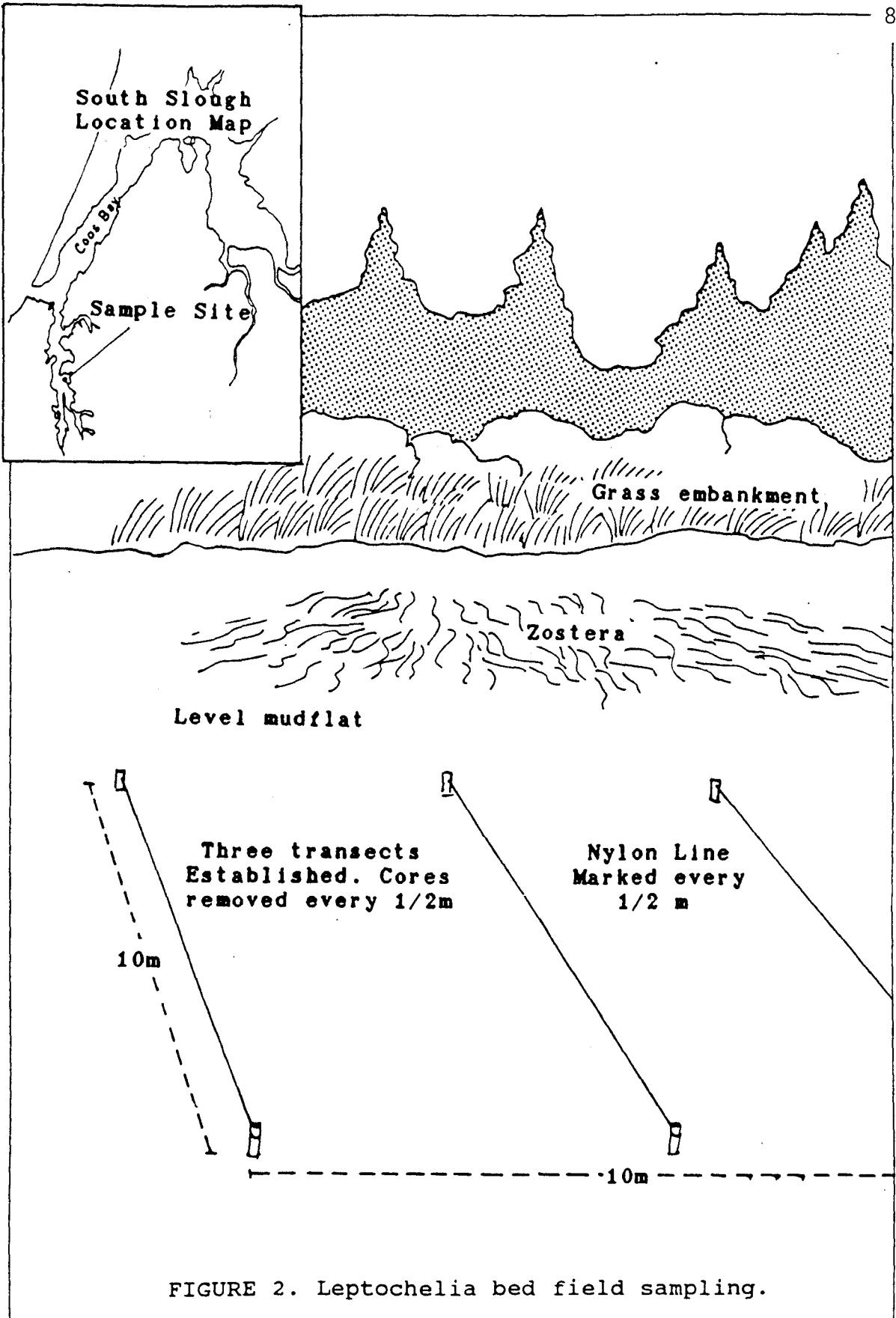


FIGURE 2. *Leptochelia* bed field sampling.

plastic (Rubbermaid) tank with opaque sides was used as a test tank which could hold 28 separate glass containers. Each container had a square perimeter with a circular depression 1.5 cm deep and 3.23 cm in diameter (figure 3). Azoic sediments were prepared for the laboratory studies by removing the upper 3 cm of sediments from the Leptochelia sampling site at South Slough. These sediments were washed through an 0.5 mm screen and air dried for seven days. Seawater was mixed with the sediments to form thick homogenous mud. This mud was used to fill 28 - 1.5 cm deep by 3.23 cm diameter watch glasses (figure 3a). Ten Leptochelia were added to each of 14 of the watch glasses. All 28 glasses were then held 48 h immersed in aerated seawater. The Leptochelia had a tendency to migrate from their respective containers. In order to prevent this the watchglasses containing Leptochelia were held separately from those with only sediments.

Hemileucon were collected from the same field location as Leptochelia within 24 h of the experiment. Three hundred adult Hemileucon were counted and placed into a one liter flask of sea water. One hour before the experiment, the watchglasses with the two treatments were removed from their respective tanks and placed in an alternating fashion into a 17 cm deep X 26 cm wide X 36 cm long experimental tank (figure 3). The cumaceans were then added. To eliminate directional light sources, to which the cumaceans are sensitive, a translucent plexiglass sheet 6.3 mm thick was

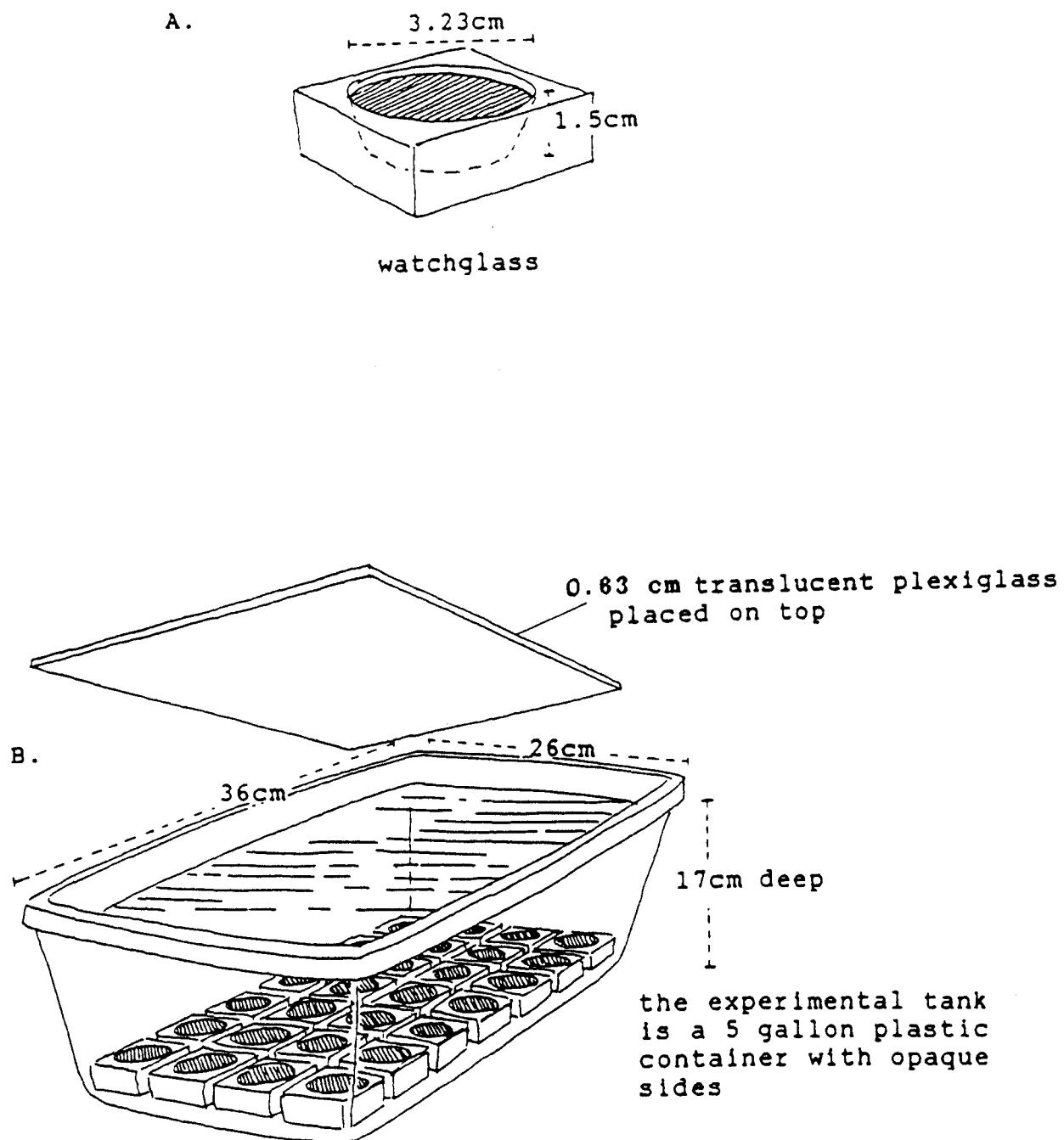


FIGURE 3. Leptochelia density experiments (setup).

placed over the top of the tank. The experiment lasted 24 hours. The water in the tank was then slowly siphoned until it was below the level of the tops of the watchglasses. The sediment from each container was sieved and the animals present were counted under a 10X dissecting microscope. Significant differences were tested for using an unpaired students t-test.

Response to Leptochelia
Presence (field)

The responses of Hemileucon and Cumella to the presence of Leptochelia were tested under field conditions. Two racks (figure 4) were placed on the mudflat where they could be submerged in a permanent standing pool of water to a depth of 30 cm to avoid disturbance from wave action at low tide. Each rack held 12 containers. The containers are 8.3 cm (inner diameter) by 6.5 cm deep with snap-on lids. Surface sediment was collected and prepared in the same manner as described above. A three centimeter deep layer of these sediments was added to each container. The containers were then filled with sea water. Leptochelia were collected near where the racks had been deployed. Approximately 300 Leptochelia were placed into each of 12 treatment containers. Most of the animals immediately burrowed into these sediments. A two to three day period was necessary for Leptochelia to establish tube densities comparable to field conditions. Therefore both treatments were partially

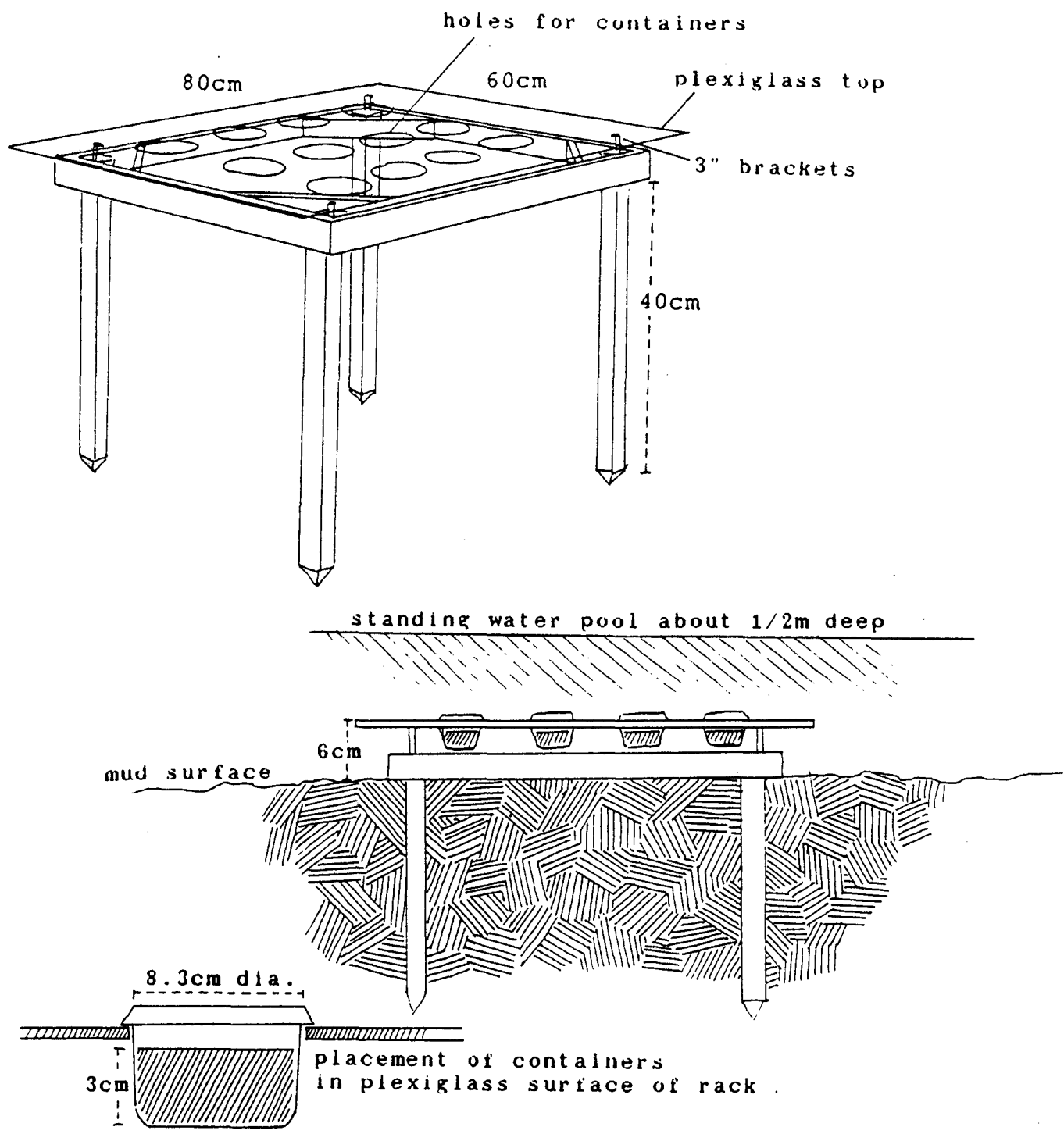


FIGURE 4. Rack construction.

immersed in an aerated seawater bath maintained at 15 ° C for three days prior to the field experiment. When prepared, the containers were placed out in the field for a 24 hour period. Each container was positioned in a randomly assigned place in one of the two racks. After 24 hours of exposure the containers were collected and the sediments from each container were washed on an 0.5 mm mesh sieve. The remaining cumaceans were counted. The data were Log_e transformed and significant differences were tested using an unpaired students t-test.

Response to Various Leptochelia Densities in the Laboratory

The responses of cumaceans to four densities of Leptochelia were examined under laboratory conditions. The design and execution of these experiments were similar to the Leptochelia presence experiment conducted in the laboratory, described above. Freshly collected Leptochelia were placed into the sediment containers in densities of 0, 1.6, 2.91, and 5.8 Leptochelia / cm^2 . Seven replicates of each Leptochelia density were used. The replicates of each density were placed around the perimeter of an 15.2 cm diameter bowl filled with seawater (figure 5). For 48 h the water was changed daily and continuously aerated while the Leptochelia were allowed to establish tubes. The experimental tank was filled with unfiltered seawater to a depth of 17 cm. The containers were placed into the test

tank in 7 rows and 4 columns. To assure the replicates were properly interspersed (Hurlbert 1984) one watchglass of each Leptochelia density was placed randomly into every row. The water was continuously aerated before the experiment.

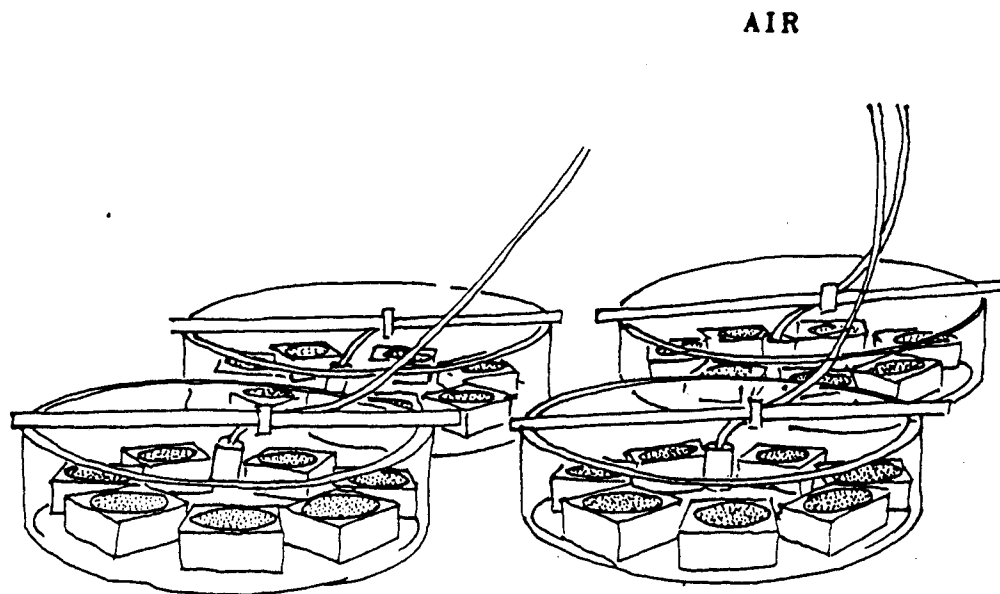


FIGURE 5. Preparation of experimental Leptochelia beds in watchglasses.

Hemileucon were collected and three hundred adults were added to the tank. The air supply was removed and the tank was covered with a 6.3 mm translucent plastic sheet to

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diffuse incoming light. After 24 hours the water was carefully siphoned from the tank and the watchglasses were removed. The sediment from each watchglass was washed through an 0.5 mm mesh sieve and any remaining animals counted. Significant differences were assessed by a one way ANOVA. The same experiment was also performed with Cumella.

Response to Various Leptochelia Densities in the Field

A field experiment similar to the lab experiment with four densities of Leptochelia was designed using 3 field racks (figure 4). This provided spaces for 36 containers. Sediment was prepared and placed in the containers as described above. Leptochelia were collected and three hundred were added to each of 12 high density containers ($5.5/\text{cm}^2$), 50 were added to 12 intermediate density containers ($1.1/\text{cm}^2$), and 12 containers remained with sediment only. The containers of each density were divided into two groups which were placed into holding tanks. The holding tanks were filled with nonfiltered seawater. The treatments were kept in these tanks for 48 h to allow the Leptochelia time to establish tubes. The water was aerated and changed daily. The placement of containers within the racks was blocked so that each row received one replicate of each treatment in random order. After 24 hours the containers were collected from the field. The samples were processed in the lab by washing the sediments on an 0.5 mm mesh sieve and removing

all remaining animals. Significant differences were tested for by a one way ANOVA.

Cumacean Response to Azoic
Leptochelia Tubes

Whether the tubes of Leptochelia affect cumacean settlement was examined in experiments using Leptochelia tubes alone. Leptochelia were established in 14 watchglasses at a density of 5/cm² and were left for two days with constant aeration and daily changes of water. Fourteen watchglasses with azoic mud were set up in a separate tank. The Leptochelia built up dense beds of tubes in all of the containers they occurred in. All sediments were then frozen for 12 hours. Freezing killed all of the Leptochelia while leaving the tubes intact. The treatments were thawed in an 15 °C seawater bath and placed into a test tank in an alternating array of tube and non tube treatments. Upon freezing some of the Leptochelia exited their tubes (about 20-30%). These were removed from the watchglasses. However, most of the dead Leptochelia could not be collected without destroying the integrity of the tube bed. The test tank was filled with unfiltered seawater and aerated for one hour. Three hundred Hemileucon freshly collected from the field were then placed into the test tank. After one day the water in the tank was carefully siphoned off and the containers removed. The sediments of each watchglass were washed on an 0.5 mm sieve and all remaining animals were removed and counted.

CHAPTER III

RESULTS

The Benthic Community

The benthic community was dominated by peracarids, polychaetes (mostly spionids), oligochaetes, and bivalves. Peracarids were the most common crustaceans and were represented by cumaceans, tanaids, and gammarid amphipods. The two most abundant species of cumaceans were Cumella and Hemileucon. Other cumaceans that were occasionally found included Diastylus dawsoni, Diastylus sp. and Lamprops quadriplicata. The most abundant polychaetes were the spionids, of which one species, Streblospio benedicti, was predominant. All other spionids were combined and treated as one group. The polychaetes Glycera and Eteone were also commonly seen. The most abundant bivalve was Transennella tantilla, occurring in densities of up to 20,000/m². Other common bivalves included Mytilus edulis, Macoma balthica, and Clinocardium nuttallii.

Hemileucon occurred in the highest densities at sites 12 and 13 (19.2 and 21 Km from the bay entrance) in March and May (figure 6). This area was characterized by fine silty sediments with a moderately high organic content at

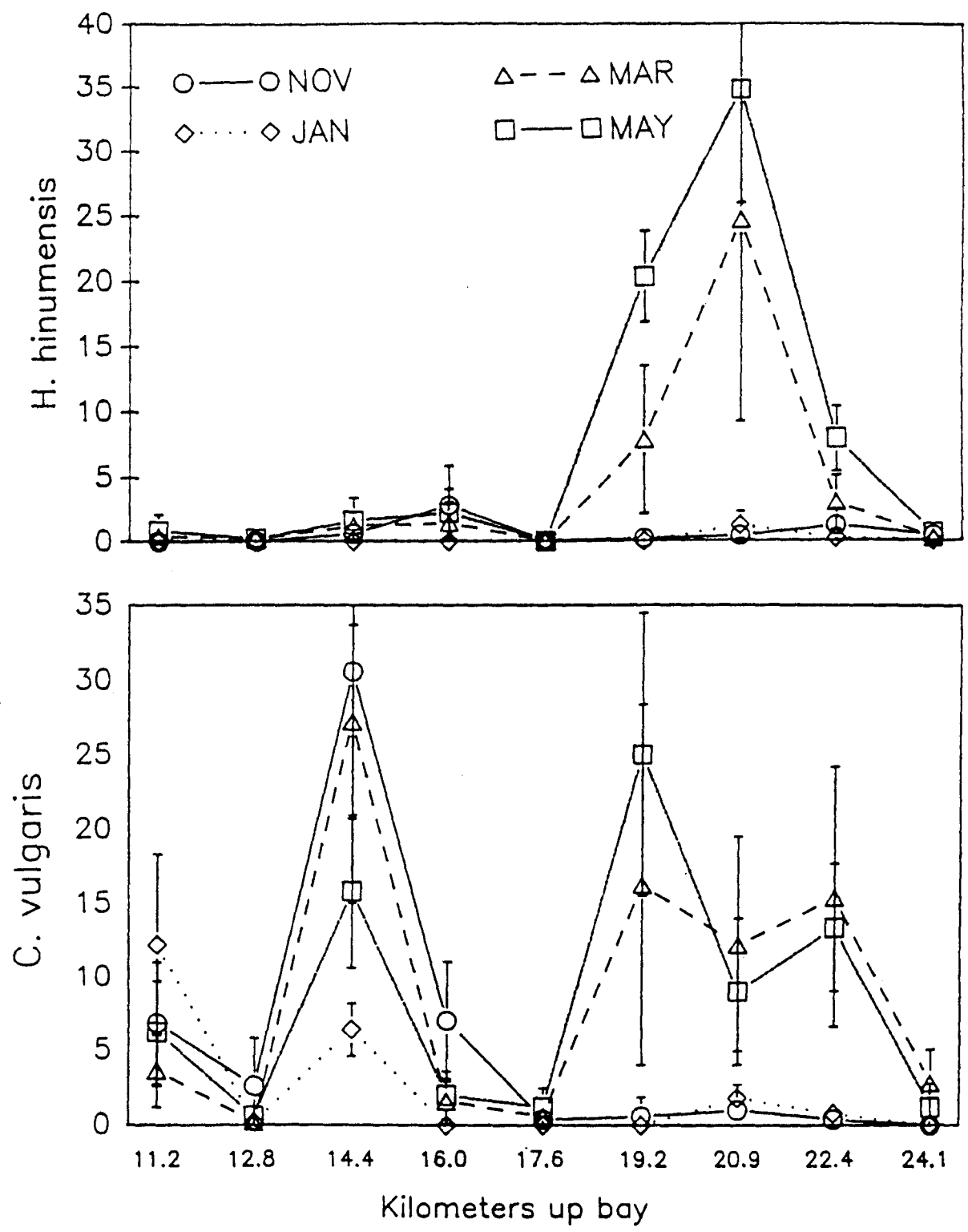


FIGURE 6. Density of *Hemileucon* and *Cumella* at nine sample sites bimonthly from November to May.

3.4% of total dry weight (table 1). The salinities at this site ranged from 10 to 15 ppt over the 6 month sampling period. Temperatures at this site were recorded between 10 to 11 °C when Hemileucon was present. The response of Hemileucon to temperature was erratic (figure 7).

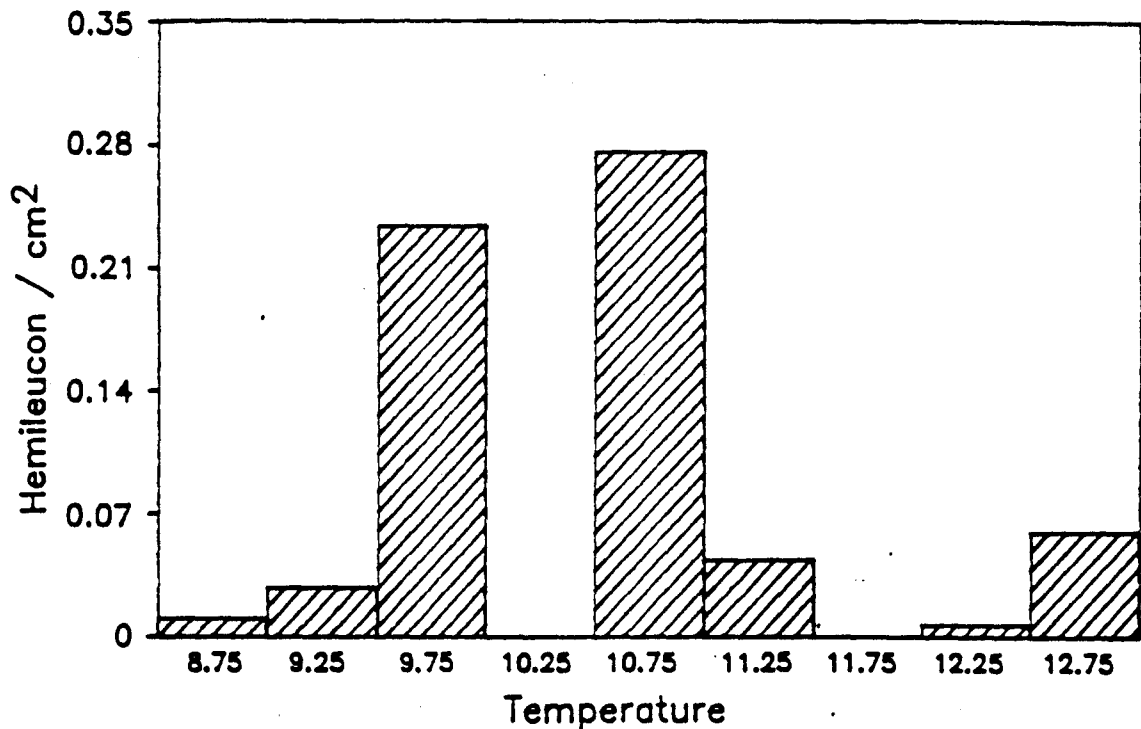


FIGURE 7. Density of Hemileucon over various field temperatures.

The other species co-occurring with Hemileucon included Cumella, Streblospio, Transennella, gammarid amphipods, and oligochaetes. One of the most interesting relationships was between Streblospio and both species of cumacean. When the numbers of Hemileucon and Cumella were plotted against the

TABLE 1. Observed Values for Salinity, Temperature, and Organic Content

| | | NOV | JAN | MAR | MAY | Average org % |
|--------------|-------|---------------|---------------|--------------|---------------|------------------|
| SITE 7 | sal | 22.0 | 29.0 | 24.0 | 32.0 | |
| | temp | 12.0 | 9.0 | 8.8 | 9.0 | |
| | org % | 1.0 | 1.1 | 0.9 | 1.0 | 1.0 ± 0.1 |
| SITE 8 | sal | 21.5 | 24.0 | 13.8 | 32.0 | |
| | temp | 13.0 | 9.5 | 9.0 | 9.0 | |
| | org % | 0.9 | 1.2 | 0.9 | 0.7 | 0.9 ± 0.2 |
| SITE 9 | sal | 21.5 | 19.0 | 16.5 | 31.0 | |
| | temp | 13.0 | 10.5 | 9.0 | 10.0 | |
| | org % | 3.6 | 3.6 | 4.2 | 3.7 | 3.8 ± 0.3 |
| SITE 10 | sal | 21.5 | 19.9 | 19.9 | 29.0 | |
| | temp | 13.0 | 10.0 | 9.5 | 9.5 | |
| | org % | 3.5 | 3.7 | 3.8 | 3.6 | 3.6 ± 0.1 |
| SITE 11 | sal | 22.5 | 17.5 | 8.5 | 28.0 | |
| | temp | 12.5 | 10.0 | 9.0 | 9.5 | |
| | org % | 1.4 | 1.4 | 1.5 | 1.6 | 5.9 ± 0.1 |
| SITE 12 | sal | 26.7 | 16.0 | 18.1 | 25.0 | |
| | temp | 12.5 | 11.0 | 10.0 | 10.0 | |
| | org % | 3.2 | 3.1 | 3.8 | 4.0 | 3.5 ± 0.4 |
| SITE 13 | sal | 22.0 | 16.0 | 12.0 | 15.0 | |
| | temp | 12.5 | 10.0 | 10.0 | 11.0 | |
| | org % | 3.0 | 3.2 | 3.3 | 3.3 | 3.2 ± 0.1 |
| SITE 14 | sal | 13.4 | 8.0 | 10.5 | 11.0 | |
| | temp | 11.5 | 10.0 | 10.0 | 13.0 | |
| | org % | 3.8 | 3.8 | 3.8 | 4.1 | 3.9 ± 0.2 |
| SITE 15 | sal | 15.5 | 2.0 | 5.3 | 10.0 | |
| | temp | 12.5 | 10.5 | 9.5 | 13.0 | |
| | org % | 5.0 | 4.7 | 4.9 | 5.3 | 5.0 ± 0.3 |
| Average temp | | 12.5 ± 0.4 | 10.1 ± 0.4 | 9.4 ± 0.5 | 10.4 ± 1.6 | |

number of Streblospio from sites 12, 13 and 14 in March and May the cumaceans were negatively correlated with Streblospio (figure 8). No other potential interactions between Hemileucon and other species were apparent.

Experimental analysis was restricted to interactions with Leptochelia. Collecting Streblospio unharmed and establishing different densities of the polychaete for experimental tests proved to be unmanageable. Leptochelia was very abundant, easily accessible and easily manipulated.

Leptochelia Bed Sampling

The mudflat sampled consisted of silt-sand sediment. The only species examined in this analysis were Cumella, Hemileucon and Leptochelia. However, gammarid amphipods, oligochaetes, polychaetes, nematodes, and copepods were also present. The highest densities of Leptochelia occurred in the first transect with up to 8 Leptochelia per square centimeter. The low densities of Leptochelia in the second and third transects indicated that the plot may have been at the edge of a Leptochelia bed (Table 2). Hemileucon and Cumella were both negatively correlated with Leptochelia (figure 9A and 9B).

Responses to Various Densities of Leptochelia

Initial results indicated that the presence of Leptochelia enhanced the settlement of both Hemileucon and

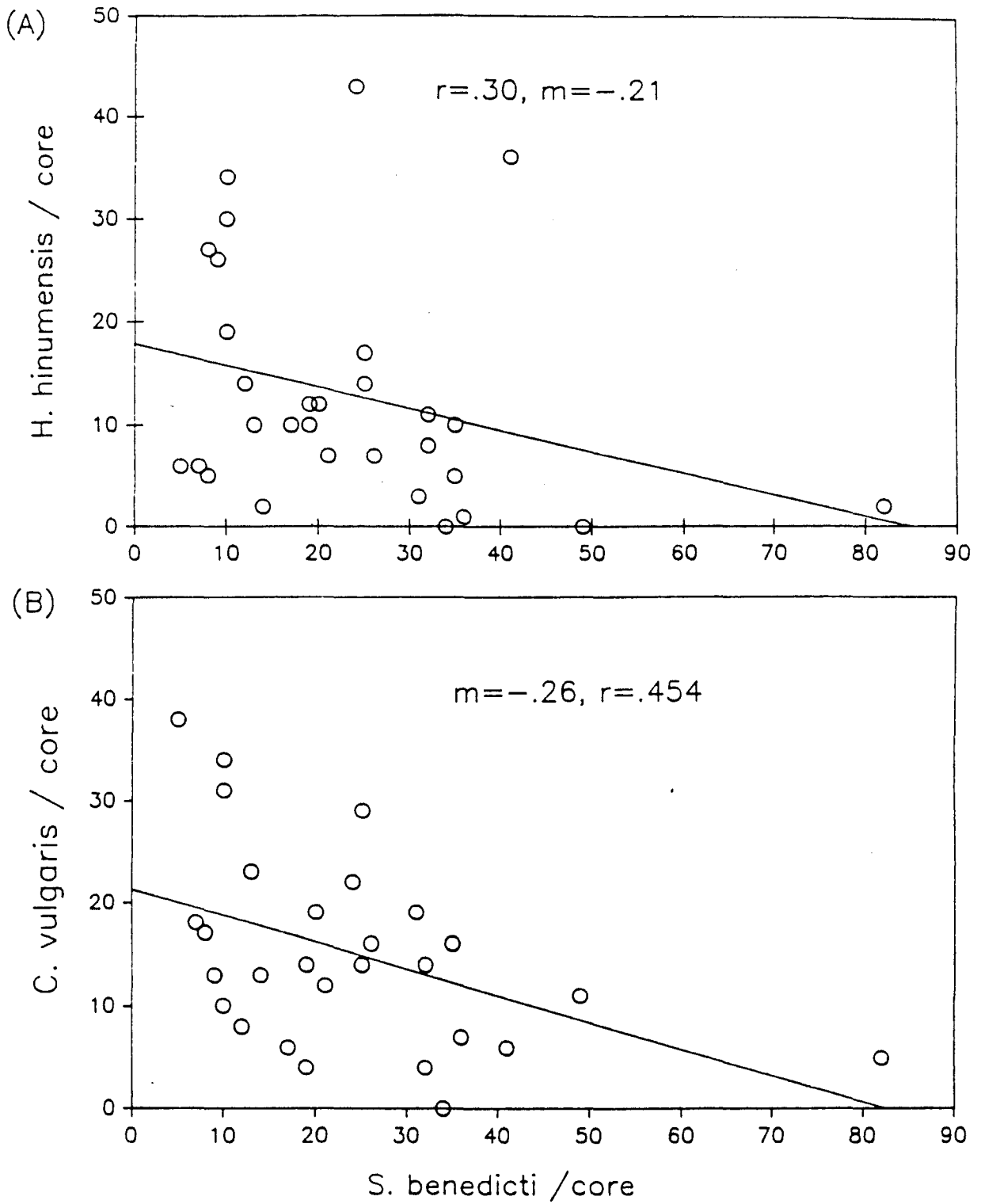


FIGURE 8. Relationship of Streblospio with Hemileucon and Cumella.

TABLE 2. Mean Densities and Standard Deviations of Cumella,
Hemileucon, and Leptochelia Over Three Transects
From South Slough

| | <u>Cumella/cm</u> ± S.D. | <u>Hemileucon/cm</u> ± S.D. | <u>Leptochelia/cm</u> ± S.D. |
|------------|-----------------------------|--------------------------------|---------------------------------|
| TRANSECT 1 | 0.08 ± 0.1 | 0.01 ± 0.03 | 1.7 ± 0.43 |
| TRANSECT 2 | 0.32 ± 0.17 | 0.20 ± 0.16 | 0.26 ± 0.27 |
| TRANSECT 3 | 0.79 ± 0.30 | 0.20 ± 0.21 | 0.23 ± 0.21 |

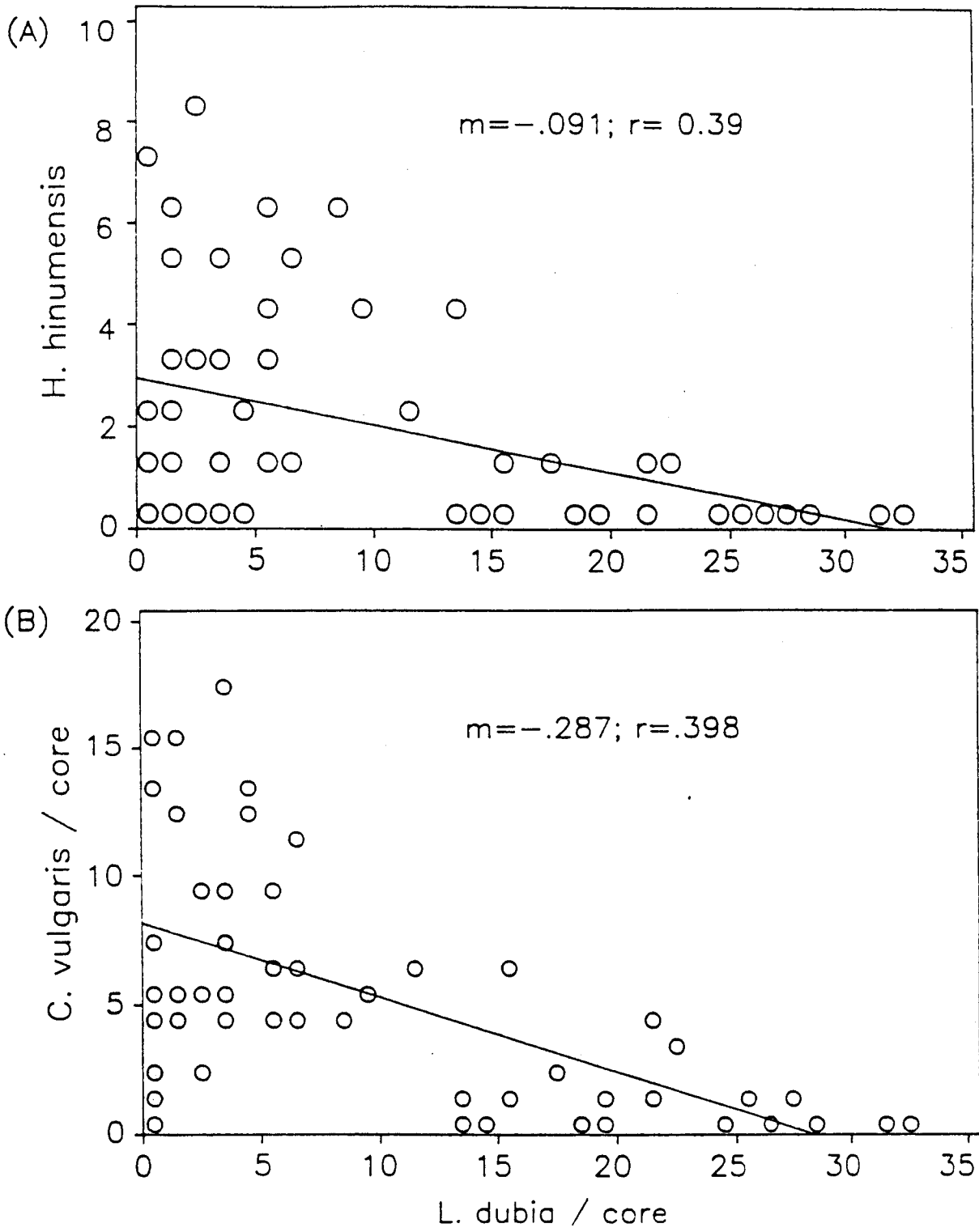


FIGURE 9. Relationship of Leptochelia with Hemileucon and Cumella.

Cumella contrary to the results from sampling the Leptochelia bed (Tables 3 and 4). In each case cumaceans settled in the Leptochelia treatment in significantly greater numbers ($p < 0.05$). The variance was high and therefore the data were Log_e transformed in order to reduce variance to mean ratios. Duplicate experiments were run for both species of cumaceans to verify the results and repeatedly the response was the same.

The first field experiment, designed to duplicate and confirm the above laboratory results, produced contradictory results. Cumella settled into the open sediment treatments at a significantly greater rate than the Leptochelia treatments (Table 4). Interestingly Hemileucon was not found in the field experimental containers even though it made up about 20 percent of the cumacean population at the site. Therefore Hemileucon's response to Leptochelia in the field could not be experimentally assessed.

Manipulation of the Leptochelia densities in the laboratory experiments made it possible to duplicate the inhibitory effect observed with high densities of Leptochelia in the field data. Both Hemileucon and Cumella settled in the moderate density Leptochelia treatment at nearly twice the numbers observed in the high density treatment (Tables 3B and 4B).

When offered four densities of Leptochelia, Hemileucon settled significantly more ($p < 0.05$) in the two intermediate and high density treatments than in the zero

TABLE 3. Settlement by Hemileucon hinumensis with Varied Densities of Leptochelia dubia. (four experiments)

| Experiment | N ¹ | <u>Leptochelia/cm</u> | <u>H. hinumensis/cm</u> ± S.D. | | p |
|--|------------------|-----------------------------|--|---------|-------|
| A. <u>Leptochelia</u> Presence/Absence (lab) | 14 14 | 0.37 2.0 | 0.68 ± 0.37 * 1.31 ± 0.8 | t=2.219 | 0.03 |
| B. High Density/Moderate Density <u>Leptochelia</u> Experiment (lab) | 14 14 | 1.6 4.2 | 1.2 ± 0.35 0.61 ± 0.56 * | t=-3.51 | 0.001 |
| C. Four density <u>Leptochelia</u> Experiment (lab) | 7 7 7 7 | 0.15 0.66 2.0 3.11 | 0.26 ± 0.16 * 0.68 ± 0.3 0.85 ± 0.28 0.63 ± 0.3 | F=6.602 | 0.003 |
| D. Azoic Tube Experiment (lab) | 14 14 | + ² - | 1.18 ± 0.4 0.9 ± 0.4 | t=1.87 | 0.07 |

* Asterisks indicate significant differences

¹ N = number of replicates per treatment

² Tubes were present (+) or absent (-)

TABLE 4. Settlement by Cumella vulgaris with Varied Densities of Leptochelia dubia. Four Laboratory Experiments, Two Field Experiments.

| Experiment | N ¹ | <u>L. dubia</u> Density (n/cm) | <u>C. vulgaris</u> Density (n/cm ± S.D.) | | p |
|--|------------------|-----------------------------------|--|--------|---------|
| A. <u>Leptochelia</u> Presence/Absence (lab) | 14 14 | 0.6 2.0 | 0.8 ± 0.4* 1.6 ± 0.7 | t=3.32 | 0.002 |
| B. High Density/Moderate Density <u>Leptochelia</u> Experiment (lab) | 14 14 | 1.1 3.7 | 1.8 ± 0.8* 0.6 ± 0.4 | t=5.14 | 0.00001 |
| C. Four Density <u>Leptochelia</u> Experiment (lab) | 7 7 7 7 | 0.4 0.6 0.9 1.3 | 0.4 ± 0.4* 2.4 ± 1.8 1.8 ± 1.4 0.3 ± 0.2* | F=6.97 | 0.002 |
| D. Azoic tube Experiment (lab) | 14 14 | + ² - | 1.2 ± 0.5 0.5 ± 0.3* | t=7.86 | 0.00001 |
| E. <u>Leptochelia</u> Presence/Absence (field) | 12 12 | 0.1 6.3 | 0.5 ± 0.2 0.1 ± 0.1* | t=4.88 | 0.0001 |
| F. Three density <u>Leptochelia</u> Experiment (field) | 12 12 12 | 0.0 1.5 6.7 | 0.4 ± 0.1 0.4 ± 0.2 0.2 ± 0.1* | F=5.35 | 0.01 |

* Asterisks indicate significant differences

¹ N = number of replicates per treatment

² Tubes were present (+) or absent (-)

density treatment (Table 3C). The identical experiment using Cumella showed a more complex result (Table 4C). Both of the two intermediate densities received significantly greater settlement than either the zero or high density treatments.

A similar variable density experiment repeated under field conditions shows a slightly different pattern that probably provides a more accurate picture of the actual relationship between cumaceans and Leptochelia. Again as in the above field experiment Hemileucon did not appear in the experimental containers in the expected densities. The results of the experiment can only describe the interaction of Cumella and Leptochelia. The relationship that showed up between Cumella and Leptochelia was negative overall. The means of the zero density and moderate density Leptochelia treatments were identical at 12.8 Cumella per container ($0.4/\text{cm}^2$). In the high density treatment the mean number of cumaceans per container was 6.08. This was significantly different ($p < 0.05$) from the two lower density Leptochelia treatments (Table 4F). Other species that also appeared in the containers included gammarid amphipods and Corophium sp. These two groups were not identified to species. The gammarid amphipods tended to increase in numbers with increasing densities of Leptochelia. The differences were significant (ANOVA, $p < .05$) and showed that not all peracarids respond the same to Leptochelia.

Response to Leptochelia Tubes

When cumaceans were provided the opportunity to settle into treatments containing only dense beds of Leptochelia tubes, without the Leptochelia, Hemileucon settled into the tube treatment at a greater rate ($p < 0.10$) than the open sediments (Table 3D). The response of Cumella was more pronounced. It settled into the tube treatment at significantly greater levels than the non-tube treatment (Table 4D).

CHAPTER IV

DISCUSSION

Hemileucon was found in the highest densities at site 13, an area of silty, organic-rich sediments, opportunistic and highly mobile species, brackish waters, seasonally variable temperatures and high disturbance. Hemileucon's distribution is dependent on a combination of these factors.

The sediment quality, in terms of grain size and the type and amount of organic material, is probably one of the most important factors governing the distribution of this species. Cumaceans generally either filter from or feed on the organic material associated with benthic sediments. The amount and quality of organic material is critical to the substrate that Cumella selects (Weiser, 1956). The amphipods, Corophium volutator (Pallas) and Corophium arenarium (Crawford) also show high sensitivity to the quality and grain size of the substrate (Meadows, 1964; 1967). Protein compounds, specifically amines and amino acids, are most effective in eliciting feeding responses from the amphipod Orchomene limodes (Meador, 1989). Therefore cumaceans probably respond to such nitrogenous compounds in a similar fashion selecting sediments based

upon the quality of the food source. A Pearson correlation matrix (Table 5) indicates that the Hemileucon is only weakly correlated with organic content.

One explanation for the weak correlation to organic content is that the amount of protein is not necessarily correlated with the quantity of organic material. If high percentages of woody materials are present then most of the carbon will be bound into cellulose and lignin. Until this wood is digested by bacteria it is unusable to macroinvertebrates. This may help explain why site 15 showed the highest amounts of organic material and yet low densities of cumaceans and other macroinvertebrates. The sediment at site 15 contained a large amount of wood chips due to the activities of wood processing industries in the area. Most of this woody material cannot be used by the benthic fauna.

Hemileucon is found in the brackish regions of Coos Bay. In its native range of Japan, Hemileucon is also found in brackish areas (Gamo 1967). Its ability to survive in low salinities may be advantageous. The low salinities may release the cumacean from competition or predation it may otherwise encounter in more saline areas (Levinton 1985). At salinities above 15 ppt the densities of Hemileucon dropped to low levels (Figure 10). This phenomenon is not due to Hemileucon's intolerance of higher salinities. It survives well in the laboratory for weeks in full salinity water (pers. obs.). In salinities below 10ppt the densities of

TABLE 5. Pearson Correlation Matrix.
Species X Organic Content.

| | ORG | CUM | HEM | GAMP | COR | SBEN | TRAN |
|------|-------|--------|-------|-------|-------|-------|-------|
| ORG | 1.000 | | | | | | |
| CUM | 0.221 | 1.000 | | | | | |
| HEM | 0.181 | 0.305 | 1.000 | | | | |
| GAMP | 0.269 | 0.433 | 0.255 | 1.000 | | | |
| COR | 0.298 | 0.499 | 0.291 | 0.404 | 1.000 | | |
| SBEN | 0.408 | -0.032 | 0.199 | 0.143 | 0.060 | 1.000 | |
| TRAN | 0.263 | 0.364 | 0.644 | 0.244 | 0.212 | 0.547 | 1.000 |

KEY: ORG = Organic Content
 CUM = Cumella
 HEM = Hemileucon
 GAMP = Gammarid Amphipod
 COR = Corophium
 SBEN = Streblospio
 TRAN = Transennella

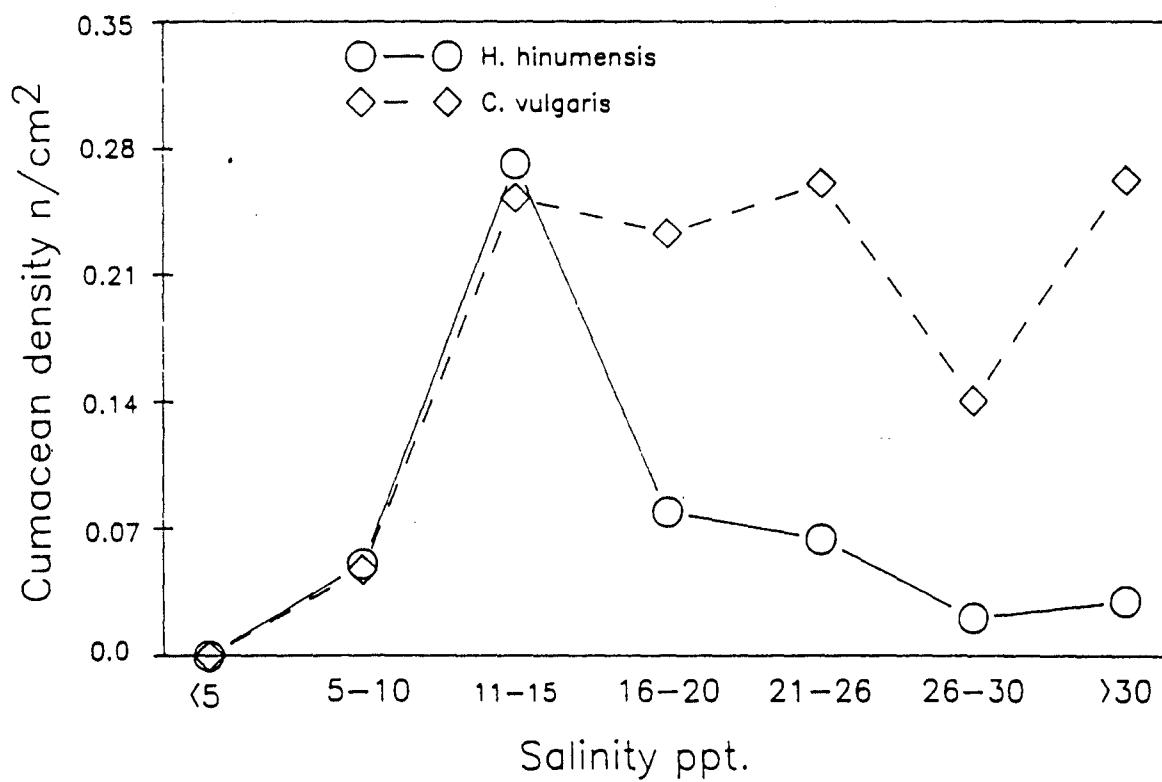


FIGURE 10. Cumacean Density vs. Salinity.

both Hemileucon and Cumella dropped dramatically. These data suggest that the distributions of both cumacean species is limited in the upper bay by low salinity.

The effects of temperature on Hemileucon's distribution were unclear. Hemileucon occurred in the highest densities at temperatures between 9.5 and 11 °C (figure 7). Its response to temperature was erratic with peaks at 9.6 to 10 °C and again at 10.6 to 11 °C. Differences in temperatures were seasonal and no changes in distribution correlating to differences in temperature were apparent.

While the overall distribution of Hemileucon in Coos Bay is probably dependent upon the above physical factors, interspecific interactions play a role as well. Hemileucon may also affect benthic successional interactions altering the normal patterns of community development and distribution. Many infaunal species have been observed to influence the distribution of other species by predation and competition (Rhoads & Young, 1970; Woodin, 1976; Brenchley, 1981; Wilson, 1984; Tamaki 1985; Committo & Ambrose 1985). Both facilitation and inhibition have been observed in benthic communities (Gallagher et al., 1983; Woodin 1976). Such species interactions can influence the successional sequences and distributional patterns of the communities on micro and macro scales (Olafsson 1986).

Species most abundant with Hemileucon include Streblospio, Transennella, Cumella, oligochaetes and in South Slough Leptochelia. The negative correlation that

exists between Hemileucon and Cumella with Streblospio and also Leptochelia may be a result of interference competition.

Streblospio tubes may affect the burrowing and feeding activities of Hemileucon and Cumella. In several studies the presence of tubes has been shown to have important effects on the distribution of mobile epibenthic species (Eckman 1979, 1981, 1983; Woodin 1976). Moderate tube densities tend to enhance cumacean settlement while high densities of Streblospio tubes interfere with cumacean presence. Densely packed tubes may prevent the cumaceans from burrowing.

It is unlikely that aggressive actions by Streblospio would inhibit cumacean settlement. Interspecific and intraspecific studies have shown that Streblospio is not territorial (Levin 1982). This finding corresponds to lab observations in which I observed that low densities of Streblospio did not appear to influence cumacean activities.

The feeding activities of Streblospio may indirectly affect cumacean settlement. Streblospio feeds on surface detritus by sweeping its tentacles across the sediment surface, or filter feeds by holding its tentacles upright in a water current (Dauer et. al. 1981). Physical disruption of cumaceans may occur by Streblospio's activities. However I have observed that a cumacean burrowed in the sediment surface does not willingly leave the sediment even after being probed with a glass rod several times (pers. obs.).

Although some spionid polychaetes have been shown to be

predators (Tamaki 1985) predation by Streblospio on cumaceans is unlikely. Streblospio has not been shown to be a predator and adult cumaceans are relatively large (5mm) and highly mobile. This is not a species that Streblospio could capture. Other benthic predators such as the polychaetes Nereis and Glycera have not been shown to affect Cumacean densities (Ambrose 1984). Cumacean larvae may be more vulnerable to predation. The young are released in the well developed manca stage. Essentially miniature adults, immature cumaceans are active and free swimming. Chances are they could not be preyed upon by Streblospio either.

Like Streblospio, Leptochelia makes dense beds of tubes in the surface mud. Data from a dense population of Leptochelia in South Slough showed a negative relationship with both species of cumaceans similar to the relationship with Streblospio (figure 9). It seems likely that the responses of cumaceans to both Streblospio and Leptochelia have a similar functional basis.

Initial laboratory experiments showed positive responses of both Hemileucon and Cumella to the presence of Leptochelia (tables 3 and 4). These results were contrary to the field data (figure 9). It may be that cumaceans find the reworked sediments provide a food source and/or the intertube spaces serve as a protective refuge for the burrowing cumaceans. The sensitivity of cumaceans and other peracarids to sediment conditions (Weiser 1956; Meadows, 1964) suggests that subtle changes in the sediment

composition due to the activities of Leptochelia may greatly influence the rate at which the cumaceans settle. The positive interaction between Leptochelia and cumaceans also suggests that Leptochelia do not actively defend territories from cumaceans. Individual Leptochelia did not aggressively respond to the presence of cumaceans when observed through a microscope (pers. obs.). Alternatively, cumaceans did not appear to disturb either the Leptochelia or the tubes that they had been built. This supports the hypothesis that relatively small bioturbators are unable to affect tube dwellers (Dewitt and Levinton 1985).

When a similar Leptochelia presence experiment was performed in the field, the cumaceans settled into open sediment containers at a greater rate than in Leptochelia treatments (Table 4 E). This was contrary to the above results. The major difference between Leptochelia treatments from the laboratory and field experiments (other than location) was the high densities of Leptochelia used in the field experiments ($5/\text{cm}^2$) and relatively moderate densities used in the lab ($1/\text{cm}^2$). The differences in cumacean settlement may be explained by Leptochelia densities.

Under laboratory conditions, both facilitation and inhibition of cumacean settlement in the same experiment could be produced by manipulating the Leptochelia density (Table 3 B-C and Table 4 B-C). Greater settlement occurred in intermediate densities of Leptochelia while open sediments did not attract cumaceans and high densities had

an inhibitory effect (Tables 3C and 4C). Crowe et al. (1987) showed comparable settlement patterns using different densities of ophiuroids and bivalves. This shows that a density dependent interaction exists between Leptochelia and Hemileucon.

Field experiments showed that there was little difference in settlement of Cumella between the zero and moderate densities of Leptochelia (Table 4F). However, settlement was reduced by high densities of Leptochelia (Table 4E-F). The high degree of settlement into the open sediment treatment could have resulted from competition. Under natural conditions unoccupied sediments may be rare and quickly colonized when found. Inhibition at high densities is probably due to the same reasons explained above, interference competition, individual aggressive interactions, or reduced amounts of food material in the Leptochelia bed. The reason why Hemileucon did not settle in the field experimental containers, even though they comprised 20 to 30 % of the benthic cumacean population, is not apparent. Hemileucon vertically migrate in laboratory tanks (pers. obs.). Therefore, the height of the field containers was probably not a barrier.

Leptochelia may not actively inhibit the presence of cumaceans, however, cumaceans do respond to the presence of biogenic structures. Settlement by cumaceans was significantly greater in azoic Leptochelia tubes (Table 3D and Table 4D) even though the tube density was the same as

that which inhibited the cumaceans when Leptochelia were present. Possibly the presence of live Leptochelia inhibited cumacean settlement in the previous experiments. However, the lack of an aggressive response by Leptochelia against cumaceans when viewed under the microscope makes this seem unlikely. The processing of the Leptochelia tube treatment by freezing may have caused some alteration in the integrity of the mucous that binds the intertube sediments. After freezing, the intertube sediments appeared to be more easily displaced. Normal tubes have mucous associated with them that binds the intertube sediment into a mat-like consistency. Altering this could have made burrowing easier for the cumaceans allowing them access into these substrates. Also many of the dead Leptochelia could not be removed from their tubes without disrupting the integrity of the tube structures. The dead bodies of Leptochelia may have attracted cumaceans even though the experiment was performed as quickly as possible after freezing to keep the Leptochelia from deteriorating too much.

CHAPTER V

CONCLUSIONS

1. Salinity affected the upper distribution of both species of cumacean similarly. At between 5 to 10 ppt the numbers of both cumaceans dropped to near zero. While in this study the numbers of Hemileucon also decreased dramatically at higher salinities (figure 10), lab data suggests that Hemileucon can easily tolerate high salinities.

2. The response of Hemileucon to different temperatures was erratic. It was found in the densest concentrations at 10 and 11 °C.

3. Most of the macrobenthic species studied showed only weak correlations with organic content. Streblospio showed the highest correlations followed by gammarid amphipods, Cumella, and Hemileucon the last was only weakly correlated.

4. Hemileucon showed a negative response to the presence of the spionid polychaete Streblospio and the tanaid crustacean Leptocheilia. Its response to the presence

of other benthic species was unclear. Cumella also showed a similar response to the presence of Streblospio and Leptochelia.

5. Further investigations into the interaction of Hemileucon with tube dwelling species indicated that the observed negative relationships in the field may involve more complex behaviors. Depending upon the density of the Leptochelia the settlement of Hemileucon into experimental containers was either facilitated or inhibited. Facilitation was observed at low to moderate densities and inhibition occurred at high densities. The response of Hemileucon to dense azoic tubes suggests that inhibition occurs because of direct interactions of the individual animals or that intertube mucus that binds sediments may have some affect.

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