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A Multivariate Characterization of Assemblages of Planktonic Mysids Decapods and Sergestids in the Chesapeake Bay Mouth Area

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A MULTIVARIATE CHARACTERIZATION OF ASSEMBLAGES OF PLANKTONIC MYSIDS, DECAPODS, AND SERGESTIDS, IN THE CHESAPEAKE BAY MOUTH AREA

by

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ABSTRACT

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OF ASSEMBLAGES OF PLANKTONIC
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John Charles Seibel
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Director: Dr. Raymond W. Alden III

This study is the first to focus on the assemblages of the planktonic mysids, decapods, and sergestids found in the lower Chesapeake Bay. The assemblages of these organisms in the lower Chesapeake Bay and nearby shelf were characterized using three different statistical approaches, and the methods used were evaluated for their effectiveness at delineating ecologically meaningful assemblages. Three stations were sampled across the Chesapeake mouth and one offshore, with oblique and neuston net tows. Twenty-seven larval stages, representing at least 23 species, were found in sufficient numbers to be analyzed statistically. The statistical approaches were each based upon a different initial clustering analysis: 1) the divisive VARCLUS analysis; 2) the ANOVA-based partitioned agglomerative approach of Williams and Stephenson (1973); and 3) the Canberra metric: a commonly used representative of traditional agglomerative clustering analyses. The VARCLUS analysis was by far the most successful at suggesting species associations, followed by the

Williams and Stephenson analysis, which was primarily useful as a summarization of major temporal and spatial patterns. Major species associations included *Uca* spp. and *Upogebia affinis* zoea; juveniles and adults of two mysid species (*Neomysis americana* and *Mysidopsis bigelowi)*; and associations between larval stages of *Callinectes* and *Squilla*. Major seasonal patterns found were the abundance of *Cancer irroratus* and *Crangon septemspinosa* in the spring, the predominance of decapod larvae in the late summer, and the fall and spring migrations of the two mysids. The major spatial pattern was the prevalence of the larvae of most taxa in oblique samples from the bay mouth. The multivariate methods proved most useful as data summaries, providing different perspectives for exploration and hypothesis generation.

DEDICATION

To Jo

ACKNOWLEDGEMENTS

I thank the many individuals who made my study possible. I begin with my major advisor, Dr. Raymond W. Alden III. His guidance throughout my graduate career is much appreciated, I learned much working with him. I also thank the other two members of my committee: Dr. Daniel M. Dauer and Dr. Cynthia M. Jones. Both of these individuals were very giving of their time and expertise. I also benefitted from the statistical knowledge of Dr. James Matta.

The data I analyzed were from a plankton monitoring program, and were the result of long hours and a lot of hard work by many people. I thank Mr. Robert J. Young and Dr. Arthur J. Butt, both of whom served as project managers of the program. I thank the crews of the R/V *Zoea*, the NOAA R/V *Laidley*, and the COE R/V vessel *Mobjack*, and I single out the field sampling efforts of Mr. John Leslie, Mr. Anthony Rodi, and Mr. Dean Devereaux. I thank the taxonomists who spent many long hours on the microscope, especially Mr. Ken Kemidy, Ms. Donna VanKeuren, Ms. Jean Stankovich, Ms. Jacqueline Annis, and Mr. Anthony Rodi. I also thank my colleagues who managed the data, Mr. David Wade, Mr. Dennis Lundberg, and Ms. Martha Norris.

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Finally, I gratefully thank my parents, my wife's parents, and especially my wife, Jo. Jo's support throughout my graduate career has been remarkable.

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INTRODUCTION

Mysids, decapods, and sergestid shrimps are all members of the crustacean sub-class Eumalacostraca (Barnes, 1980), a group whose early life stages comprise an important component of the estuarine and coastal macrozooplankton communities. Mysids are commonly captured in macrozooplankton samples from the Chesapeake Bay (Birdsong, 1991), are important in the diet of estuarine fishes (Hopkins, 1965), may play a major role in the structuring of holoplankton communities (Fulton, 1982), and act as a link in the recycling of detrital material (Zagursky and Feller, 1985). Decapods, the common shrimps, crabs, and lobsters, are among the best known and well-studied estuarine and coastal fauna, with numerous species found in the Chesapeake Bay (Wass, 1972), as well as along the entire Atlantic coast of the United States (Williams, 1984). Also, larval decapods are very abundant seasonally in the plankton of the Chesapeake and Delaware Bays, and in the coastal estuaries of North Carolina (Birdsong, 1991; Epifanio, 1988; Sandifer, 1975; Williams, 1971). In addition to their ecological importance, some decapods are commercially valuable, for example, the blue crabs and rock crabs are the bases for fisheries in the mid-Atlantic and in the northeastern coastal areas of the United States, respectively. Sergestids, while not as well studied as mysids or decapods, are common to abundant in the shallow waters of estuaries (Woodmansee, 1966).

While the planktonic stages of these eumalacostracans have been extensively studied in the estuaries of the mid-Atlantic coast, there has not been a study of assemblages of these organisms. Because of the preliminary nature of this study, I am using the term assemblage, and specifically avoiding the term community. The term community is used to describe groups of interacting organisms (Whittaker, 1975), and information on the interactions among the Chesapeake Bay's planktonic eumalacostracans is not available. Also, when I use the term association, I am referring to the degree of correlation (not necessarily statistical correlation) between two or more taxa's abundances.

Multivariate statistics are the method of choice for the study of assemblages as they offer an objective way to characterize assemblages of species, and thus serve as a mechanism to generate hypothesized associations for future directed studies (Green, 1980). While a few of the most abundant eumalacostracans have been included in the multivariate statistical analyses of the zooplankton monitoring program of the Chesapeake Bay Program (Birdsong, 1991), the emphasis of these analyses has been the holoplankton, and those few eumalacostracan plankters that were included represented a small subset of those commonly found in the Chesapeake Bay. There have also been studies done in the Chesapeake Bay, which included several larval decapods (Sandifer,1975,1973; Goy, 1976; Sadler, 1983; Johnson, 1985; Maris, 1986). However, only one (Maris, 1986) included an analysis which examined the intercorrelations of these organisms, and multivariate methods were not used in this study. Holt and Strawn (1983), working in the western Gulf of Mexico, have

published the only multivariate analysis which focused on this important component of the plankton.

A multivariate assemblage analysis begins with an examination of the groups of species encountered during the study, and cluster analysis is the preferred statistical method to find such groups, when none are known *a priori* (Manley, 1986). Cluster analysis can be used to group species with one another, based upon shared preferences for sites, seasons, or combinations of both. It may also be useful, for example, to cluster sites based upon similar species composition (*ie* most of the same species are found at each site within a cluster of sites, and in like numbers). Clustering of sampling sites may be done solely to identify ecologically similar areas, or it may be part of a nodal analysis which is used to further delineate the spatial patterns of groups of species (Boesch, 1977).

There are many different types of clustering methods, each having distinct properties - some of which may prove more useful with certain types of data than with others. While various methods have been commonly used and evaluated in marine ecology for the examination of benthos (*eg* Boesch, 1973), holoplankton (*eg* Angel and Fasham, 1973, 1974; Cassie, 1963), and phytoplankton (*eg* Kaneta *et al*, 1985), these organisms do not exhibit the extreme seasonality of the eumalacostracan plankton, where larvae can be extremely abundant during the peak of the spawning season and absent during the rest of the year. Therefore, the properties understood for these statistical methods as applied to non-eumalacostracan organisms are not necessarily the same properties as those for eumalacostracans. Because of the highly

seasonal nature of eumalacostracans, the wide variety of available clustering methods, and because only one multivariate statistical study has been published for these organisms, a variety of approaches is indicated. The use of multiple approaches has three advantages: 1) if two or more of the approaches show the same pattern, then the pattern is more likely to be real (Green, 1979); 2) if one or more of the approaches fail, that is, an approach is not supported by diagnostic analyses, then one or more of the remaining approaches may be useful and all is not lost; and 3) distinct approaches offer distinct viewpoints of the data, and this diversity of result, when each viewpoint is carefully evaluated by diagnostic analyses, can be advantageous in suggesting useful and interesting hypotheses for future studies.

Replication in the field and proper subsampling in the laboratory are important for any study involving quantitative analysis of the data. Field replication leads to known confidence in estimates of abundance, while subsampling is done rather than completely enumerating a sample in order to save time and money, and is especially important when surveying a number of species. However, traditional subsampling methods, such as the use of a Folsom splitter or Stempel pipet can lead to different levels of precision for rare and abundant species. This is due to different levels of enumeration effort, in a given subsample more individuals of an abundant species are counted. The Coefficient of Variation Stabilization (CVS) method corrects for this problem (Alden *et al*, 1982).

Assemblages of estuarine planktonic eumalacostracans are numerically dominated by larval and juvenile forms, leading to the extreme seasonality discussed

earlier. To maintain populations, estuarine organisms with planktonic stages must possess mechanisms to insure that these stages are not transported from the estuary and lost forever. Therefore, retention or re-invasion mechanisms for estuarine plankton are important, and this has long been recognized (*eg* Ketchum, 1954; Rogers, 1940). Since plankton cannot swim horizontally and fight the currents of outflowing estuarine surface waters, they must vary vertical position in a strategic manner over the course of a day, a tidal cycle, or throughout their larval development, to maintain estuarine populations. Thus, a major objective of many past studies of decapod larvae of the Chesapeake Bay has been to establish the dispersal-recruitment strategy employed by a species (Johnson, 1985,1982; Maris, 1986; Sandifer, 1975,1973; Goy, 1976). I will be referring to dispersal-recruitment strategies, because they effectively summarize the complicated patterns of movement during an organism's planktonic larval development.

Two studies which categorized dispersal-recruitment patterns for larval decapods of the Chesapeake Bay were conducted by Johnson (1982) and Maris (1986). Johnson used three categories to describe early decapod life histories in his work on brachyuran megalopae: 1) retained estuarine - larvae remain in the estuary throughout development; 2) expelled estuarine - larvae pass out of the estuary, and return at some stage of development; and 3) retained shelf - larvae are released on the shelf, and remain there throughout development. Maris (1986) expanded this to six classes (splitting Johnson's retained estuarine category in thirds, and his expelled category in two): 1) retained estuarine - larvae develop entirely within the estuary;

2) retained estuarine-transitional - larvae are released and develop in the estuary's mouth area; 3) retained transitional-nearshore - larvae develop outside of the bay mouth, in the nearshore area; 4) retained offshore - development takes place entirely on the shelf; 5) expelled with estuarine spawning - larvae are released well within the estuary, pass out of the estuary, and return to the estuary at a later stage of development; and 6) expelled with transitional spawning - larvae are released in the estuary's mouth area, develop offshore, and return at a later stage of development. In this paper I will be using Maris's (1986) categories as summaries of early life histories, recognizing that as more is known about the early life history of eumalacostracans, more distinctions will be possible. However, Maris's categories offer a sufficient level of resolution for my purposes.

In addition to using these hypothesized mechanisms as summaries of early life-history spatiotemporal patterns, this study can also qualitatively support or not support a hypothesized recruitment mechanism. For this study to offer a quantitative test, it would need to include lower Bay sampling, as well as additional offshore sampling. However, certain general patterns can be expected, given the hypothesized early life-history strategies, this study's sampling regime, and the circulation of water in the Chesapeake Bay mouth area (Table 1).

In order to understand Table 1, its components must be understood: the life-history strategies, this study's sampling regime, and the circulation of water in the bay mouth area. The early life-history strategies were summarized above. The sampling regime of this study consisted of three stations across the bay mouth, and

Table 1. Expected dispersal-recruitment spatiotemporal patterns for this study, using Maris's six dispersal-recruitment strategies. Expected patterns for dispersal-recruitment strategies are a function of the Chesapeake Bay's circulation, and the placement of this study's stations (see text for details).

Dispersal-recruitment pattern	Neuston vs. Oblique	Mouth vs. Offshore	North vs. South Mouth
retained estuarine	oblique	mouth	primarily south
retained estuarine-transitional	both, but primarily oblique	both, but primarily mouth	primarily north
retained transitional-nearshore	both, but primarily oblique	both, but primarily mouth	primarily north
retained offshore	oblique	offshore	north, if at all
expelled with estuarine spawning	both	primarily mouth, but with significant number offshore	primarily north
expelled with transitional spawning	both, neuston as abundant as oblique	both	primarily north

one 20 km offshore. Each of these stations was sampled using two different types of plankton gears (with the same net mesh): a bongo-net which was towed obliquely (sampling the entire water column), and a neuston net which was towed across the surface of the water. The circulation in the Chesapeake Bay mouth is two-layered (Boicourt, 1982). The low salinity estuarine water flows out on top of a wedge of denser, more saline, oceanic water from the nearby shelf. Due to the Coriolis force, both the estuarine and the oceanic waters bear to their right. This leads to oceanic waters flowing primarily into the northern bay mouth, and the outflowing estuarine waters flowing south on the nearby shelf. This nearshore southern flow is modified during the late summer, when winds offshore are from the south, keeping surface water from flowing south (Leming and Johnson, 1986). These winds are important to the retention of blue crab larvae to the Chesapeake Bay, as blue crab larvae are released at the bay mouth, develop in the surface waters of the shelf, with later stages re-invading the bay (Maris, 1986). Without this wind from the south in the summer, and the positioning of the blue crab larvae at the surface, the later stages of the blue crab would flow south with the prevailing currents and be lost to the blue crab population of the Chesapeake Bay.

Therefore, based upon this study's sampling regime and the water's circulation, I expect to find the larvae of an organism with a retained estuarine dispersal-recruitment strategy to be primarily in the oblique tows of the bay mouth (Table 1). I do not expect to find them offshore, nor do I expect to find them in the mouth neuston layer, because they would be carried offshore. I expect to find them

predominantly in the southern waters, because the estuarine waters flow out mainly through that end of the mouth. For reasons similar to those for the retained estuarine larvae, I expect to see those larvae retained offshore to be mostly in the oblique tows of the offshore station. These larvae have no need to be in surface waters, as would the blue crab, for example, because their adults are not estuarine. This study's lack of stations between the offshore station and the bay mouth stations prevents me from distinguishing between species with retained estuarine-transitional and retained transitional-nearshore strategies. I can expect to see larvae of both types primarily in mouth oblique tows, because the mouth stations of this study are closer to these areas. I can also expect to see larvae of both types primarily at the northern end of the bay mouth, as both types of larvae have nearshore distributions, and may be brought into the bay. Larvae in the two expelled categories would be expected to share a pattern of a primarily northern mouth distribution, as they may also be brought into the bay. While both can be expected to be found offshore, the expelled with estuarine spawning larvae would be more likely to be abundant at this study's relatively distant offshore station.

In addition to the multi-species surveys in the Chesapeake Bay, there has been a long-term multi-species survey of macrozooplankton in the estuaries of North Carolina which resulted in several publications including one concerning brachyuran larvae (Williams, 1971) and one about mysids (Williams, 1972). In addition, there have also been several specialized studies focusing on one to a few species of larval decapods from the Chesapeake and Delaware Bays. The early life history of both

Callinectes and *Uca* were recently summarized by Little and Epifanio (1991), based upon several specialized studies in the Chesapeake and Delaware Bays. *Rhithropanopeus* has been the subject of both specialized field surveys (Lambert and Epifanio, 1982) and laboratory studies of the behavioral basis for vertical migration (Cronin and Forward, 1982). *Ovalipes oscellatus* was studied on the continental shelf near the Delaware Bay by Epifanio (1988) as part of a three species project, along with *Callinectes* and *Uca*. Dittel and Epifanio (1982) studied the recruitment patterns of fifteen species of crab larvae, by investigating their seasonal and vertical distributions. Species of special focus were *Cancer irroratus*, *Ovalipes oscellatus*, *Pinnixa chaetopterana*, *Pinnixa sayana*, and *Callinectes* spp.

In this study, three multivariate approaches were taken to characterize eumalacostracan communities from the Chesapeake Bay mouth and nearby shelf. Each of these three approaches was based upon a wholly different type of clustering analysis. The first method, the Canberra metric, is a well-respected distance metric, and I am using it as a representative of the agglomerative clustering analyses: as a group, the most commonly used clustering methods in marine ecology (Boesch, 1977). The second method, proposed by Williams and Stephenson (1973), which I will refer to as W&S, is a unique agglomerative technique which segregates the variance into temporal and spatial factors, an approach that is potentially useful for highly seasonal data. The third method is the VARCLUS method, a widely available divisive technique (SAS, 1989). The results from each of these three multivariate

statistical techniques were evaluated through the use of supporting statistics and graphics.

I have two objectives:

1) To characterize the assemblages of eumalacostracan plankton (*ie* mysids, sergestid shrimps, and larval decapods) in the Chesapeake Bay mouth area:
   a) to identify assemblages of species;
   b) to delineate the spatial and temporal patterns of these assemblages;
   c) to characterize the physicochemical characteristics of the plankter's habitats; and

2) To evaluate these clustering approaches, suggesting the best method(s) for future investigations of eumalacostracan assemblages. Evaluation criteria include:
   a) accuracy of the final result (*ie* do simple diagnostics of individual species's spatiotemporal patterns support the multivariate descriptions?);
   b) ease of interpretation, and usefulness as summarization of individual species patterns (*ie* do accurate multivariate

methods save effort when compared with exhaustive and subjective species-by-species evaluations?).

METHODS

Field

From March of 1982 through December of 1983, three stations were monitored in the mouth of the Chesapeake Bay, along with a fourth station 27 km offshore (Figure 1). Physical measurements, and replicated neuston and oblique plankton tows were taken approximately once per month, resulting in 19 cruises during the period of study. While on station, salinity, temperature, and dissolved oxygen were measured one meter below the surface and one meter above the bottom. Salinity and temperature measurements were taken using a Beckman RS-5 induction salinometer, while dissolved oxygen was measured using an air calibrated YSI probe. Four sequential replicate samples were collected from the neuston, using a flow-metered 355μ mesh net mounted on a rectangular (1.28m x 0.30m) frame. On average, half of this net was submerged, giving a frontal area of 0.1905m^2. Two sequential replicate oblique tows, each using a bongo unit with two one-half meter diameter nets (0.1964 m^2 per net), were also made at each station. Like the neuston net, each of the two one-half meter oblique nets had a mesh-size of 355μ.

Figure 1. Map of study area indicating stations. Each of the four stations was sampled using both oblique and neuston tows, resulting in eight sites.

Chesapeake
Bay
North Mouth
Middle Mouth
South Mouth
Off
Shore
0 4 8km
N

Laboratory

In the laboratory, the replicates were separated into four size classes using 2000μ, 850μ, 600μ, and 300μ sieves. All samples were split and counted so that abundant and less common organisms would have equal variance, using the coefficient of variation stabilization (CVS) method of Alden *et al* (1982). Species were identified to the lowest possible taxonomic level.

Analysis of Taxonomic Data

Site designations. Two locations, neuston and below neuston, were sampled at each of the four stations of this study. The resulting eight combinations of station and location (portions of water column sampled with neuston tow or oblique tow) were treated in all statistical analyses as separate sites. Thus, in this paper, site refers to a combination of station and net tow-type. These combinations were used in order to obtain an objective view of areas of similar species composition. For example, it would allow a cluster analysis to group the neuston samples from one station with the oblique samples taken at another station. This flexibility is important when dealing with species with recognized movements between the neuston layer of one area and the lower water column (sampled by oblique tow) of another, as in the case of *Callinectes* spp., where a pattern of movement between the neuston and the remainder of the water column is known (Maris, 1986; McConaugha *et al*, 1983).

The eight sites in this study and the abbreviations used are: southern mouth oblique (SM_O), southern mouth neuston (SM_N), middle mouth oblique (MM_O), middle mouth neuston (MM_N), north mouth oblique (NM_O), north mouth neuston (NM_N), offshore oblique (OS_O), and offshore neuston (OS_N).

Initial Calculations. For each taxon, the size class splits and counts were combined with the flowmeter readings to determine the number of each size class per cubic meter. The size class densities for each taxon were then summed, and this total was used for most statistical analyses. All data analyses were performed upon $\log(x+1)$ transformed data, except for the percent occurrence/abundance portion of the taxa reduction.

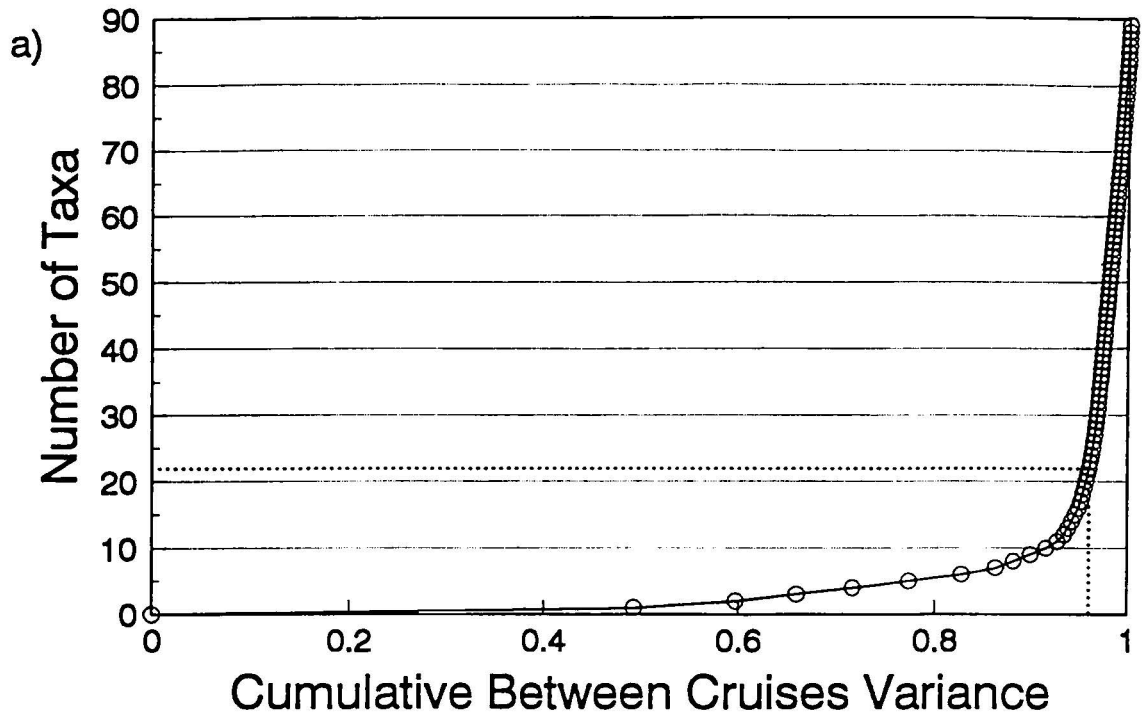
Taxa Reduction. The taxa reduction was performed using the consensus of three independent screens. Two of these screens were taken from the method of Williams and Stephenson (1973), and the third is a percent occurrence/abundance based reduction.

The W&S taxa reduction method is composed of a site screen and a cruise screen. In the site screen, those few taxa which cumulatively explain most of the variance between sites are retained, and likewise for the cruise screen. This method was modified for this study by using a graph of the cumulative variance, rather than the 1% cut-off recommended by the authors. In this graphical modification, once the variance per taxa is obtained, the taxa are sorted in descending order by variance

explained, and the cumulative variance is calculated. The number of taxa is plotted against cumulative variance, resulting in a curve which begins with a small positive slope and ends with an exponential rise (Figures 2a and 2b). The region of small positive slope corresponds to the few taxa which typically explain the bulk of the variance, and the exponential increase in the number of taxa necessary to explain the next increment in variance represents the inclusion of the many taxa which individually explain very little variance. The taxa corresponding to the part of the curve just before the exponential rise are retained for further analyses.

The percent occurrence/abundance method is begun by finding the percent occurrence of each taxa at or above a series of planktonic abundances: zero to 20/m^3 in 0.5/m^3 increments was used in this study. Then these percent occurrences are compared with a series of percent occurrences. In this study, a series of percent occurrences from 0 to 50% in increments of 2.5% was used. Counts are then made of the number of taxa meeting or exceeding each combination of abundance level and percent occurrence. The resulting three variables: number of taxa, density, and percent occurrence are plotted against one another (Figure 3). Because a subset of taxa account for most of the high abundances observed, this surface has a plane of low positive slope followed by an exponential rise. The taxa represented by the plane of low positive slope are those which occur most often in highest number, and these taxa are retained when using this method. The increments for the planktonic abundance and percent occurrence series used for a particular data set are chosen by trial and error to give a three-dimensional surface of sufficient resolution to choose

Figure 2. Plots used for Williams and Stephenson method of taxa reduction: a) variance between cruises, b) variance between sites. For both the cruise and site reductions, variances were calculated for each taxa. Taxa were then ranked from highest to lowest variance, and cumulative variance calculated. Number of taxa was plotted against cumulative variance. The number of taxa to retain (keeping taxa ranked at or above that number) was that number corresponding to the rapid rise in the curve (see dotted reference lines). In this manner, those taxa explaining the bulk of the inter-cruise and inter-site variances were kept.


a)
Number of Taxa
90
80
70
60
50
40
30
20
10
0
0
0.2
0.4
0.6
0.8
1
Cumulative Between Cruises Variance

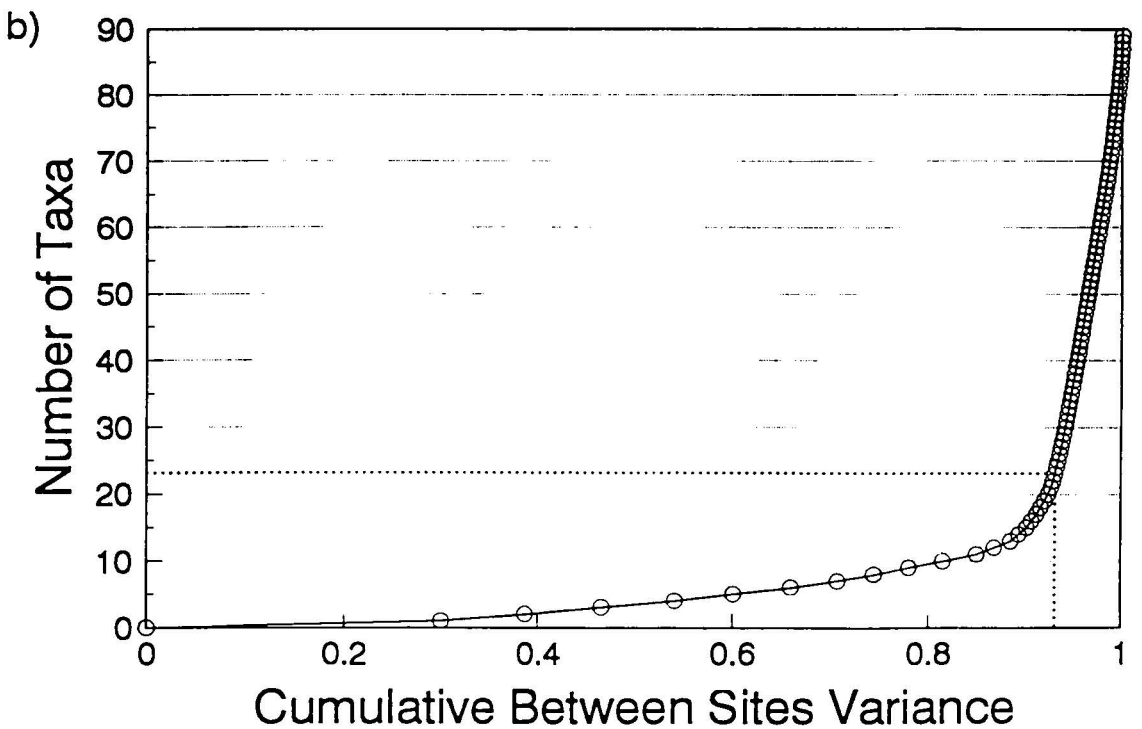
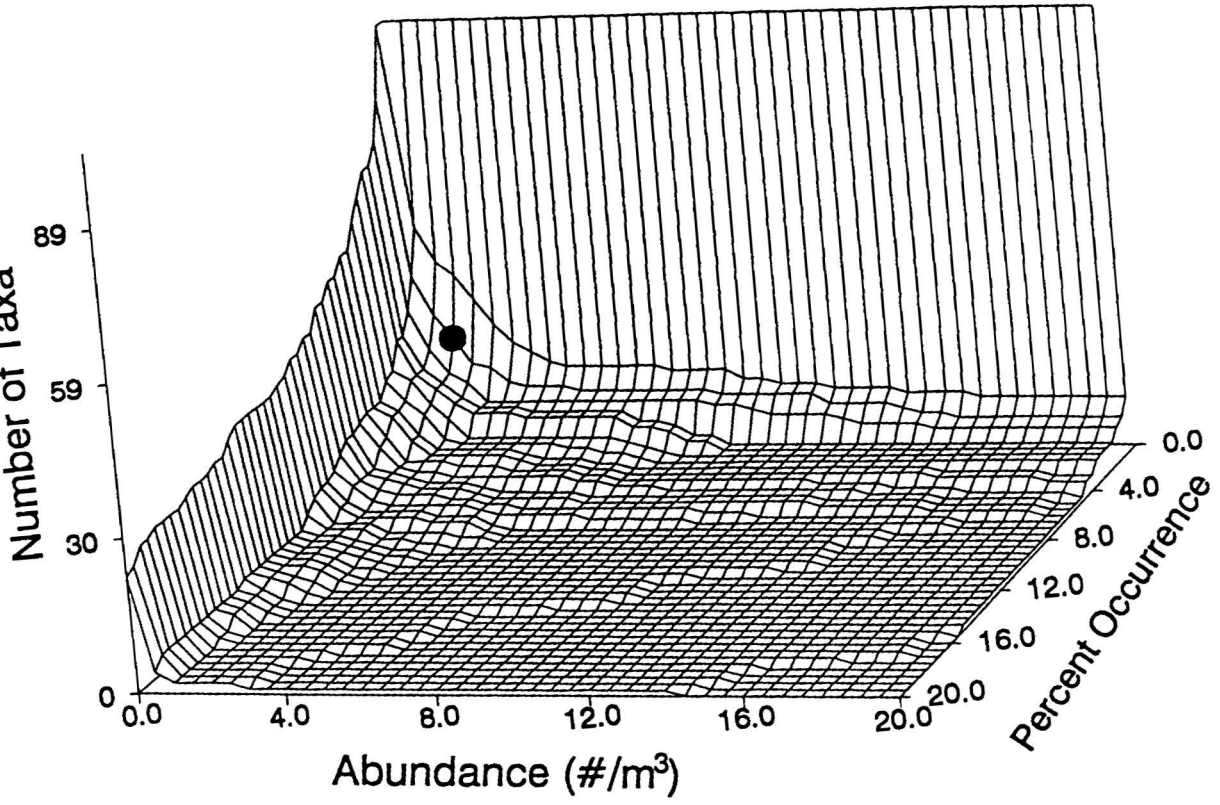

b)
Number of Taxa
90
80
70
60
50
40
30
20
10
0
0
0.2
0.4
0.6
0.8
1
Cumulative Between Sites Variance

Figure 3. Plot used for percent occurrence reduction. Each point on the surface represents the number of taxa exceeding the corresponding percent-occurrence/abundance combination. For example, the dot corresponds to 25 taxa occurring at or above 1.5 individuals per cubic meter at least one percent of the time; these were the criteria used for this study's reduction. These criteria were selected because they correspond to the point on the surface prior to the rapid rise in taxa. By choosing the data reduction criteria at this point, as many taxa as possible are included, without retaining a large number of uncommonly captured taxa.


Number of Taxa
89
59
30
0
0.0
4.0
8.0
12.0
16.0
20.0
Abundance (#/m3)
0.0
4.0
8.0
12.0
16.0
20.0
Percent Occurrence

the percent occurrence and abundance criteria. Choosing the percent occurrence and abundance criteria by use of this graph ensures an objective choice of criteria. Including this percent occurrence/abundance reduction avoids omission of ubiquitous and possibly important taxa, a criticism of the Williams and Stephenson method (Boesch, 1977).

Cluster-based Analyses

I searched for species associations using three different statistical approaches, each approach based upon a distinct multivariate clustering analysis. In this portion of the paper, I first present background information common to all three approaches, consisting primarily of definitions of clustering terminology. Following the definitions, I provide an overview of the steps in common among the three approaches. After that, I describe each method in turn, providing a general description of the method first, followed by a description of how it was specifically used in this study. I finish by reviewing the end products (*ie* graphical summaries) of the three approaches, describing how each graph is used and pointing out which graphs serve the same role for the different approaches.

In general, clustering is a multivariate statistical method of finding groups in nature, when one has no predetermined idea of which groups exist. It is used in an exploratory fashion to generate hypotheses (Green, 1980), and in a descriptive fashion to illustrate multivariate patterns which otherwise would not be apparent. As a

descriptive method, clustering has the advantage of being quantitative, and therefore objective. An example of an application of clustering analysis would be sites in a estuarine study area grouped according to patterns of occurrence of several species of zooplankton. Sites which are grouped with one another in this type of analysis may be similar to one another in the habitat requirements of the zooplankters surveyed. In this application, cluster analysis would be used to identify the various zooplankton habitats within the estuarine study area. Cluster analysis might also be used to objectively find groups among the species of zooplankton, indicating which zooplankters have similar habitat requirements.

The examples above illustrate two main applications of cluster analysis in ecology: 1) identifying similar habitats or times of the year (*ie* grouping sampling sites or dates); and 2) identifying taxa with similar habitat requirements (*ie* clustering species). Boesch (1977) introduced two terms which are useful in describing a particular application of any type of clustering analysis: entity and attribute. Entities are grouped together based upon their attributes: for example, when one is clustering sites based upon the abundance of various species within them, then the sites are the entities and the species are the attributes used to group those sites.

There are other terms useful in describing applications of clustering analysis. One of these terms describes the end product of any clustering analysis: a dendrogram. A dendrogram is a tree-like diagram which has each entity as a terminal branch, these branches fuse with one another in pairs, which in turn fuse with entities or previously grouped entities, until all groups of entities have been fused into one

group at the trunk of the dendrogram. Determining where on the dendrogram (*ie* how far up the tree) to draw a line and identify the groups of entities is often done by eye, and is therefore subjective.

Another set of terms important to any discussion of clustering analysis refers to the general manner of conducting the analysis. Divisive clustering refers to a process by which groups are formed by starting with the overall group of entities, which is then split into smaller and smaller groups until all of the individual entities are separated from one another. In contrast, agglomerative clustering procedures cluster by starting with the individual entities, grouping them in larger and larger clusters until all are members of one group.

Finally, a term which is sometimes used in conjunction with a clustering analysis is nodal analysis (Boesch, 1977). In a nodal analysis, the results of two cluster analyses on the same data are combined. For example, the first of these analyses may have had species as the entities with sites as the attributes and the other had sites as the entities with species as the attributes. A nodal diagram is the end product of this type of analysis, and for this example it would be a cross-tabulation of species versus site, using species and site groups as the categories for the two dimensions of the table. The entries in each cell are some function of the abundance of the species group within that site group. I will be using the terms defined above throughout my description of the three clustering-based approaches taken in this study.

The three approaches used in this study had the same basic steps. Each of the approaches began with a clustering of the reduced subset of eumalacostracan plankton, selected earlier using the consensus of the three data screens. The resulting species dendrogram was inspected and the groups chosen by eye (choice of groups was supplemented by supporting statistics in the VARCLUS method, see next paragraph). For each approach, this was followed by supporting analyses to determine the spatial and temporal patterns of the groups of species. All three methods were evaluated for accuracy using three-dimensional plots of the log-transformed abundances of individual species versus sampling site and sampling date. These plots provided a simple and objective view of any species's spatiotemporal pattern. The plots of species which had been grouped together by the clustering analysis were visually compared to one another to see if they had similar patterns.

The VARCLUS method is divisive, and it is performed by SAS's VARCLUS procedure (SAS, 1989). It is fundamentally different from the other two methods which are both agglomerative. VARCLUS finds clusters by calculating cluster components which maximize the sum of the between cluster variance of the original variables, as explained by the cluster components. It begins by calculating the correlation matrix for the entities. It then finds clusters based upon this matrix through an iterative process of splitting a pre-existing group, and then reassigning entities between all groups until the sum of the between cluster variance for all groups is at its maximum. The first split is of the initial group of all entities, afterwards the group to be split is the one with the largest second eigenvalue: a measure of how

much variance remains in that group. During the overall process the hierarchy may be maintained (*ie* once an entity is assigned to a cluster by the iterative process it remains in that cluster: all the reassignment takes place between the two new clusters within the group being split) or members may be allowed to join any cluster in the iteration process. Also, the initial splitting of selected groups during each step of a run can either be done at random, which may lead to a subsequent lengthy iteration period, or can be done based upon a factor analysis (PCA, followed by a varimax rotation): the first 'proposed' group consists of those entities correlated with the first factor and the second group are those entities correlated with the second factor. Each split and subsequent iteration is one step in the overall process of constructing a dendrogram. Following construction of the dendrogram, an objective measure of determining the point on the dendrogram at which to draw the line, and thus define the clusters of entities, occurs when none of the remaining second eigenvalues ares greater than one (*ie* in an eigenanalysis of a correlation matrix, an eigenvalue of one is equivalent to the variance contained in one of the original variables). In addition to the dendrogram and its groupings, this method also can produce cluster component scores, similar to principal component scores, which can be used in further analyses. To produce these scores, the number of clusters must be chosen (*ie* where to draw the line on the dendrogram), and this is accomplished by specifying the lower limit for the second eigenvalue (generally one).

In my application of the VARCLUS method, I used log-transformed taxa's abundances to calculate the correlation matrix. I constructed the dendrogram using

the hierarchy-preserving option, and then confirmed that dendrogram by comparing it with the results of a non-hierarchical run. After deciding which eigenvalue to use to choose the clusters, I checked the stability of these clusters using the random-split option. I ran the program 100 times with this random option, and I compiled a table containing the number of times taxa were paired with one another. I compared the number of times taxa within a group from the dendrogram were paired with one another against how often taxa in different groups were paired. Finally, I produced cluster components scores for each of the taxa's groups, and plotted the scores for each group in a three-dimensional plot against sampling sites and sampling dates, to summarize the spatiotemporal patterns of that taxa cluster.

The two remaining methods, both agglomerative, had an additional step in common. Most agglomerative methods have two major steps: 1) calculation of the distance or similarity matrix, and 2) combination of the entities into groups based upon the distance or similarity matrix (Boesch, 1977). The two methods I chose, the Canberra metric and the Williams and Stephenson (1973) partitioned variance metric, only supply the distances between entities; there are many methods of combination which may be used with either. In this application, I used the same combinatorial method for both, the flexible-beta method of Lance and Williams (1967). I constructed all the agglomerative dendrograms for this study by using values of beta between 0.25 and -0.75, a range recommended by Boesch (1977), choosing the dendrogram with the most clearly defined clusters.

I used the Canberra metric as a well-respected representative of the most commonly used types of cluster analyses in marine ecology (Boesch, 1977). It is a simple distance measure: the distance between two taxa (for example) is the mean over all site-cruise combinations of the ratio of the absolute difference in the abundances of the two taxa to the sum of their abundances. Double zero matches are ignored: they do not contribute to the sum, and the number used as the denominator in the mean is decremented by one for every zero/zero match. Also, to insure that for example, zero/one matches contribute less to the distance than zero/one thousand matches, zeros in these cases are replaced by an arbitrary small number (usually one-fifth). This method can also be used as the basis for the quantitative nodal analysis proposed by Boesch (1977): the taxa's abundances within a node are first divided by each taxon's mean abundance, and then the mean of all such numbers within that node is calculated. When using this method a value of one indicates that the taxa within a node were at their average value.

In my application of this method, I used log-transformed abundance data, and used one-fifth to replace zeros in zero/non-zero matches. I also built Boesch's (1977) quantitative nodal analysis table. I slightly modified Boesch's approach by subtracting one from the results of the nodal analysis, so that below average values would be indicated by negative numbers, and above average values by positive numbers. I presented the results graphically, as recommended by Boesch (1977).

The second agglomerative method, and the final clustering method overall, is the partitioned clustering analysis proposed by Williams and Stephenson (1973). This

method uses the two-way ANOVA sums of squares model to partition cluster distances due to temporal effects from those distances due to spatial effects. It results in four matrices: distances between 1) sites, 2) cruises, 3) taxa based upon occurrence at sites, and 4) taxa based upon occurrences during cruises. These analyses also provide methods for producing two kinds of supporting tables. The first of these contains the percent of the total variance associated with differences in taxa abundance due to sites, cruises, and the site-cruise interaction. And the second, called "B-tables" by the authors: nodal tables illustrating the relative abundances of each site-based or cruise-based plankton group in each site or cruise group. It is important to realize that the numbers used in the B-table are relative both to the taxa's mean abundances and to the mean abundance of all plankters within the group. For example, for a site-based taxa group to have a high value in the table, those taxa must either be especially abundant with respect to their own mean abundance, especially abundant with respect to the mean abundance of all taxa (members and non-members of the taxa group alike) within that site group, or both.

In my application of this method I used log-transformed abundances, and produced both the mean-variance per comparison table and the B-table. In this study, the results of these B-tables are presented graphically, using shaded boxes instead of the raw numbers. I also used canonical discriminant analysis, which is separatory rather than classificatory (*cf* Williams, 1983), to test the site and cruise groups resulting from the W&S analyses, and to illustrate differences in taxa composition between these groups. In my application of canonical discriminant analysis, I selected

taxa for discriminant function loadings based upon two criteria. First, they were significantly different among the groups in a univariate ANOVA ($p=0.05$). Second, they had large coefficients. The coefficients in a canonical discriminant analysis are the cosines of the angle between the taxa's abundance variable and the canonical discriminant function. I considered a taxon which had an angle of intersection with the discriminant function of less than or equal to an angle of 45 degrees to have a high degree of similarity to the discriminant function. I chose 45 degrees because it is midway between 0 degrees, corresponding to the highest possible coefficient (one), and 90 degrees which corresponds to the lowest possible coefficient (zero). Since the cosine of 45 degrees is 0.7071, I considered coefficients with an absolute value of greater than or equal to 0.7071 to be large.

The VARCLUS analysis produced a taxa dendrogram, which, along with supplementary statistics, was used to identify taxa groups. It also produced cluster scores plots which were used to delineate and summarize the spatiotemporal patterns of these groups. The Williams and Stephenson analysis produced a taxa dendrogram based solely upon sites as attributes and a taxa dendrogram based solely upon cruises as attributes. It also produced clusters of both sites and cruises (using taxa as attributes), used to summarize spatial and temporal patterns of the plankters as a whole and, as part of the B-table nodal plots, to make summaries of individual taxa group's spatiotemporal patterns. Canonical discriminant analysis was also used with the W&S results to identify those individual taxa with strong site or cruise (time of year) preferences. And finally, the Canberra metric-based analyses produced a taxa

dendrogram, which was used to identify taxa associations. It also was used to produce a sample (site-cruise) dendrogram, used in the quantitative nodal diagram to delineate and summarize spatiotemporal patterns.

Analysis of Physical Data

Taking the basic approach of Green and Vascotto (1978), canonical discriminant analysis was used to identify which of the physicochemical measurements, temperature, salinity or dissolved oxygen, varied the most between the W&S cluster analysis site groups and between the W&S cruise groups, separately. These cluster analysis groups were used as representatives of the different spatial and temporal habitats of these taxa. By identifying which of these measures is most different between habitats, I hoped to find the measure most important to the spatial and temporal distributions of the plankters.

The physicochemical data for these analyses were standardized to a mean of zero and a standard deviation of one, in order to insure against dominance of the analyses due solely to a physical measurement's units. Variance due to temporal effects was removed for site analyses, and vice versa for cruise analyses, to provide more powerful and more easily interpretable tests. Temporal variance was removed by producing residuals in a polynomial regression which used powers of date. These residuals, with temporal variance removed, were used in the discriminant analyses between site groups. Likewise, data for the W&S cruise group discriminant analyses were first site-centered, to remove site effects, and these residuals used in the discriminant analysis.

RESULTS AND DISCUSSION

In this section, I first present the results of the data reduction, as this was used by all three approaches. I begin with the results of the VARCLUS-based analyses, because its taxa clusters were the most realistic, based upon comparisons with the simple three-dimensional plots of individual taxa. I also present the results and literature-based discussion of the individual taxa in the VARCLUS section; this is consistent with earlier work, all done taxon-by-taxon. This presentation is important both to demonstrate the credibility of the results of the VARCLUS analysis, and to establish that these data are typical of eumalacostracan plankton. I follow the VARCLUS results with a presentation of the W&S results, because, although the W&S results did not always hold up well when compared with the individual taxa plots, they did provide some unique and useful insights into multi-taxa associations and patterns of abundance, as well as providing good summaries of spatial and temporal patterns. In the W&S section, I also present the results of the physicochemical discriminant analyses of the spatial and temporal habitat of the plankters. I do this because I consider the W&S site and cruise clusters to be accurate summaries of the spatial and temporal habitats of these organisms. Finally, I close with the results of the Canberra analyses; my representative of traditional clustering approaches. The Canberra metric fared poorly: based upon the individual taxa plots, most of the associations it proposed were nonsensical. When the results

were more realistic, this method was redundant, with these associations already having been made apparent from the result of one or both of the other two approaches.

Within the VARCLUS section, I present the VARCLUS groups one at a time, first presenting the results for each individual taxa, then comparing this study's results with the literature, followed by a discussion of the implications for the taxa early life-history strategy, and closing with a summary of the cluster's shared pattern and the possible ecological explanations and consequences. Then, within the W&S section I first present the results of the partitioning of variance, as this is information applicable to the rest of the W&S results. Following, I present all of the temporal patterns, within which I present the cruise groups, then the taxa groups (with a separate discussion of each taxa group), and I finish with a summary of the temporal patterns. The spatial patterns are next, subdivided in the same manner as the temporal patterns. The Canberra results are presented in a similar manner, with the results and discussion of the sample groups followed by a presentation of the results and discussion of each taxa group.

Taxa Reduction

Twenty-seven eumalacostracan taxa, from a total of 89 crustaceans, were retained by the consensus of the percent occurrence and the Williams and Stephenson (1973) reductions (Table 2). In the percent occurrence reduction, 25 taxa occurring at or above 1.5 individuals per cubic meter at least one percent of the time were

Table 2. List of all eumalacostracan plankton sampled, with retained taxa indicated by inclusion of their code. Taxa are ranked by the percent occurrence criteria, and Williams and Stephenson site and cruise reduction results are indicated by boldfacing of site or cruise reduction rank. (Table covers multiple pages: 32-34.)

Taxon	Code	Percent Occurrence		Site Reduction		Cruise Reduction	
		Rank	% > 1.5/m^3	Rank	Variance	Rank	Variance
Callinectes spp. zoea	BLUEZ	1	33.3	7	0.047	1	0.494
Crangon septemspinosa zoea	CRANGON	2	27.6	1	0.300	2	0.104
Upogebia affinis zoea	UPOGEB	3	15.1	2	0.087	4	0.057
Neomysis americana	NMYSIS	4	13.8	4	0.075	5	0.057
Uca (*minax*?) sp. #2 zoea	UCAZ2	5	13.8	5	0.059	3	0.062
Pagurus longicarpus zoea	PAGURLZ	6	12.5	3	0.080	8	0.019
Lucifer faxoni	LUCIFER	7	7.9	10	0.035	7	0.035
Callianassa sp. A zoea	CALIANA	8	7.2	9	0.036	9	0.018
Mysidopsis bigelowi	MYSIDOP	9	6.6	13	0.017	6	0.054
Callinectes spp. megalopa	BLUEM	10	4.6	6	0.059	11	0.012
Ovalipes quadulpensis zoea	OVALIPZ	11	4.6	16	0.005	13	0.004
Pinnotheres ostreum zoea	PINTHOZ	12	4.6	11	0.035	14	0.004
Cancer irroratus zoea	CANCERZ	13	3.9	8	0.037	10	0.016
Pinnixa spp. zoea	PINSPZ	14	3.9	12	0.018	12	0.007
Squilla (*empusa*?) protozoea	SQUILLA	15	3.9	20	0.004	16	0.003
Emerita talpoida zoea	EMERITA	16	3.3	14	0.009	15	0.004
Euceramus praelongus zoea	EUCERAM	17	2.6	15	0.008	19	0.002
Rhithropanopeus harrisi zoea	RITHROZ	18	2.6	29	0.001	24	0.001
Hexapanopeus angustifrons zoea	HEXAPZ	19	2.0	73	0.001	29	0.001
Acetes americanus carolinae	ACETES	20	1.3	80	0.001	21	0.002
Libinia spp. zoea	LIBINZ	21	1.3	24	0.002	81	0.000
Pinnixa cylindrica zoea	PINCYZ	22	1.3	17	0.005	18	0.002
Squillid antizoea	SQUILID	23	1.3	19	0.004	20	0.002
Uca (*minax*?) sp. #1 zoea	UCAZ1	24	1.3	18	0.004	17	0.002
Uca (*minax*?) sp. #3 zoea	UCAZ3	25	1.3	22	0.002	83	0.000
Bowmaniella dissimilis		26	0.7	79	0.001	23	0.001
Megalopa A	MEGA	27	0.7	21	0.003	22	0.002
Megalopa B		28	0.7	42	0.001	27	0.001
Mysid		29	0.7	84	0.001	28	0.001

Neopanope texana sayi zoea		30	0.7	86	0.000	34	0.001
Ogyrides limicula		31	0.7	88	0.000	26	0.001
Pagurus longicarpus juvenile		32	0.7	77	0.001	86	0.000
Pagurus sp.		33	0.7	34	0.001	25	0.001
Paleomonetes spp.		34	0.7	81	0.001	67	0.001
Panopeus herbstii zoea		35	0.7	87	0.000	31	0.001
Pinnixa chaetopterana zoea		36	0.7	25	0.002	87	0.000
Uca spp. megalopa		37	0.7	26	0.002	82	0.000
Alpheus heterochaelis		38	0.0	63	0.001	39	0.001
Alpheus normanni		39	0.0	67	0.001	69	0.001
Callinectes crab (juvenile)		40	0.0	43	0.001	53	0.001
Callianassa sp. C		41	0.0	53	0.001	56	0.001
Callianassa sp. A		42	0.0	71	0.001	85	0.000
Callianassa spp.		43	0.0	89	0.000	57	0.001
Cancer spp. megalopa		44	0.0	27	0.002	30	0.001
Dissodactylus mellitae zoea		45	0.0	69	0.001	70	0.001
Eurypanopeus depressus zoea		46	0.0	62	0.001	76	0.000
Hexapanopeus angustifrons megalopa		47	0.0	74	0.001	79	0.000
Hippolyte pleuracantha		48	0.0	70	0.001	68	0.001
Lepidopa websteri		49	0.0	83	0.001	88	0.000
Leptochela serratorbita		50	0.0	40	0.001	33	0.001
Libinia dubia megalopa		51	0.0	75	0.001	72	0.001
Libinia emarginata megalopa		52	0.0	50	0.001	46	0.001
Libinia spp. juvenile		53	0.0	51	0.001	43	0.001
Megalopa C		54	0.0	47	0.001	49	0.001
Megalopa D		55	0.0	35	0.001	74	0.001
Megalopa E		56	0.0	49	0.001	44	0.001
Megalopa F		57	0.0	39	0.001	64	0.001
Metamysidopsis spp.		58	0.0	32	0.001	36	0.001
Naushonia crangonoides		59	0.0	82	0.001	78	0.000
Ocypode spp. zoea	OCYPDEZ	60	0.0	23	0.002	65	0.001

Ovalipes crab (juvenile)	61	0.0	36	0.001	40	0.001
Ovalipes quadulpensis megalopa	62	0.0	44	0.001	37	0.001
Ovalipes zoea	63	0.0	46	0.001	84	0.000
Paguridae sub-adult crab	64	0.0	33	0.001	63	0.001
Pagurus pollicaris zoea	65	0.0	30	0.001	80	0.000
Panopeus spp. megalopa	66	0.0	55	0.001	45	0.001
Peneid shrimp	67	0.0	38	0.001	71	0.001
Penneus spp.	68	0.0	41	0.001	60	0.001
Percephone punctate	69	0.0	31	0.001	54	0.001
Pinnixa sp. A zoea	70	0.0	48	0.001	48	0.001
Pinnixa spp. megalopa	71	0.0	61	0.001	42	0.001
Pinnotheres spp. crab subadult	72	0.0	72	0.001	77	0.000
Pinnotheres ostreum adult	73	0.0	58	0.001	47	0.001
Pinnotheres spp. zoea	74	0.0	68	0.001	55	0.001
Pinnixa sayana zoea	75	0.0	85	0.001	89	0.000
Pinnotheres maculatus zoea	76	0.0	64	0.001	61	0.001
Polyonyx gibesi	77	0.0	66	0.001	75	0.001
Portunidae spp. crab	78	0.0	45	0.001	52	0.001
Portunidae spp. zoea	79	0.0	59	0.001	35	0.001
Portunus spp. zoea	80	0.0	37	0.001	58	0.001
Sesarma spp. zoea	81	0.0	65	0.001	38	0.001
Shrimp 6	82	0.0	60	0.001	41	0.001
Shrimp 7	83	0.0	54	0.001	50	0.001
Trachypenaeus spp.	84	0.0	56	0.001	59	0.001
Uca spp. megalopa	85	0.0	57	0.001	62	0.001
Uca spp. zoea	86	0.0	52	0.001	51	0.001
Xanthidae zoea	87	0.0	78	0.001	73	0.001
Xanthid zoea	88	0.0	76	0.001	66	0.001
Cancer sp. #2 zoea	89	0.0	28	0.001	32	0.001

kept:these criteria were chosen based upon Figure 3. In the cruise portion of the Williams and Stephenson reduction, 22 taxa were selected: accounting for 96 percent of the between-cruise variance (Figure 2a). Ninety-three percent of the between-site variance was explained by the 23 taxa retained by the site part of the reduction (Figure 2b). Most of the taxa were retained by all three screens.

Of the twenty-seven taxa retained, at least twenty-three species were represented. In three cases, more than one stage of what were most likely the same species were retained: *Callinectes* spp. zoea and *Callinectes* spp. megalopa; *Squilla empusa* protozoea and Squillid antizoea; and *Uca* spp. zoea numbers 1,2 and 3. Twenty three of the taxa are meroplanktonic; two of the taxa are holoplanktonic: *Lucifer faxoni* and *Acetes americanus carolinae*; and *Mysidopsis bigelowi* and *Neomysis americana* are epibenthic as adults.

VARCLUS Analysis

Eight clusters, one with nine members and the rest with two or three members, were found with this method (Figure 4). These groups were robust: the same groups were found whether or not the hierarchy was maintained. These results were also reproducible within this data set; in the runs with random splits, taxa within a cluster were paired far more often with each other than with taxa outside of that cluster (Figure 5). Table 3 contains the correlations of the various cluster members with their VARCLUS scores, indicating which members are strongly associated with the cluster and with its other members, and which members are only weakly

Figure 4. Taxa dendrogram from VARCLUS clustering method. Groups are labeled as VC1 to VC8. These groups were chosen based upon the second eigenvalue criterion (see text for explanation), and were confirmed by running 100 randomly seeded trials (see Figure 4 for results). Validity of groups was also evaluated by examination of diagnostic taxa abundance plots (Figures 7 through 14).

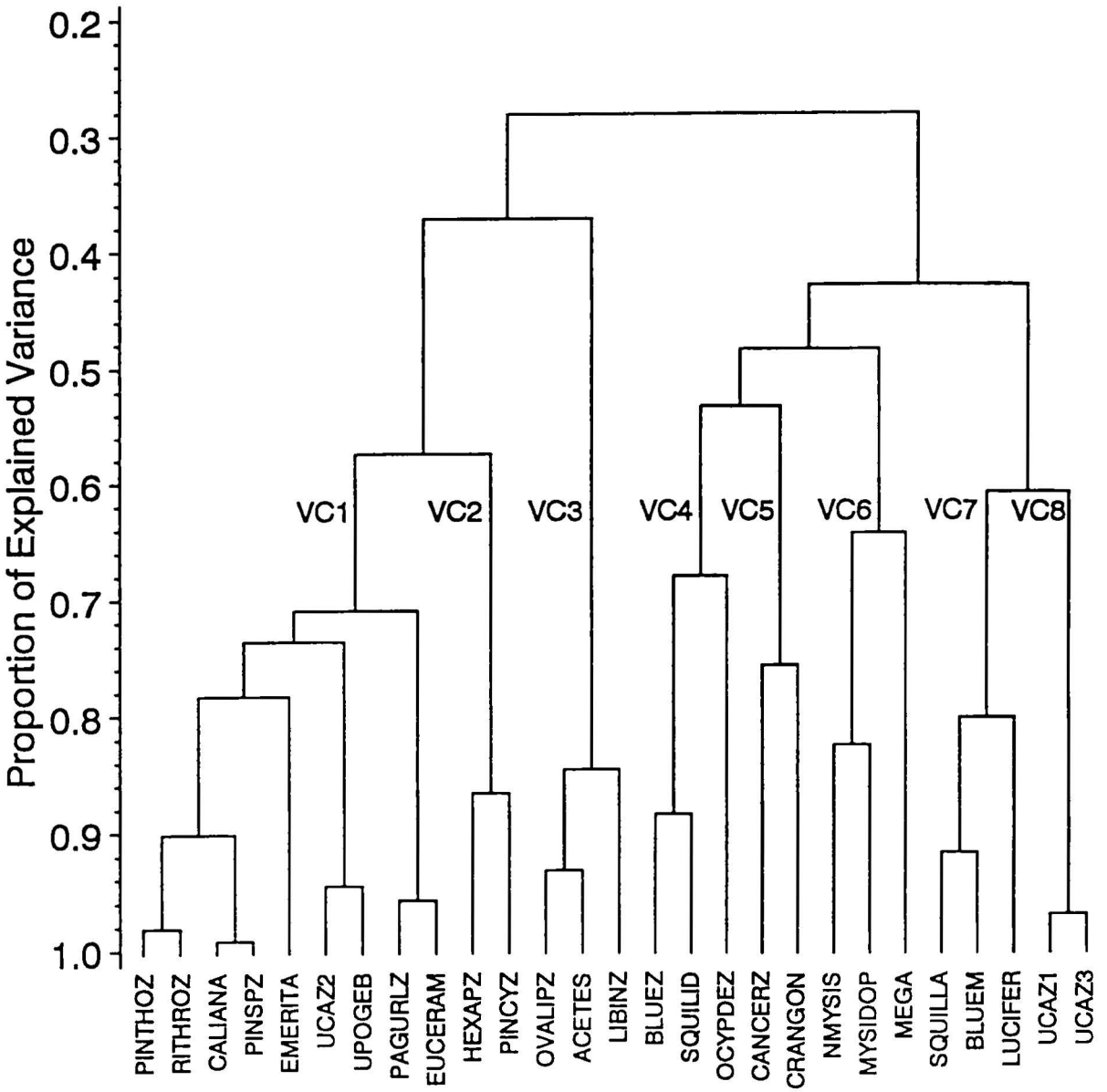
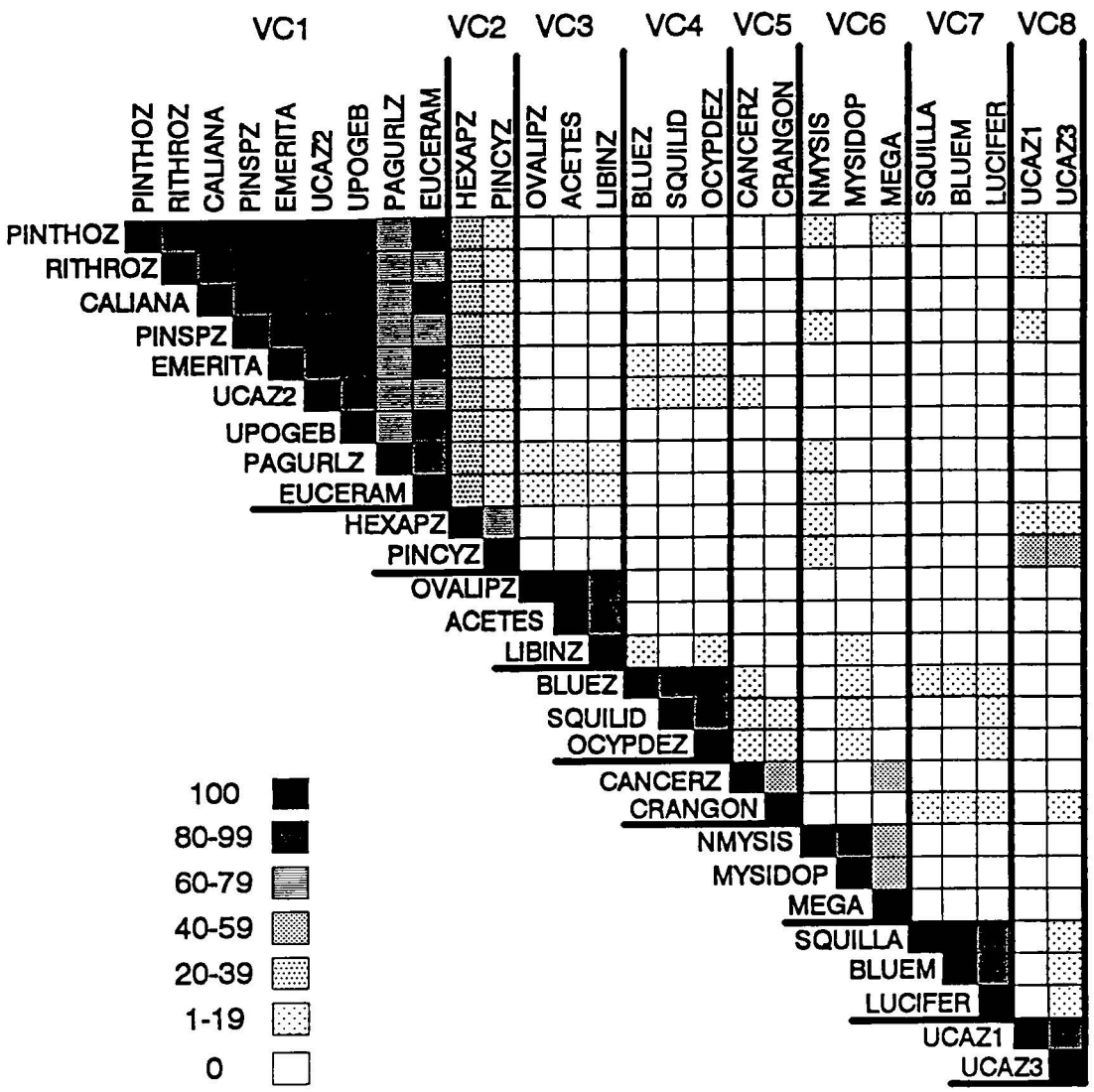

Proportion of Explained Variance
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
VC1
VC2
VC3
VC4
VC5
VC6
VC7
VC8
PINTHOZ
RITHROZ
CALIANA
PINSPZ
EMERITA
UCAZ2
UPOGEB
PAGURLZ
EUCERAM
HEXAPZ
PINCYZ
OVALIPZ
ACETES
LIBINZ
BLUEZ
SQUILID
OCYPDEZ
CANCERZ
CRANGON
NMYSIS
MYSIDOP
MEGA
SQUILLA
BLUEM
LUCIFER
UCAZ1
UCAZ3

Figure 5. Results of random VARCLUS runs. Patterns represent the percentage of times taxa were paired with one another. Results are from 100 runs with random splitting of clusters prior to sum of squares maximization, rather than the use of factor analysis for the initial split. Each run was stopped using one for the maximum second eigenvalue criterion (see Methods text for details).



Percentage of Time Pair of
Taxa in Same VARCLUS Cluster

Table 3. VARCLUS results table. The correlation coefficients between the member and the cluster are given in the "own cluster" column, and the coefficients between the member and the next closest cluster are given in the "next closest" column. The ratio found in the right-most column indicates whether or not the taxon is faithful to the cluster to which it is assigned. The smaller the number the greater the fidelity of the taxon.

Taxon	r^2 own cluster	r^2 next closest	$\frac{(1-r^2 \text{ own})}{(1-r^2 \text{ next})}$
VC1			
Pinnotheres ostreum zoea	0.6624	0.2799	0.4688
Rhithropanopeus harrissi zoea	0.5973	0.1904	0.4973
Callianassa sp. A zoea	0.8092	0.1944	0.2369
Pinnixia spp. zoea	0.6499	0.2974	0.4983
Emerita talpoida zoea	0.5372	0.1432	0.5402
Uca (*minax*?) sp. #2 zoea	0.4162	0.2447	0.7729
Upogebia affinis zoea	0.7892	0.2447	0.2791
Pagurus longicarpus zoea	0.4602	0.2669	0.7363
Euceramus praelongus zoea	0.6401	0.2893	0.5065
VC2			
Hexapanopeus angustifrons zoea	0.7534	0.2267	0.3189
Pinnixia cylindrica zoea	0.7534	0.3470	0.3777
VC3			
Ovalipes quadulpensis zoea	0.7685	0.1613	0.2761
Acetes carolinae	0.7107	0.0871	0.3168
Libinia spp. zoea	0.6168	0.2027	0.4807
VC4			
Callinectes spp. zoea	0.7591	0.2417	0.3177
Squillid antizoea	0.5967	0.0647	0.4313
Ocypode spp. zoea	0.3682	0.0249	0.6480
VC5			
Cancer irroratus zoea	0.6437	0.0243	0.3652
Crangon septemspinosa zoea	0.6437	0.0386	0.3706
VC6			
Neomysis americana	0.7099	0.0234	0.2970
Mysidopsis bigelowi	0.7032	0.0114	0.3002
Megalopa A	0.0351	0.0321	0.9969
VC7			
Squilla (*empusa*?) protozoea	0.6516	0.1432	0.4066
Callinectes spp. megalopa	0.7718	0.1772	0.2774
Lucifer faxoni	0.5562	0.1701	0.5348
VC8			
Uca (*minax*?) sp. #1 zoea	0.8476	0.2242	0.1964
Uca (*minax*?) sp. #3 zoea	0.8476	0.2878	0.2139

affiliated. The scores are plotted for each cluster versus site and cruise in Figure 6a to 6h. Following is the VARCLUS cluster-by-cluster results and discussion.

VC1

Assemblage:

Pinnotheres ostreum zoea (oyster crab), *Rhithropanopeus harrisii* zoea (mud crab), *Callianassa* sp. A zoea (mud shrimp), *Pinnixa* spp. zoea (pea crabs), *Emerita talpoida* zoea (mole crab), *Uca* sp. #2 zoea (fiddler crab), *Upogebia affinis* zoea (mud shrimp), *Pagurus longicarpus* zoea (hermit crab), and *Euceramus praelongus* zoea.

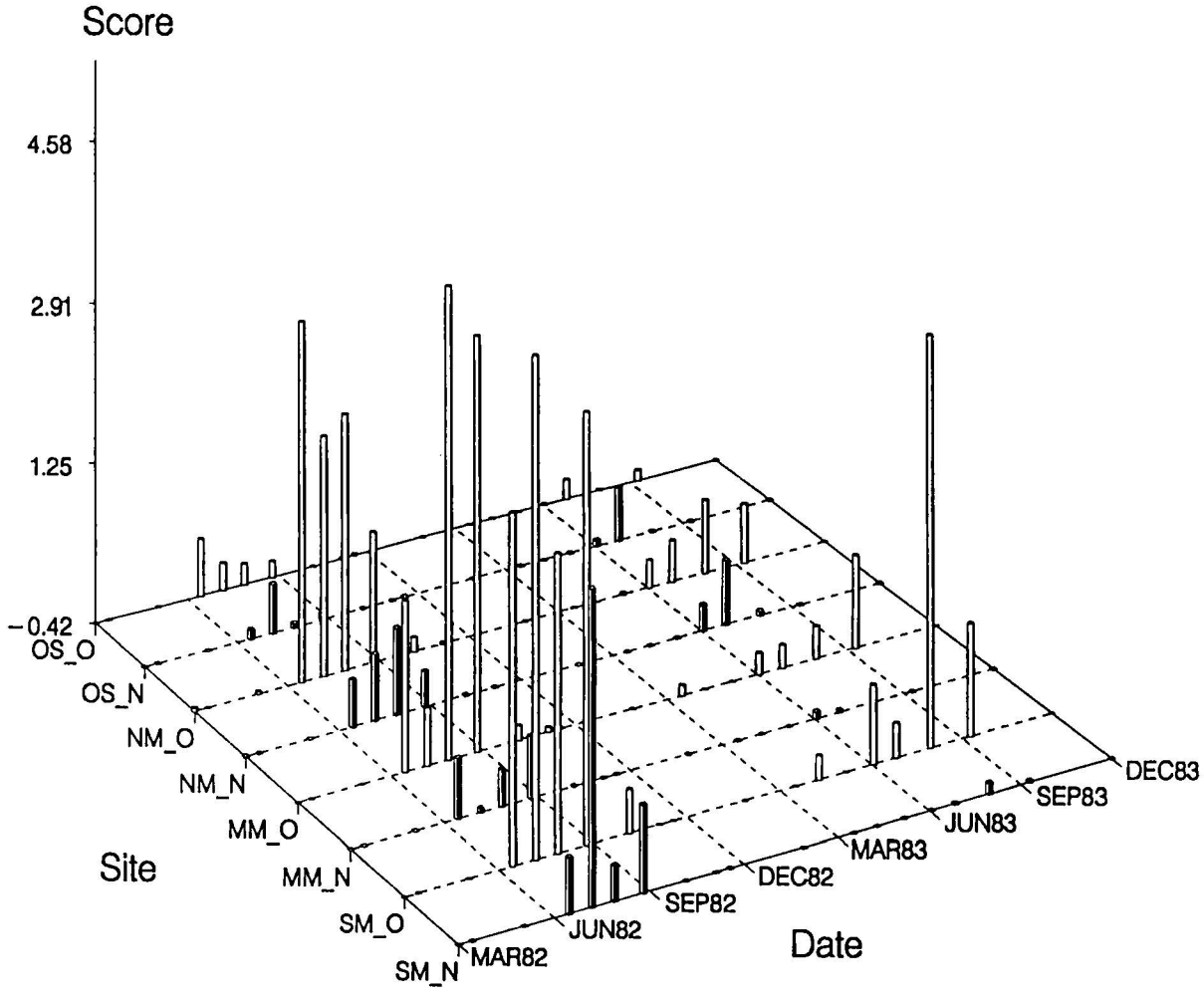
Individual Members:

***Pinnotheres ostreum* zoea** Zoeal stages of this species were found predominantly in the oblique sites of the middle and southern bay mouth (Figure 7a). These plankters were more abundant in the sampling area in 1982 than in 1983, and were present in the plankton from June to early fall (September-October), with peak abundance in July of both years.

Larvae of *P. ostreum*, the oyster crab, have been found in the lower bay and bay mouth (Sandifer, 1973; Goy, 1976; Johnson, 1982; Maris, 1986), during the months of June through September with peaks in July (Sandifer, 1973; Goy, 1976), a larval distribution consistent with this study's results. The adults of this species are primarily found in oysters (Williams, 1984), and

Figure 6. Spatiotemporal plots of VARCLUS cluster scores: a) VC1 (p.40), b) VC2 (p.41), c) VC3 (p.42), d) VC4 (p.43), e) VC5 (p.44), f) VC6 (p.45), g) VC7 (p.46), h) VC8 (p.47). For each of the eight VARCLUS score plots, scores were calculated using the abundances of the group's member taxa, and the VARCLUS function for that group. Shaded bars are neuston samples, and unshaded bars are oblique samples.

VC1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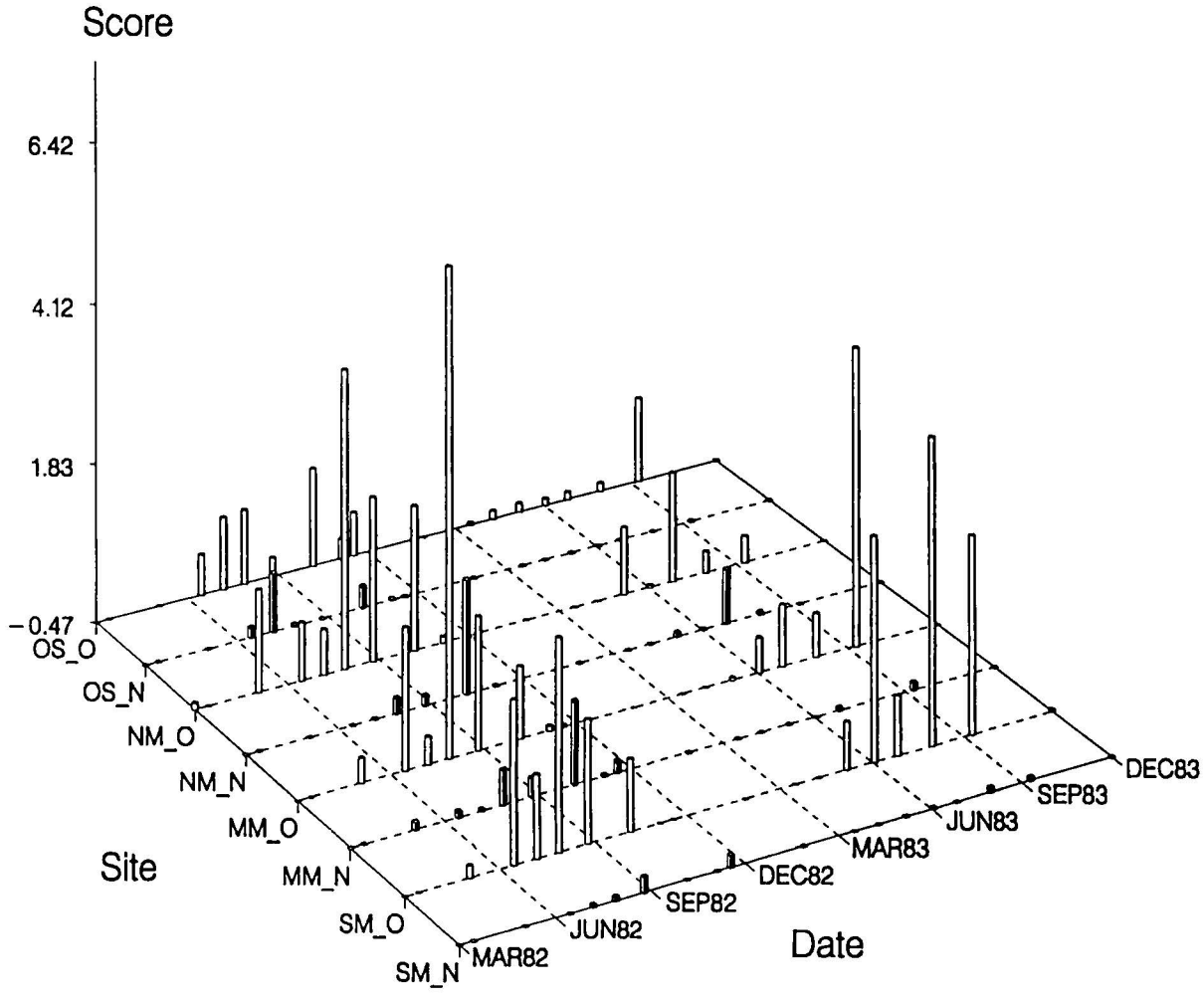
MAR83
JUN83
SEP83
DEC83
Date

VC2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Date

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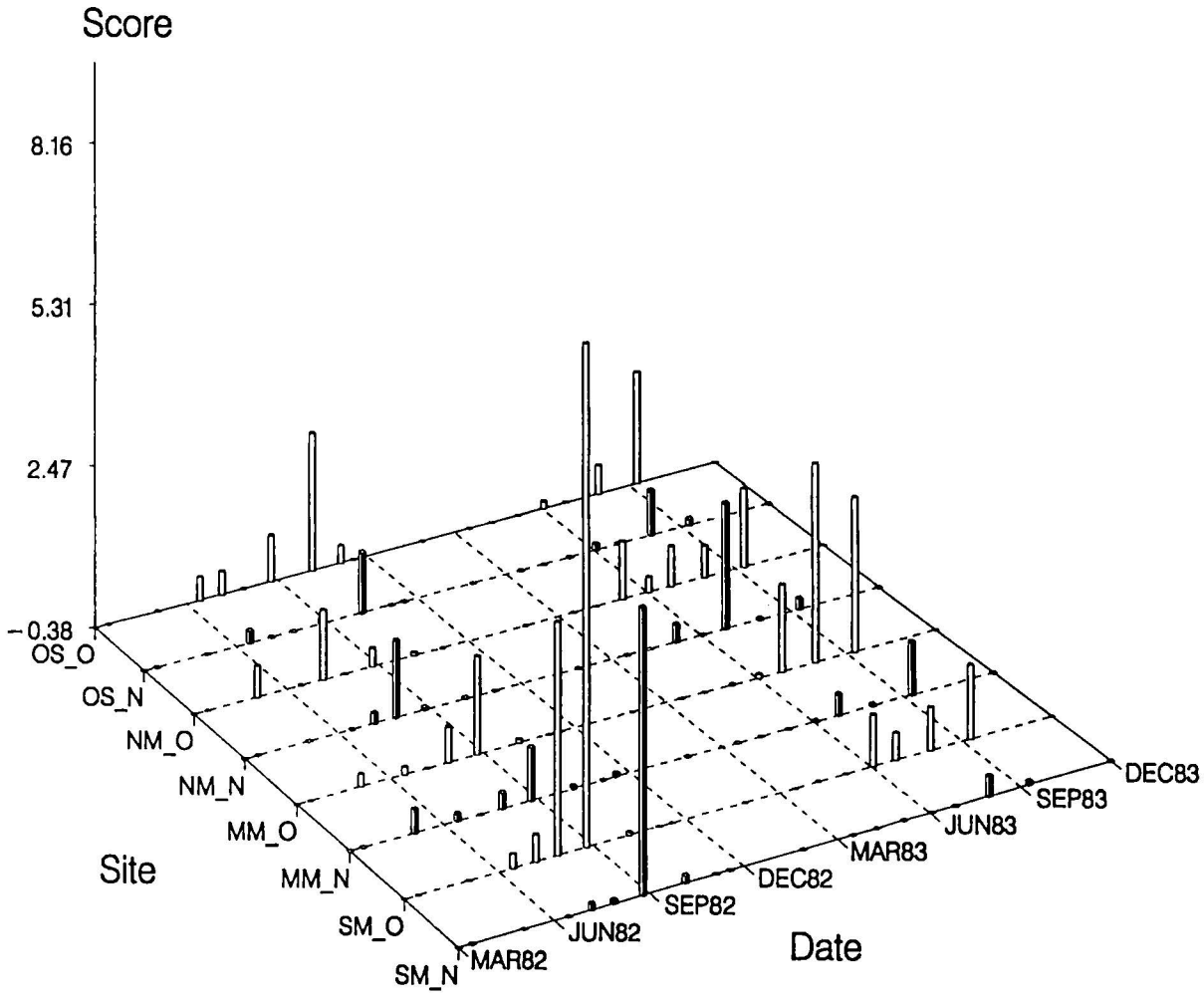
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DEC82
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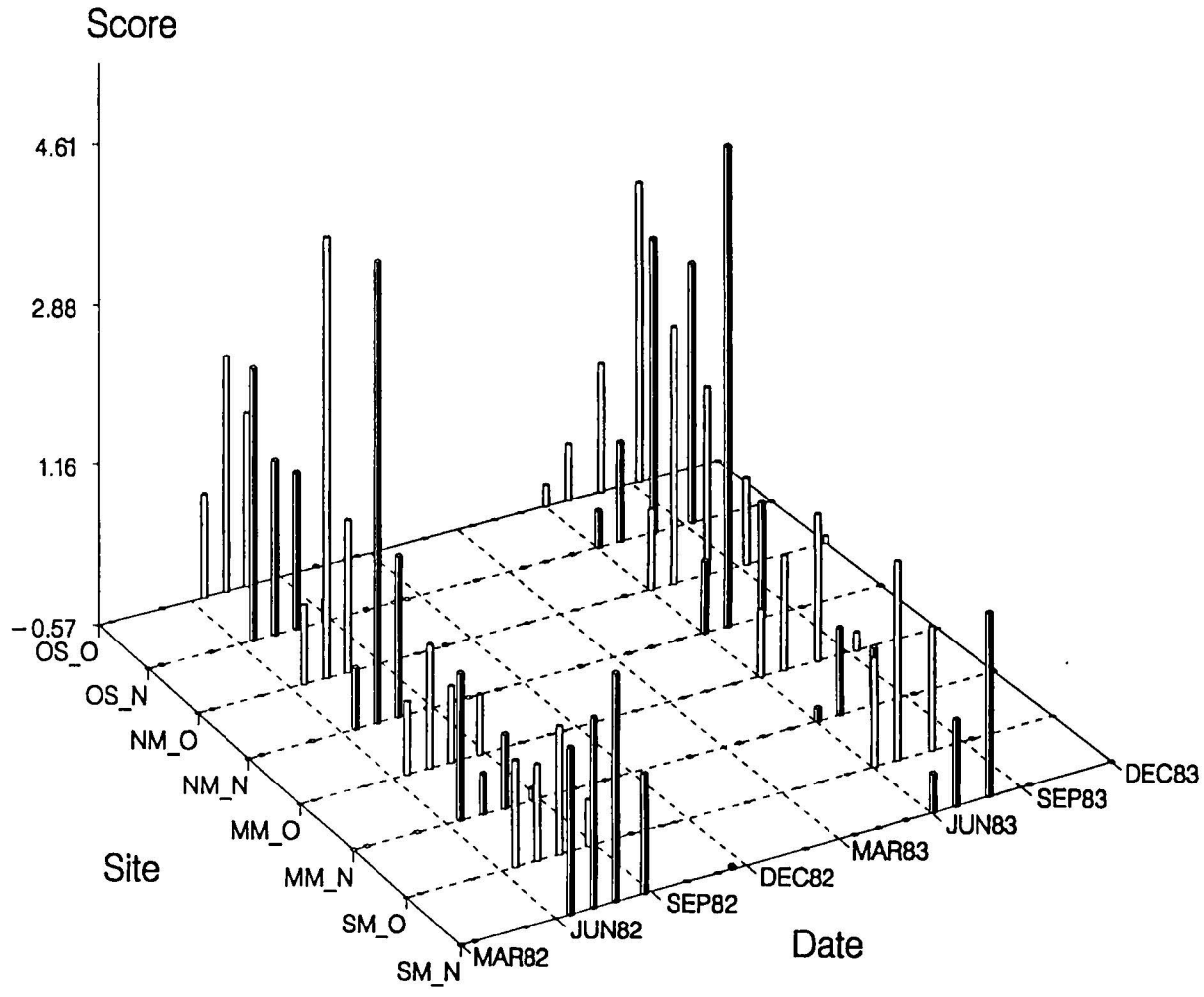
JUN83
SEP83
DEC83
Date

VC4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SEP82
DEC82
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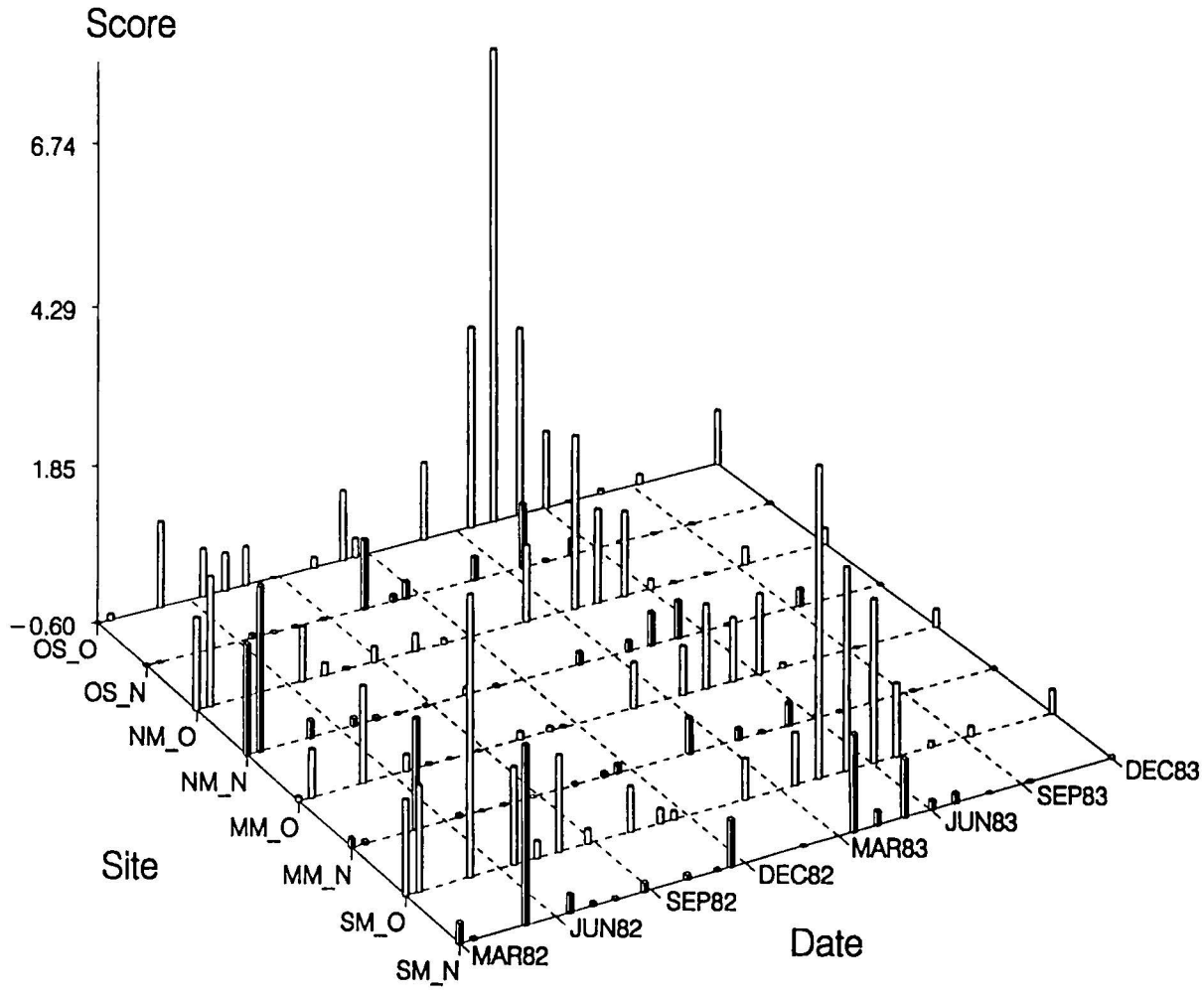
SEP83
DEC83
Date

VC5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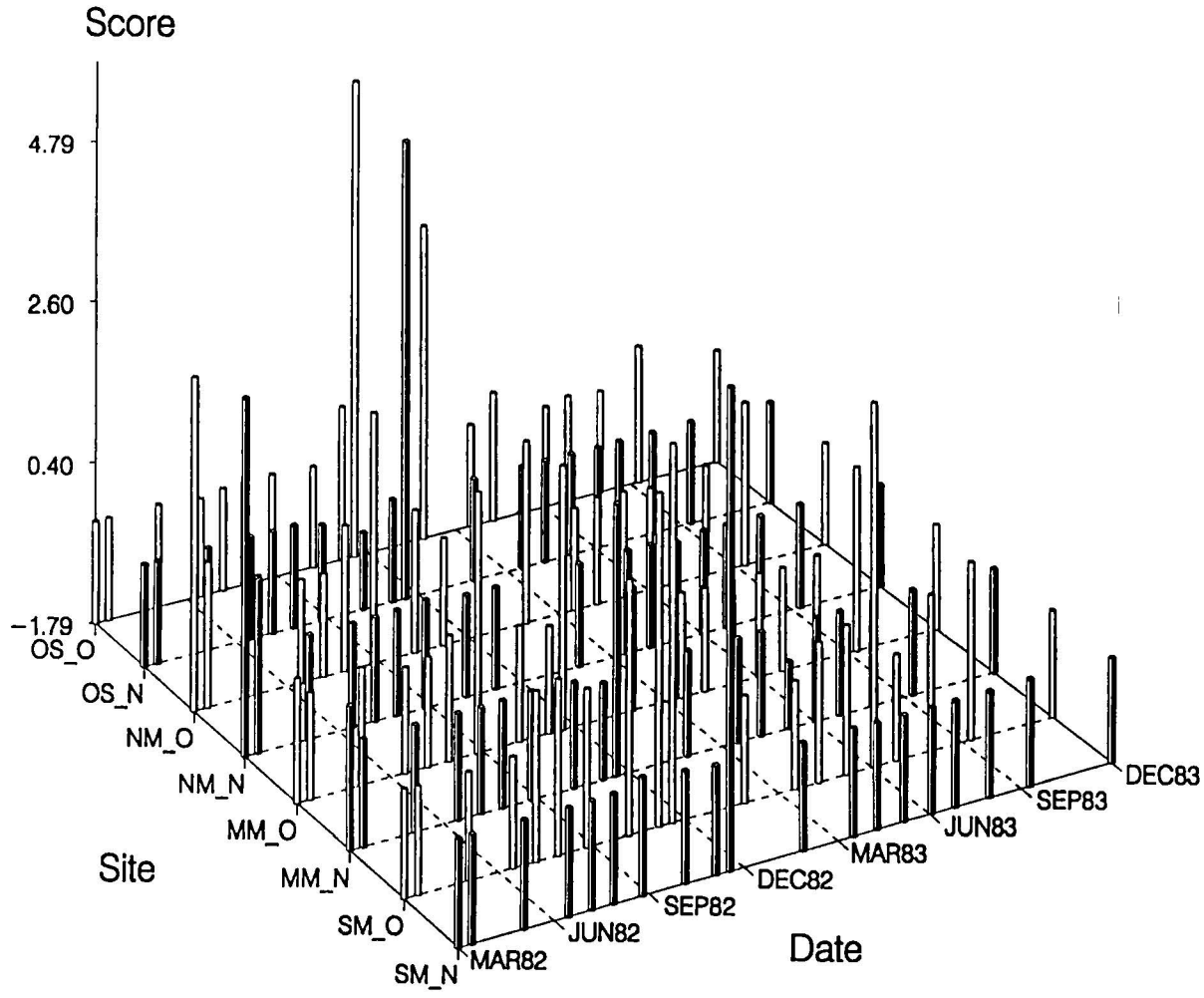
JUN83
SEP83
DEC83
Date

VC6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SEP82
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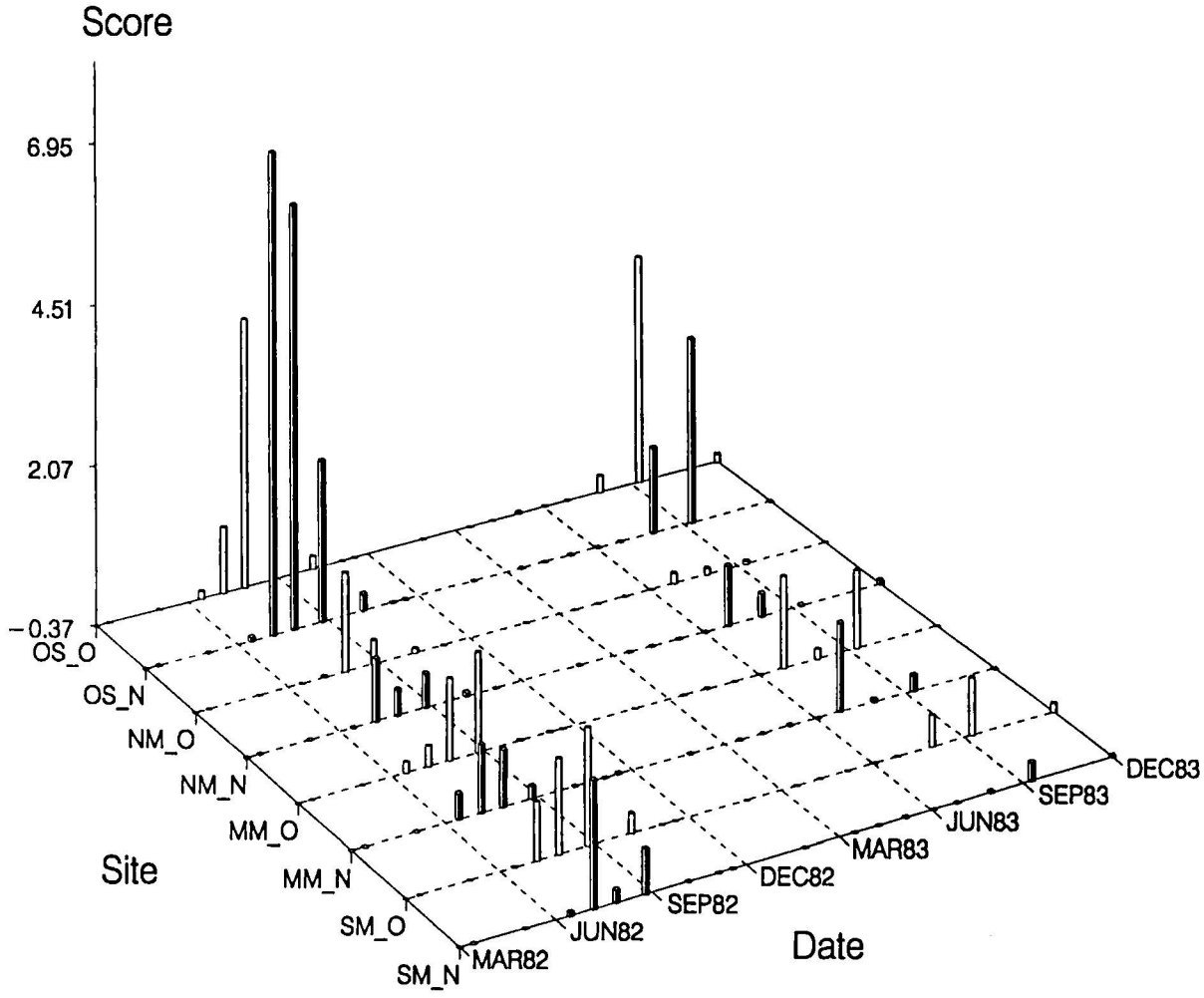
JUN83
SEP83
DEC83
Date

VC7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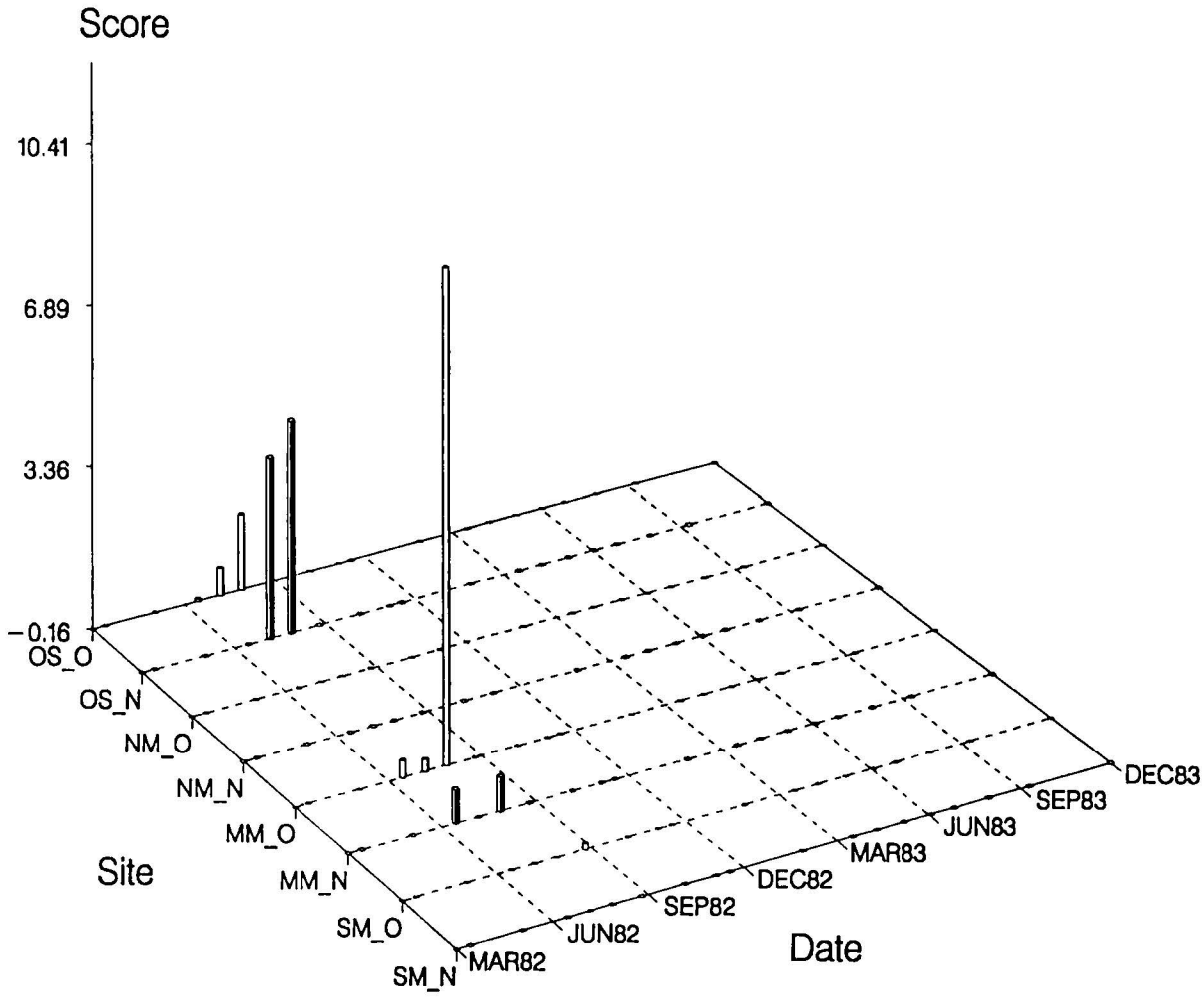
SEP82
DEC82
MAR83
JUN83
SEP83
DEC83
Date

VC8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NM_N
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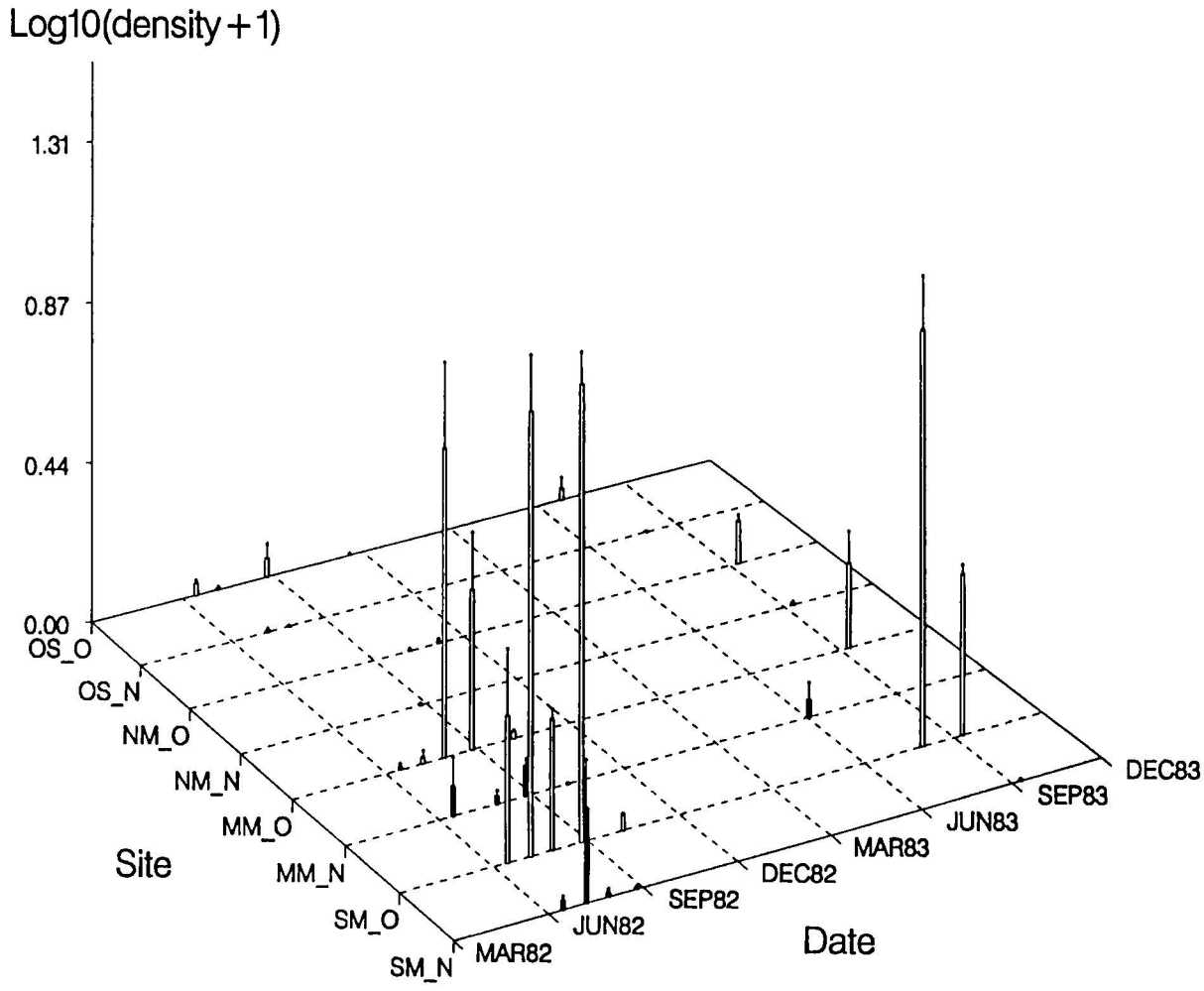
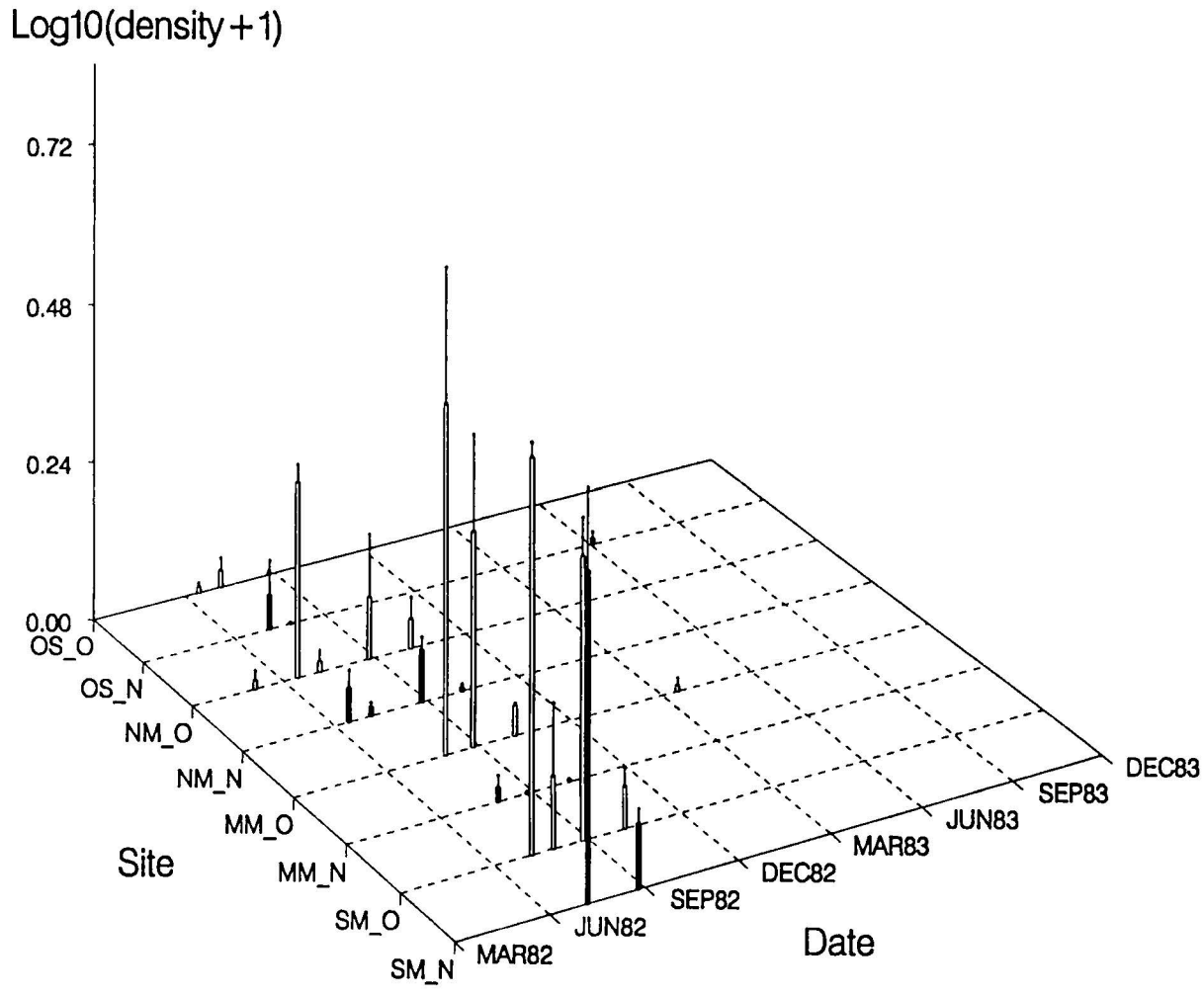
MM_N
SM_O
SM_N
Site
MAR82
JUN82
SEP82
DEC82
MAR83
JUN83
SEP83
DEC83
Date

Figure 7. Three-dimensional spatiotemporal plots of log-transformed individual taxon's mean abundance (+ 1 SE) for each member of VC1. Taxa are ordered according to VARCLUS dendrogram (Figure 4): a) *Pinnotheres ostreum* zoea (p.48), b) *Rhithropanopeus harrisii* zoea (p.49), c) *Callianassa sp. A* zoea (p.50), d) *Pinnixa* spp. zoea (p.51), e) *Emerita talpoida* zoea (p.52), f) *Uca* sp. #2 zoea (p.53), g) *Upogebia affinis* zoea (p.54), h) *Pagurus longicarpus* zoea (p.55), i) *Euceramus praelongus* zoea (p.56). Shaded bars are neuston samples, and unshaded bars are oblique samples.

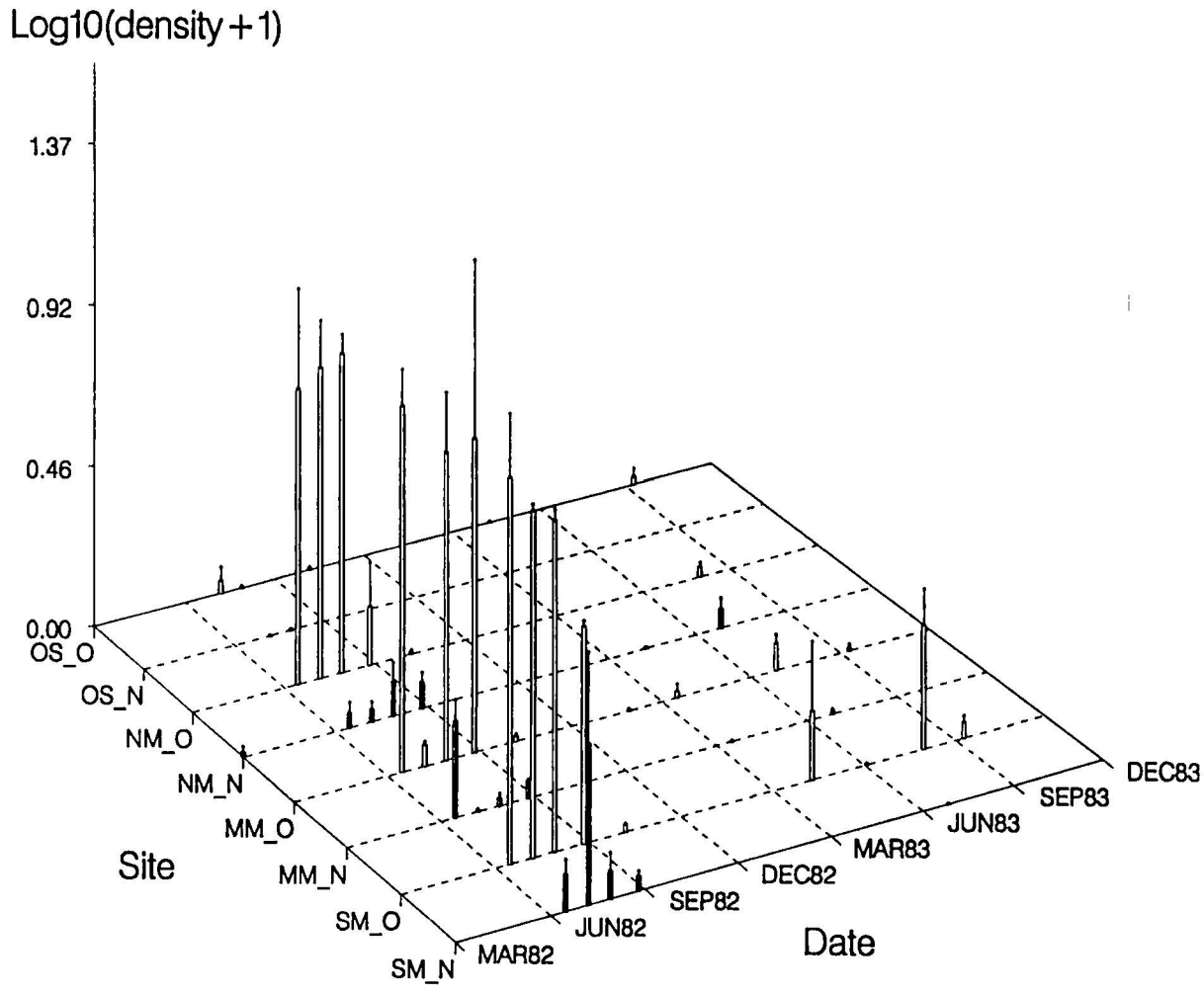
Pinnotheres ostreum zoea



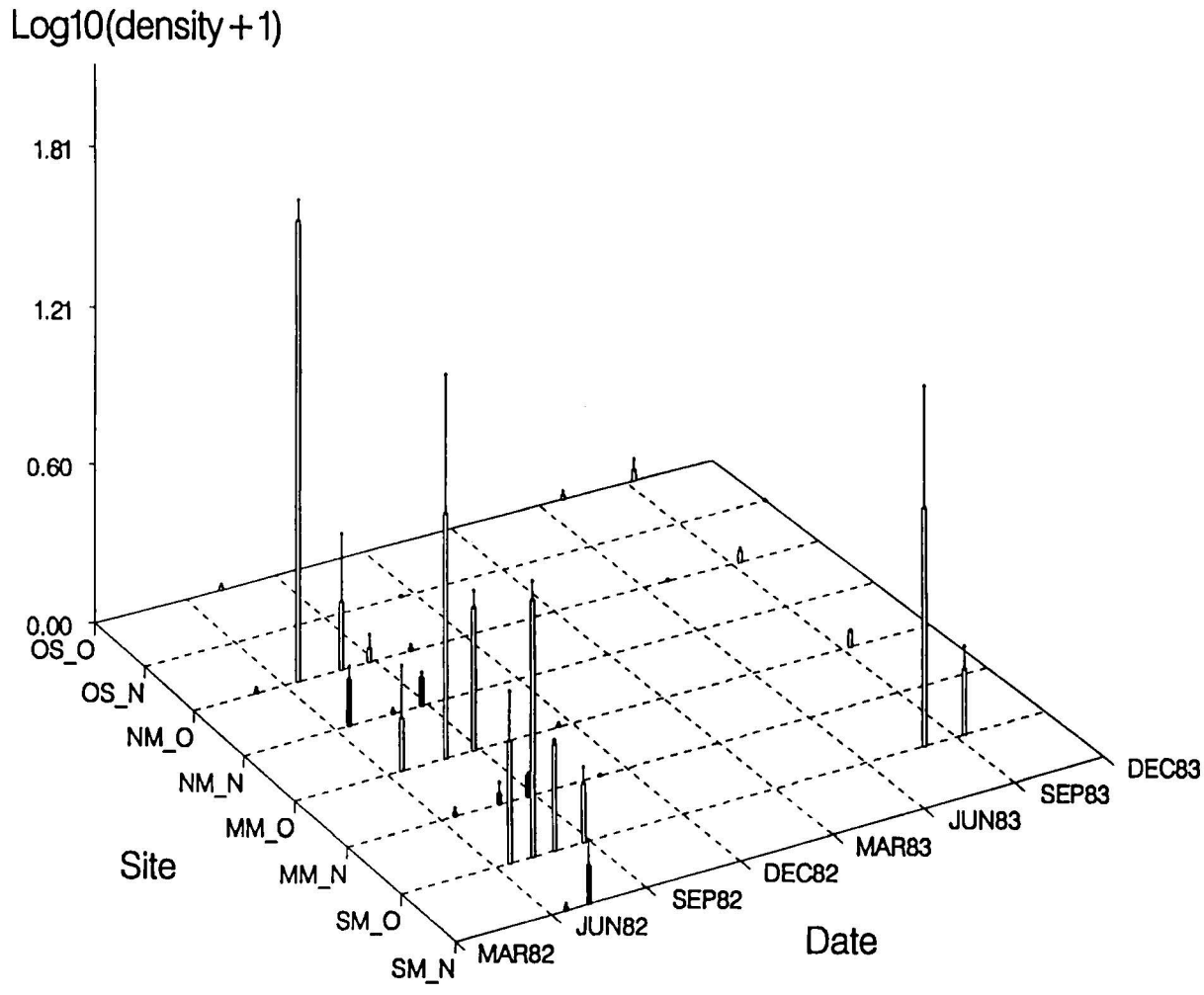
Rhithropanopeus harrisii zoea



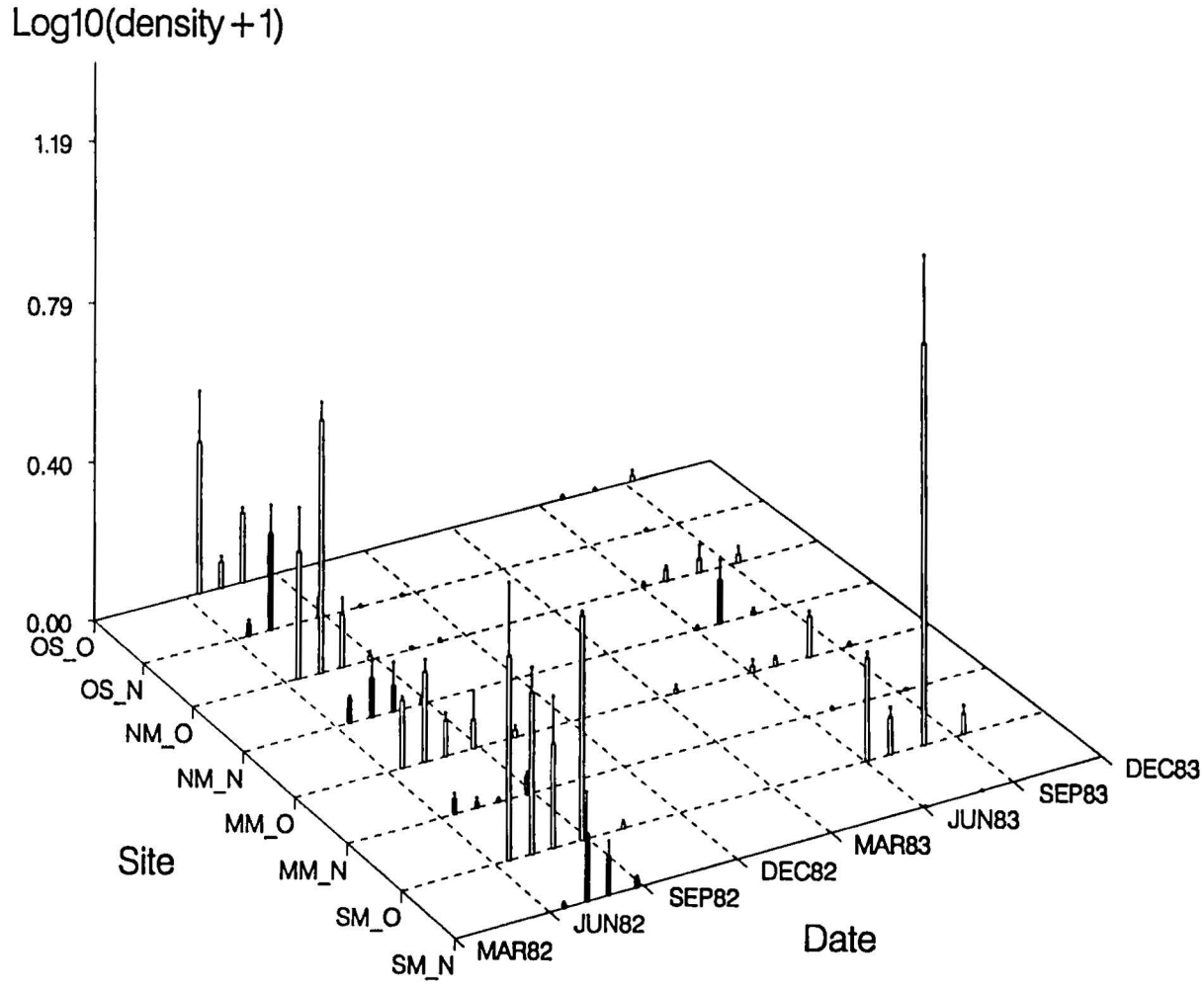
Callianassa sp. A. zoea



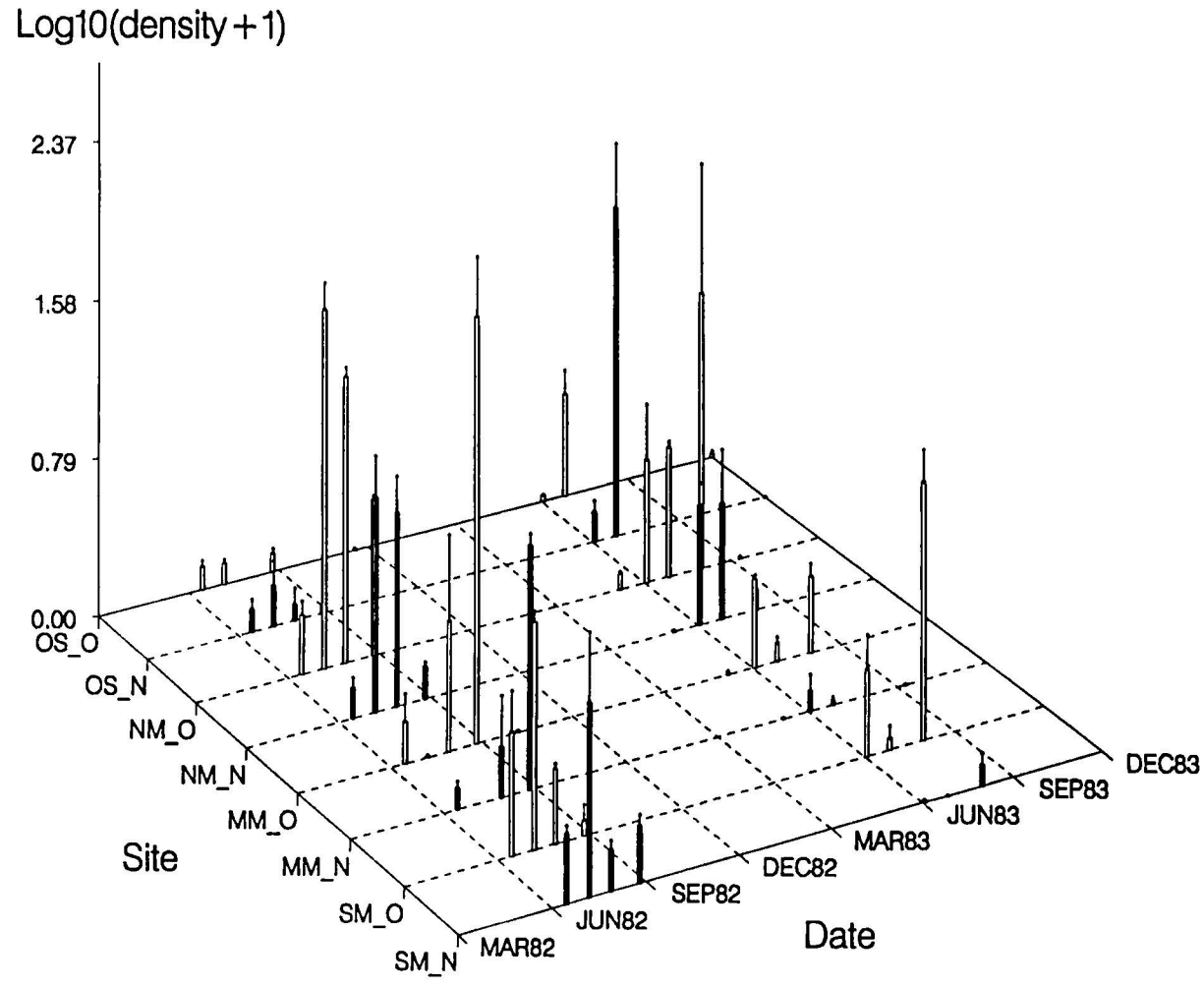
Pinnixa spp. zoea



Emerita talpoida zoea



Uca sp. #2 zoea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0.79
0.00
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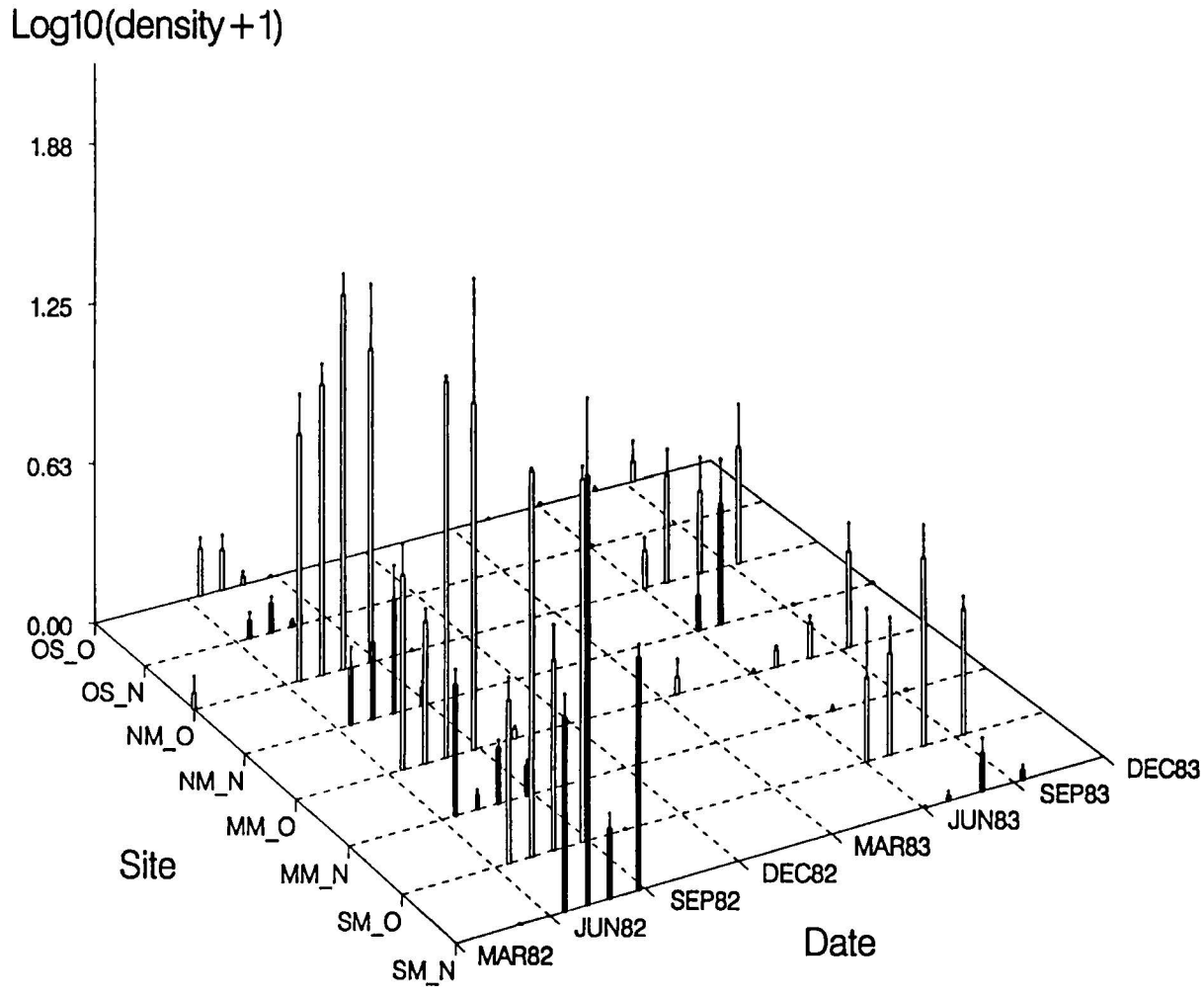
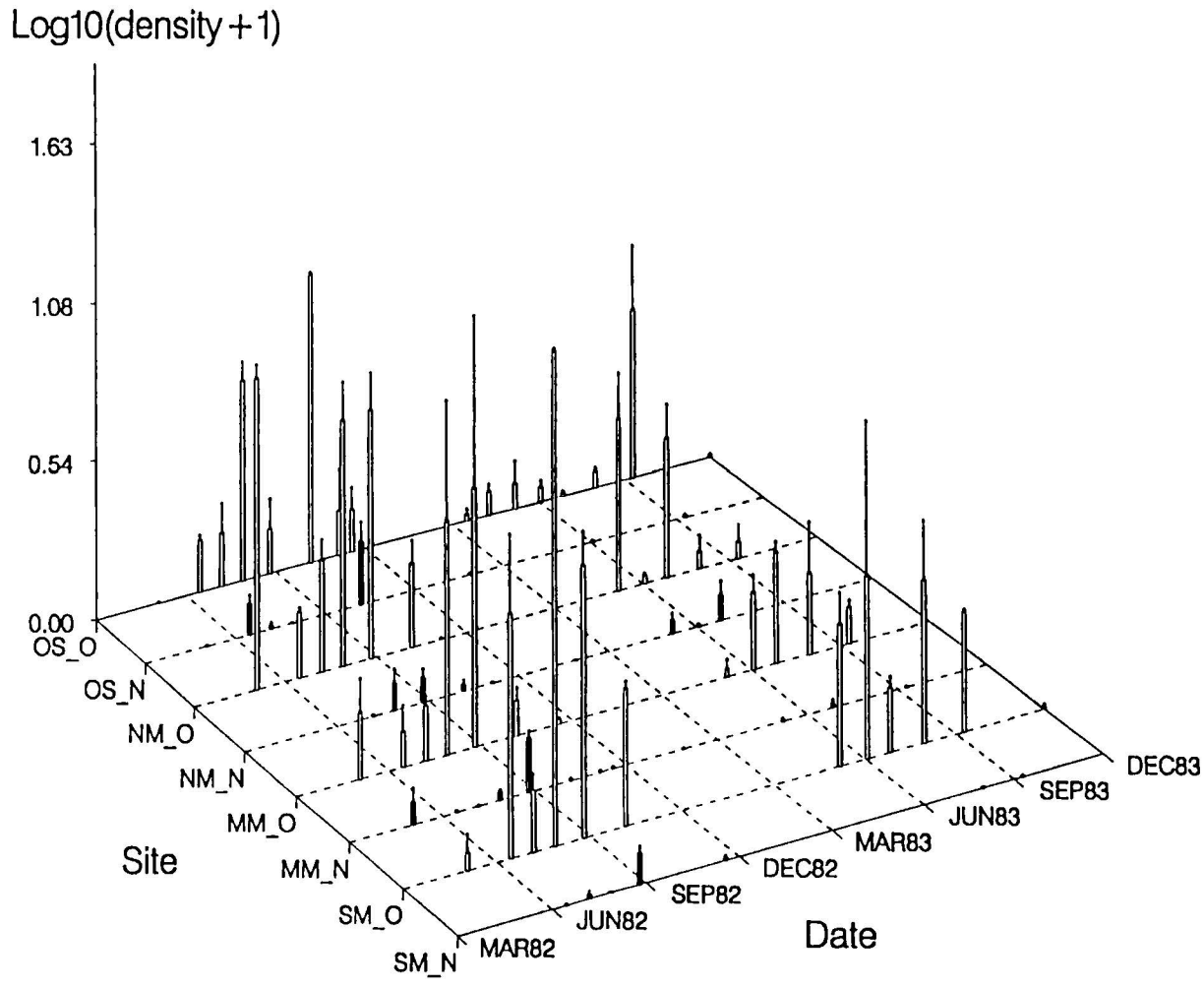
OS_N
NM_O
NM_N
MM_O
MM_N
SM_O
SM_N
Site
MAR82
JUN82
SEP82
DEC82
MAR83
JUN83
SEP83
DEC83
Date

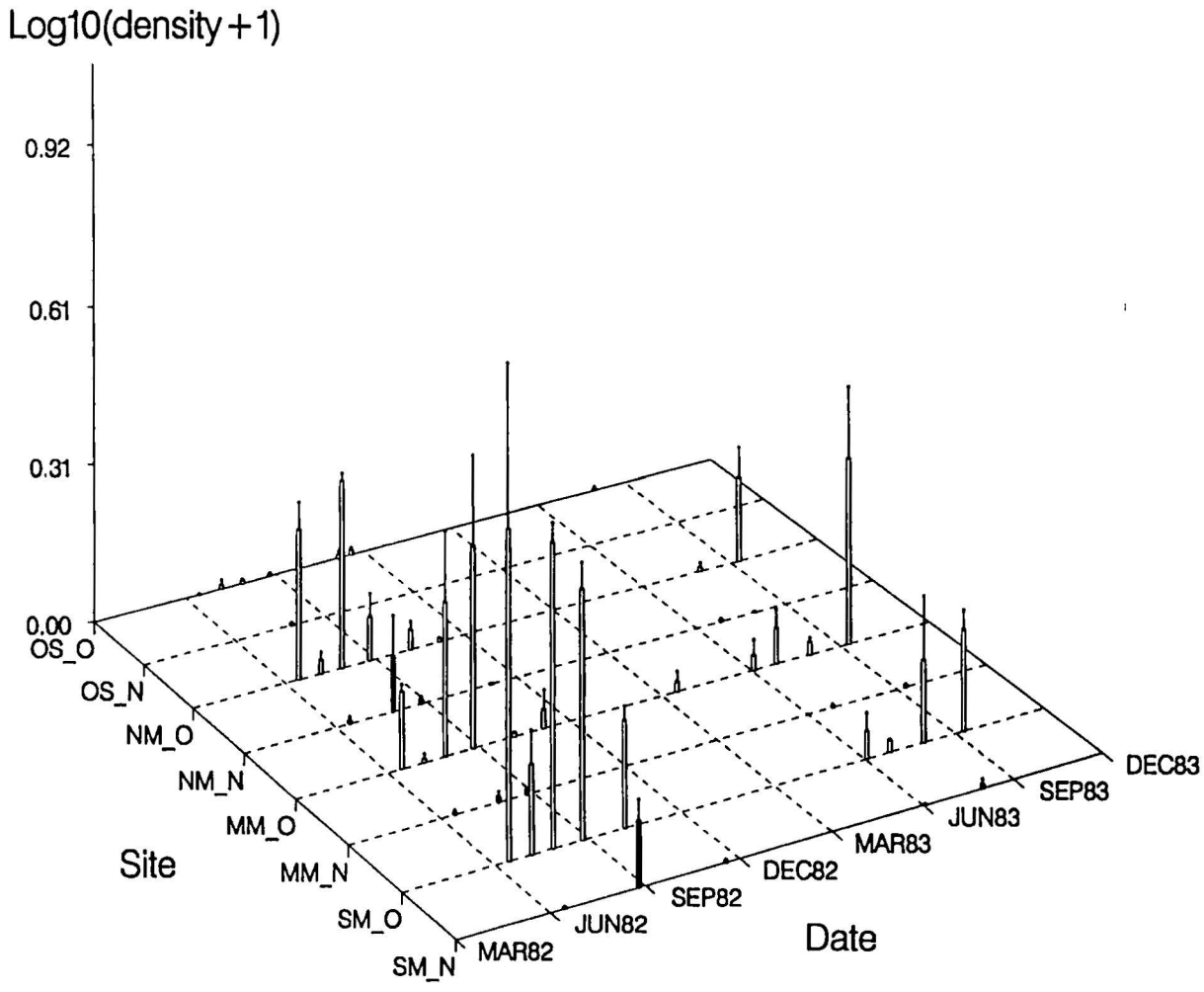
Upogebia affinis zoea



Pagurus longicarpus zoea



Euceramus praelongus zoea



are distributed throughout the waters inside the Chesapeake Bay (Wass, 1972). The estuarine habitat of the adults, combined with the estuarine to nearshore occurrence of the larvae lead to classifications of retained estuarine and retained estuarine-transitional by Johnson (1982) and Maris (1986) respectively. The results of this study generally support this hypothesized larval strategy.

***Rhithropanopeus harrisii* zoea** Zoeae of this species, a member of the mud crab family (Xanthidae), were present from June-July to October of 1982, with peaks in July and August, and were most abundant in the oblique sites of the bay mouth area (Figure 7b). These larvae were not found in the sampling area in 1983.

This pattern of late summer abundance, with *Rhithropanopeus* larvae remaining in the estuary, has been seen in earlier studies in the Chesapeake Bay, and in other mid-Atlantic estuaries. Planktonic stages of *R. harrisii* were previously found in the lower bay and York River system (Sandifer, 1973; Goy, 1976; Johnson, 1982; Maris, 1986), first appearing in samples taken in May or June, and last in samples from October, with peaks typically in the months from July to September (Sandifer, 1973; Goy, 1976). In contrast to this study, Sandifer (1973) did not find this species at his bay mouth station, however, they were found in the bay mouth by others (Goy, 1976; Johnson, 1982; and Maris, 1986). Similar patterns of estuarine prevalence have been

noted in the Delaware Bay and in North Carolina estuaries (Lambert and Epifanio, 1982; Williams, 1971).

This species of mud crab is common within the estuaries of the Atlantic Coast (Williams, 1984), and the adults of this species are found from the freshwater portions of the Chesapeake Bay into areas with salinities of 18 ppt, generally on bottoms with some relief: *eg* with rocks or gravel, in oyster beds, among trash (Wass, 1972).

Because both the adults and larvae are found within the bay, both Johnson (1982) and Maris (1986) consider this species to be retained estuarine in the Chesapeake Bay. In the Delaware Bay, this species also shows a spatiotemporal pattern of abundance consistent with a retained-estuarine early life history (Lambert and Epifanio, 1982), and a pattern of larval behavior has been described which could result in this pattern of estuarine retention (Cronin and Forward, 1982). The results of this study are also consistent with a retained-estuarine recruitment strategy for *Rhithropanopeus*.

***Callianassa* sp. A. zoea** These larvae were found predominantly in mouth oblique samples taken from June to September of 1982, with peak abundances in June, July, and August (Figure 7c). They were found sporadically in 1983. These zoeae were called "sp. A." because they were the first members of this genus to be encountered during this study by the taxonomists (Butt, *pers comm*).

Larvae of this genus have been previously found in the Chesapeake Bay by Sandifer (1973), Goy (1976), and Maris (1986). Sandifer was only able differentiate between three species, calling them *Callianassa* sp. A,B & C; while Goy and Maris were able to identify two species: *C. atlantica* and *C. biformis*. Goy found *C. atlantica* to be predominant in the lower bay, but Maris found mostly *C. biformis* in his lower bay samples. Because neither *C. atlantica* nor *C. biformis* was consistently found to be more abundant in these earlier works, I will not attempt to speculate which species was taken in this study.

Goy's and Sandifer's most abundant *Callianassa* larvae were present from July to September, predominantly in the lower Chesapeake Bay, contrasting somewhat with the June start of this study. Adults of the genus *Callianassa*, members of the mud shrimp superfamily (Thallanassidae), are polyhaline in their Chesapeake Bay distribution (Wass, 1972), and generally are found in burrows in estuarine and nearshore sediments along the Atlantic coast (Williams, 1984). Maris (1986) found both *Callianassa atlantica* and *Callianassa biformis* overwhelmingly more common in his bay mouth samples than in samples from other areas, and combined this with the estuarine and nearshore distribution of the adults, he concluded that both of these species are retained estuarine-transitional. This hypothesis is supported by the spatial distribution defined by this study.

***Pinnixa* spp. zoea** Larvae of *Pinnixa* were found predominantly from June to September of 1982, and in July and August of 1983 (Figure 7d). They were taken in greatest numbers in mouth oblique samples, and were much less abundant in 1983 than in 1982.

The temporal pattern observed was similar to seasonal occurrences found for Pinnixid larvae in earlier studies. Both Sandifer (1973) and Goy (1976) found three species of *Pinnixa* in their samplings of the bay: *Pinnixa cylindrica*, *P. chaetopterana* and *P. sayanna* were all most abundant in the late summer to early fall. *Pinnixa chaetopterana* has been found from June to November (Goy, 1976), primarily in the lower bay (Goy, 1976), as well as in the York River (Sandifer, 1973). Peak abundances of these larvae have been found in July (Goy, 1976; Sandifer, 1973), as well as August and September (Goy, 1976). *Pinnixa cylindrica* was found by both investigators from July or June to October, with a peak in October during Goy's (1976) sampling, and was found primarily in the mouth area of the bay. *Pinnixa sayana* was found in both Sandifer and Goy's surveys in the lower bay, during July or June to October, with maxima in September and October, respectively. Goy also had a category of *Pinnixa* spp. zoea, which contained latter stages of *P. cylindrica* and all larval stages of *P. lunzi* and *P. retinens*. He found these larvae primarily in lower bay and bay mouth samples from July to November, with peaks in September. This genus is represented by several species, predominantly within the Chesapeake Bay, with members generally commensal with other invertebrates (Wass, 1972; Williams, 1984). This estuarine

distribution of the adults, combined with a generally estuarine nearshore distribution of the larvae in his study, led Maris (1986) to consider this species retained estuarine-nearshore. Johnson (1982) found the megalopa most abundant outside of the bay mouth and considered this species to be expelled estuarine. The zoeae found in this study were found in the bay mouth, and not in high numbers at the offshore sites. However, the megalopal stage was not considered in this study and therefore I can not support either of these positions.

In support of Johnson, in studies done in the Delaware Bay, evidence has been presented which indicates offshore development (Brookins and Epifanio,1985): *Pinnixa* spp. larvae are most abundant on ebbing tides in the Indian River Inlet of Delaware. Additionally, Dittel and Epifanio (1982) found larvae of *Pinnixa chaetopterana* and *P. sayanna* with highest numbers in bottom waters of Delaware Bay, possibly catching these larvae during the reinvasion process.

***Emerita talpoida* zoea** *Emerita talpoida* zoeae were found throughout the sampling area in 1982, both offshore and in the mouth, although predominantly in the oblique collections (Figure 7e). These zoeae were more prevalent in 1982 than 1983 in the sampling area. Seasonally, they were found most commonly from June through September in both years.

Larvae of this species have also been found during the summer in the lower bay, and especially in the mouth, by Sandifer (1973), Goy (1976) and

Maris (1986). Adult mole crabs are found in high energy sandy beaches (Williams, 1984), and are found in the polyhaline waters within the Chesapeake Bay, as well as in the euhaline beaches of the nearby coast. Maris found it heavily at his offshore station, leading him to conclude that it was retained offshore. It has been found in greatest numbers in the waters near Delaware Bay in July and August (Dittel and Epifanio, 1982).

***Uca* spp. #2 zoea** Zoeae of the genus *Uca* were taken throughout the sampling area in both years (Figure 7f). Oblique tows had somewhat higher densities than neuston tows taken on the same cruise at the same station. In 1982, more larvae were taken in the mouth than in the offshore area. In 1983, two samples were taken at the offshore station that were of the same order of magnitude as those in the mouth area. Also in 1983, mouth oblique samples generally had much higher abundances than their neuston counterparts. Seasonal patterns were similar in both years, with most zoeae taken from June to August-September, and maxima found in July and August.

Larvae of this genus have been commonly found in the Chesapeake Bay (Sandifer, 1973; Goy, 1976; Johnson, 1982; Maris, 1986). The seasonal pattern found in my analyses reflected the results of earlier studies, *Uca* larvae have been present in the plankton from as early as June or May to as late as October or September (Sandifer, 1973 and Goy, 1976, respectively), with peaks in July or August. The adults of three species of fiddler crab, *Uca minax*, *U. pugnax* and *U. pugilator*, are found in the salt marshes and mudflats

of the Atlantic coast (Williams, 1984), and commonly in the Chesapeake Bay (Wass, 1972). The estuarine distribution of the adults, combined with Johnson's (1982) observation of significant numbers of megalopae offshore, led him to consider this larvae to be expelled-estuarine in its dispersal-recruitment pattern, and Maris (1986) further delineated its pattern as expelled offshore with estuarine spawning, in order to differentiate its pattern from that of *Callinectes*, whose females travel to the estuarine-ocean interface to spawn. Larvae were not found in high numbers offshore in my study, however Johnson (1982) had several stations he considered offshore which were nearer the bay mouth than my offshore station.

These larvae have also been extensively studied in the Delaware Bay area. Epifanio *et al* (1988) reviewed the literature concerning *Uca* larvae distribution and summarized it as follows: the zoeae are released in tidal creeks, they are taken out of these areas on ebbing tides, through the estuary and onto the continental shelf, and their megalopal stages reinvade the estuary. Support for this mechanism comes from a study of *Uca* larvae in the Indian River, a small inlet near the Delaware Bay, when first stage zoeae had been observed at their maximum in surface waters on ebbing tides, and megalopal stages were most abundant in the bottom waters of incoming tides (Brookins and Epifanio, 1985). In the Delaware Bay, they have the same late summer distribution as has been observed for the Chesapeake Bay, both by this and the other studies cited earlier, with peaks in July and August (Dittel and Epifanio, 1982).

***Upogebia affinis* zoea** These larvae were found in number from June to September of both 1982 and 1983, with maximum abundances from July through September (Figure 7g). They were generally less abundant in 1983 than they were in 1982, especially in the mouth neuston tows. Mouth areas had much higher numbers of *Upogebia* than did offshore areas in both years.

These larvae were found by Sandifer (1973), Goy (1976) and Maris (1982), with spatiotemporal patterns similar to those I observed. Sandifer and Goy found this species in the lower bay, from June to October with peaks in July to September. The adults of this species, a mud shrimp in the superfamily Thalassinoidea, are found intertidally and to depths of 29 meters in estuaries (Williams, 1984), and are found throughout the Chesapeake Bay in its polyhaline waters (Wass, 1972). Maris (1986) considered *U. affinis* to be retained estuarine-transitional, and, while this study had no stations in the transitional area between the mouth and the offshore station, the results of this study do not conflict with Maris's conclusion.

***Pagurus longicarpus* zoea** Zoeae of *P. longicarpus* were found into the late fall, later than the other members of this cluster (Figure 7h). They were found in significant numbers from May-June to October of 1982, with larvae still found in November at the offshore oblique site during this year. In 1983 they also had a broad seasonal distribution, but were seen in overall lower number than in 1982. They were found in both the mouth and offshore areas of both years, with much higher numbers in the oblique samples. Due

to the relatively strong showing in offshore samples, the assignment of this species to this group is questionable. The distribution of the adult hermit crabs at depths of up to 200 meters along the Atlantic coast (Williams, 1984), and its local distribution in euhaline offshore waters as well as in the polyhaline waters of the Chesapeake Bay (Wass, 1972), also brings into question its inclusion in this group.

The spatial and temporal patterns of distribution found in this study, are supported by the results of Sadler (1984), and Goy (1976). In both of their studies, *Pagurus longicarpus* was found from May through the fall, with peaks in the late summer months of August and September. Both found these larvae in abundance in the lower bay. Sadler also found late stages in abundance in his nearshore stations.

***Euceramus praelongus* zoea** These larvae were found in the mouth oblique samples from June to September of both years with some found in October of 1982; they were less abundant in 1983 than they were in 1982 (Figure 7i).

While the sampling interval of this study prevented me from identifying a temporal peak, the seasonal occurrence was similar to past studies. Sandifer (1973) and Goy (1976) found this species in the lower bay, during the months of June to October or November, with peaks in August and September. The adults of this species are found, uncommonly, on beaches from Delaware to Texas (Williams, 1984), and within the Chesapeake Bay (Wass, 1972). Maris

considered this species retained transitional-nearshore, finding the majority at his bay mouth station.

Cluster summary

The pairings in this group were loosely defined, with all members but *Pagurus longicarpus* found primarily in the mouth oblique samples in 1982, and in much lower numbers in 1983 (Figure 6a). These plankters were most common from June to September or October, with maximum numbers in July and August. Examination of individual taxa plots (Figures 7a to 7i) showed most taxa followed this pattern of summer abundance followed by occurrence into the early fall, with the exception of *Pagurus longicarpus*, which was present in the plankton through November of 1982 (Figure 7h, note: no samples were taken in November of 1983). The decrease from 1982 to 1983 was not found for *Uca*, while *Pagurus* did not have the extreme decrease shown by the most of the other taxa (Figures 7h and 6a, respectively).

The literature shows a variety of detailed spatiotemporal patterns, and accompanying assignments of dispersal-recruitment modes for these organisms. With the exception of *Pagurus*, *Emerita* and *Euceramus*, the adult stages of the species in this group are estuarine, found primarily in the polyhaline reaches of the Chesapeake Bay. The inclusion in this group of *Emerita* and *Euceramus* may be explainable, because the adults of both species are beach dwelling, and are thus not found far onto the shelf. With the exception of *Pagurus*, the general seasonal (late summer) and areal (lower estuarine) patterns reported in

the literature for the larvae of these species were similar, and were corroborated by the patterns found in this study.

VC2

Assemblage:

Hexapanopeus angustifrons zoea (mud crab) and *Pinnixa cylindrica* zoea (pea crab).

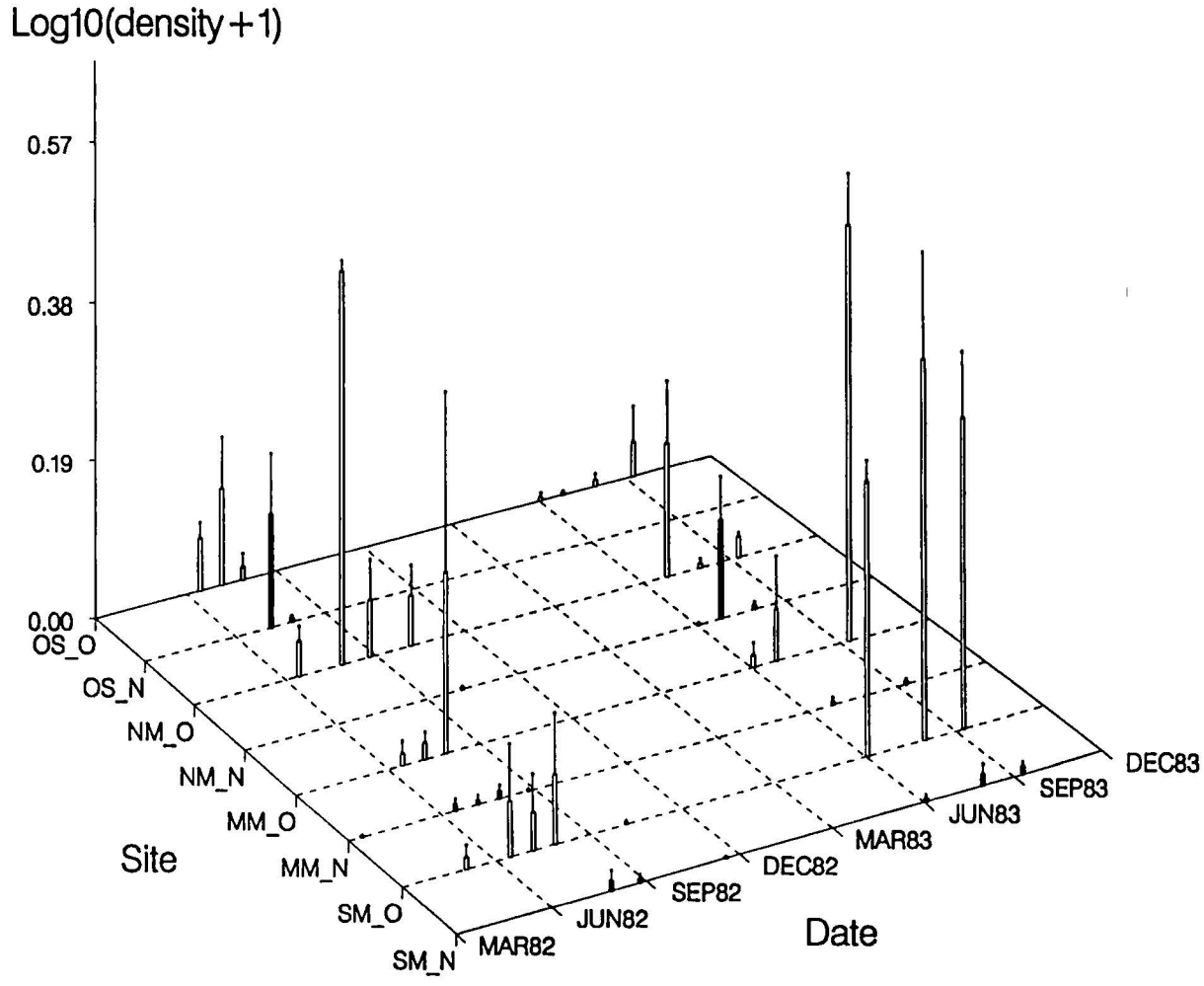
Individual Members:

***Hexapanopeus angustifrons* zoea** The overall pattern of abundance for this zoea was very similar to that of the members of VC1, although its pattern of occurrence was spottier in 1982 than many of the members of VC1. Larvae of this species were prevalent from June to September in both years, with greatest abundance at the mouth oblique sites (Figure 8a).

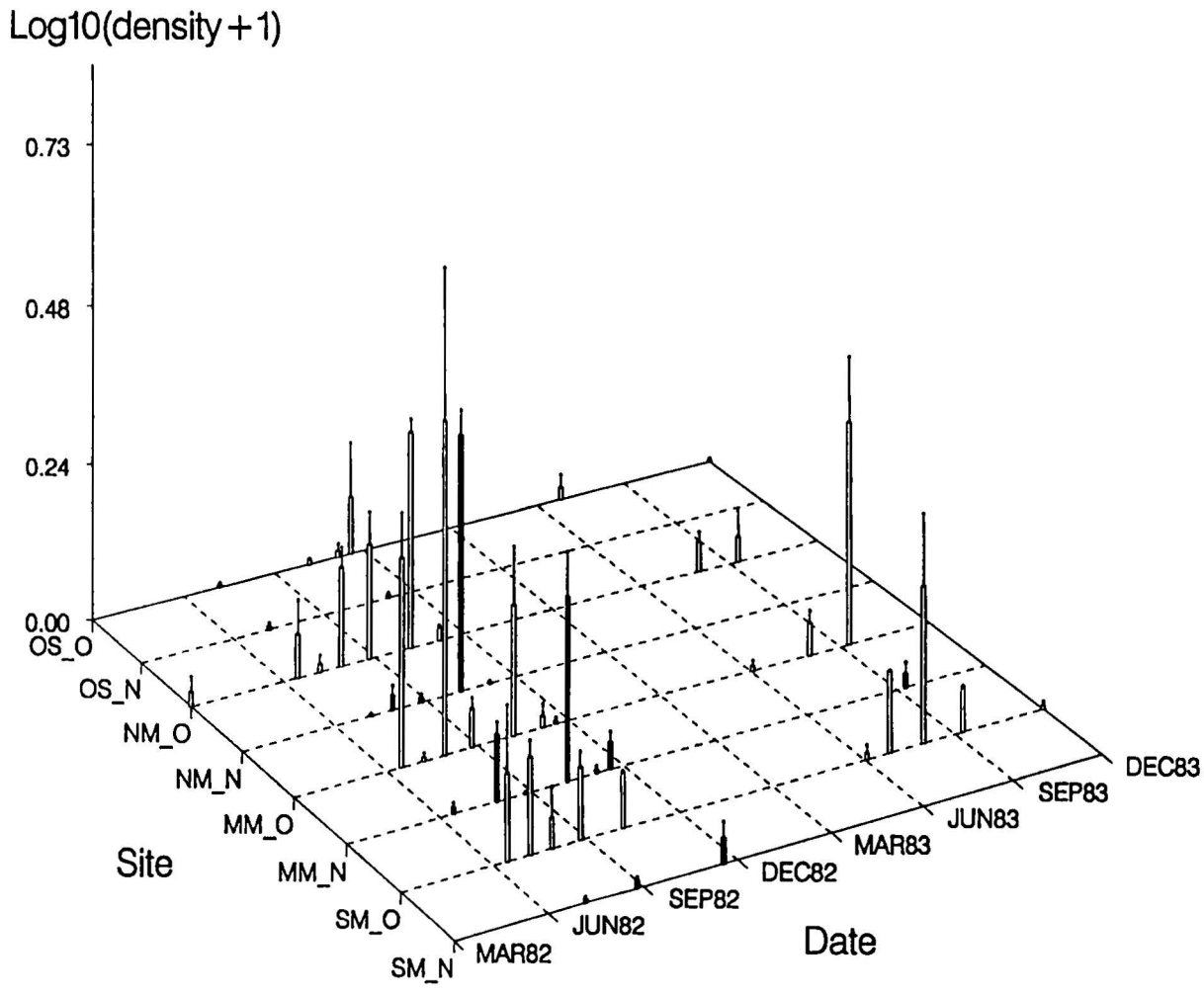
The results found for this species were consistent with earlier studies. Sandifer (1973) and Goy (1976) found this species from June through October or November, with peaks in July through September, with most larvae found in the lower bay. The adults of this species, a mud crab of the family Xanthidae, are found in estuaries and nearshore regions along the Atlantic coast, including the Chesapeake Bay (Williams, 1984; Wass, 1972). Based upon this general adult distribution and, his and earlier reported larval distributions, Maris considered this larvae to be retained transitional-nearshore.

Figure 8. Three-dimensional spatiotemporal plots of log-transformed individual taxon's mean abundance (+ 1 SE) for each member of VC2. Taxa are ordered according to VARCLUS dendrogram (Figure 4): a) *Hexapanopeus angustifrons* zoea (p.68), b) *Pinnixa cylindrica* zoea (p.69). Shaded bars are neuston samples, and unshaded bars are oblique samples.

Hexapanopeus angustifrons zoea



Pinnixa cylindrica zoea



These larvae have also been found in the mouth areas of other Atlantic coast estuaries. In a single station in the mouth of Delaware Bay, these larvae were found from June to September with some found in October (Dittel and Epifanio, 1982). Larval stages, including megalopae, were also found at the estuarine-oceanic interface in North Carolina (Williams, 1971).

***Pinnixa cylindrica* zoea** The general pattern of abundance for this species was similar to its congener(s), *Pinnixa* spp zoea, and the other members of VC1. It was most commonly found in samples from June to October of 1982, with fewer occurrences in 1983 (Figure 8b). Like *Hexapanopeus* and the members of VC1, it was most common in oblique samples.

The spatial pattern found for *P. cylindrica* was very similar to that of *Pinnixa* spp. zoea. It did differ from its fellow Pinnixid(s), by having individuals found in October, which made its seasonal pattern of occurrence more similar to that found for Pinnixids in earlier studies (see discussion of the results of Sandifer, 1973 and Goy, 1976 in VC1 section), than that found for *Pinnixa* spp. in this study. *Pinnixa cylindrica* is a pea crab, as are all members of its genus. The adults are found primarily within the Chesapeake Bay, leading Maris (1986) to classify it as retained-estuarine nearshore, even though the megalopal distribution found by Johnson (1982) led him to consider it expelled-estuarine. Because this study had only one offshore station, and

megalopae of *Pinnixa cylindrica* were not observed, I cannot support one or the other of these explanations.

Cluster Summary

The two species of this cluster had the same general pattern as the members of VC1, with high scores in summer mouth oblique samples (Figure 6b), though *Pinnixa* had significant numbers into October. These patterns were also reported in the literature for these larvae. *Pinnixa cylindrica* shared VC1's precipitous drop in 1983, but *Hexapanopeus* showed only a modest decrease, if any. This cluster was not as strong as was VC1 (Table 3).

VC3

Assemblage:

Ovalipes spp. zoea (lady crab), *Acetes americanus carolinae*, and *Libinia* spp. zoea (spider crabs).

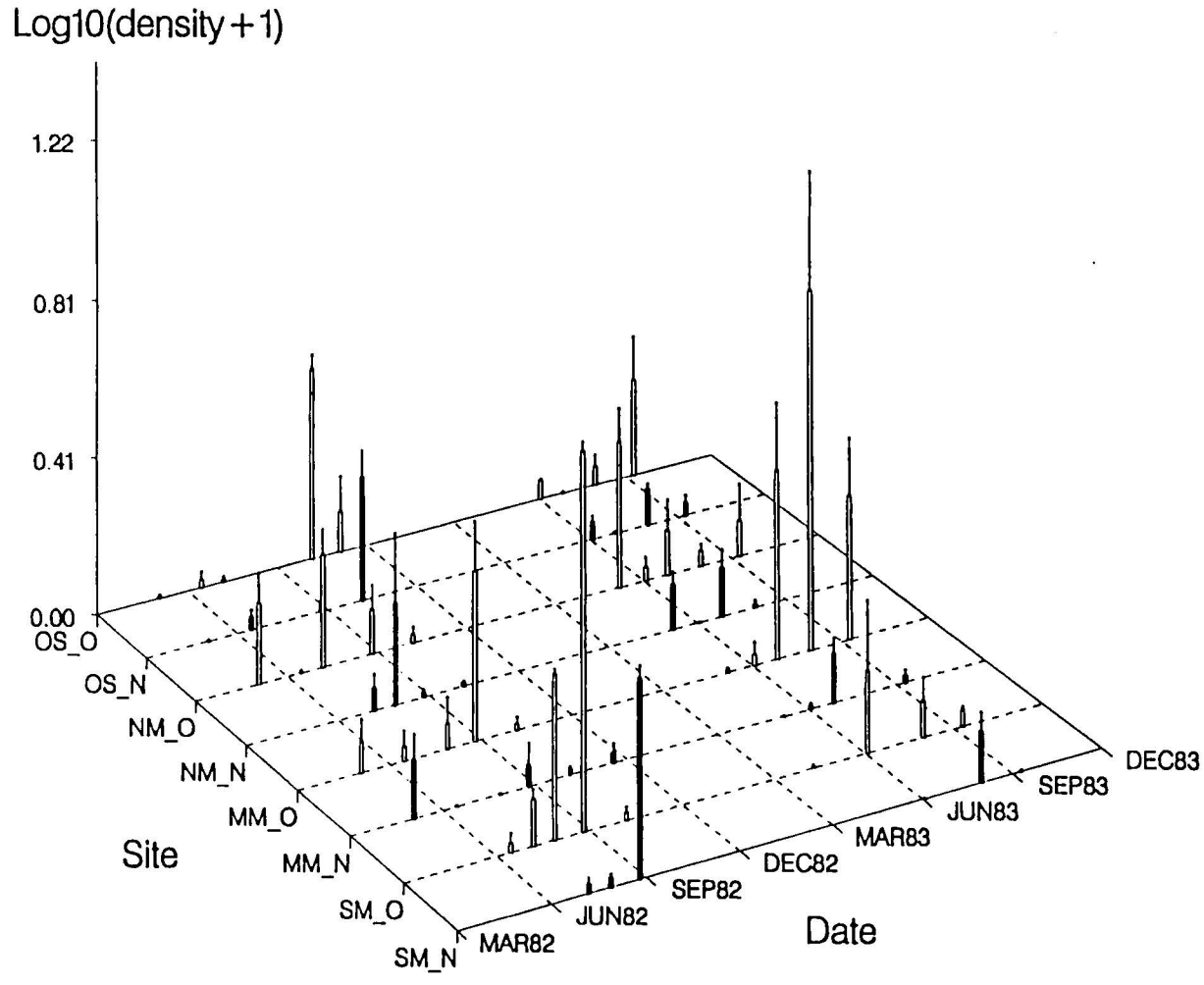
Individual Members:

***Ovalipes spp.* zoea** Plankters of this genus were abundant from May-June to September-October of both 1982 and 1983 (Figure 9a). *Ovalipes* larvae were prevalent at the oblique sites, with similar numbers in the bay mouth and offshore.

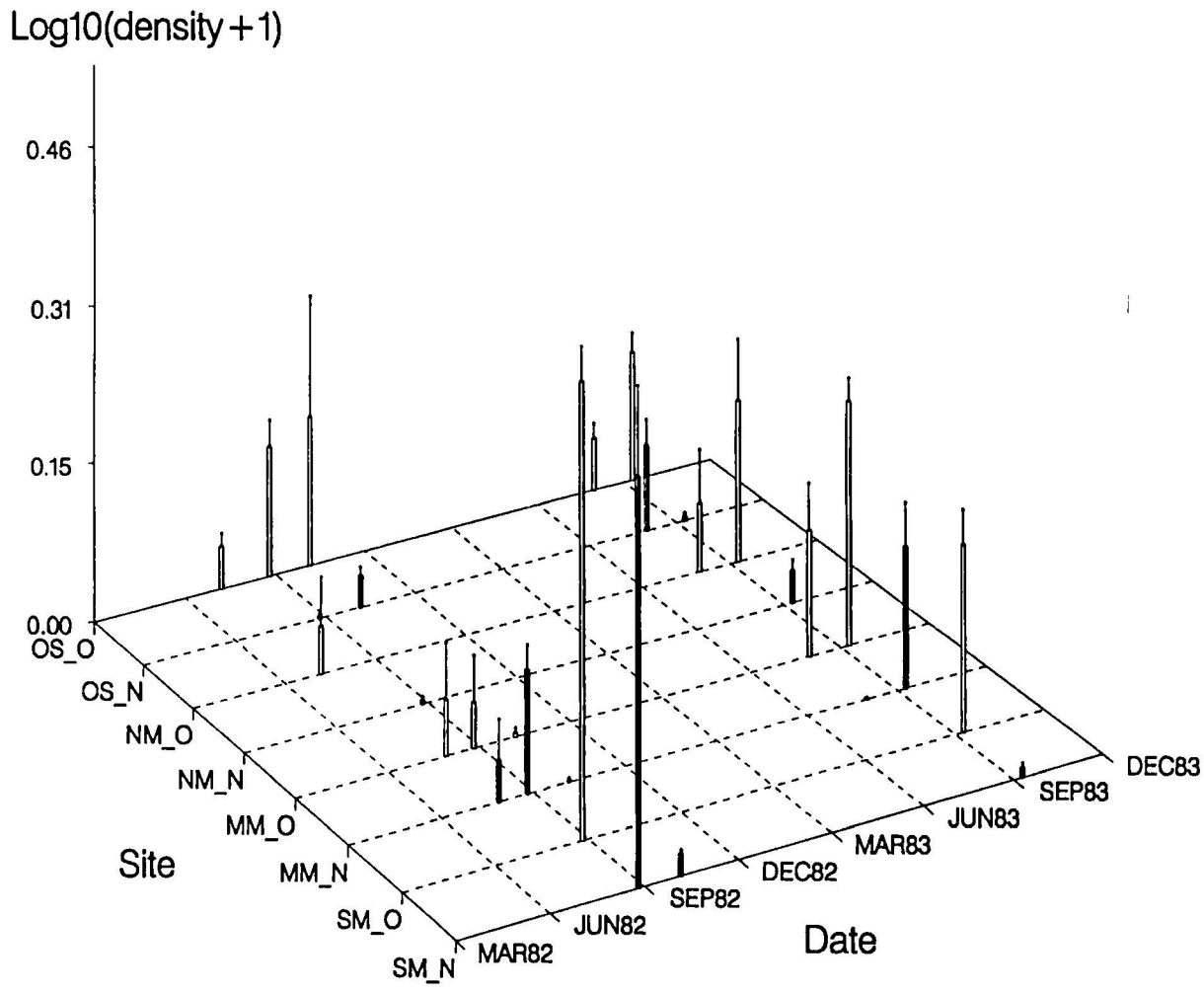
Two species of *Ovalipes* have been found in the bay, with *O. oscellatus* being much more common than its congener *O. quadulpensis*. Larvae of

Figure 9. Three-dimensional spatiotemporal plots of log-transformed individual taxon's mean abundance (+ 1 SE) for each member of VC3. Taxa are ordered according to VARCLUS dendrogram (Figure 4): a) *Ovalipes* spp. zoea (p.72), b) *Acetes americana carolinae* postlarva and larva (p.73), c) *Libinia* spp. zoea (p.74). Shaded bars are neuston samples, and unshaded bars are oblique samples.

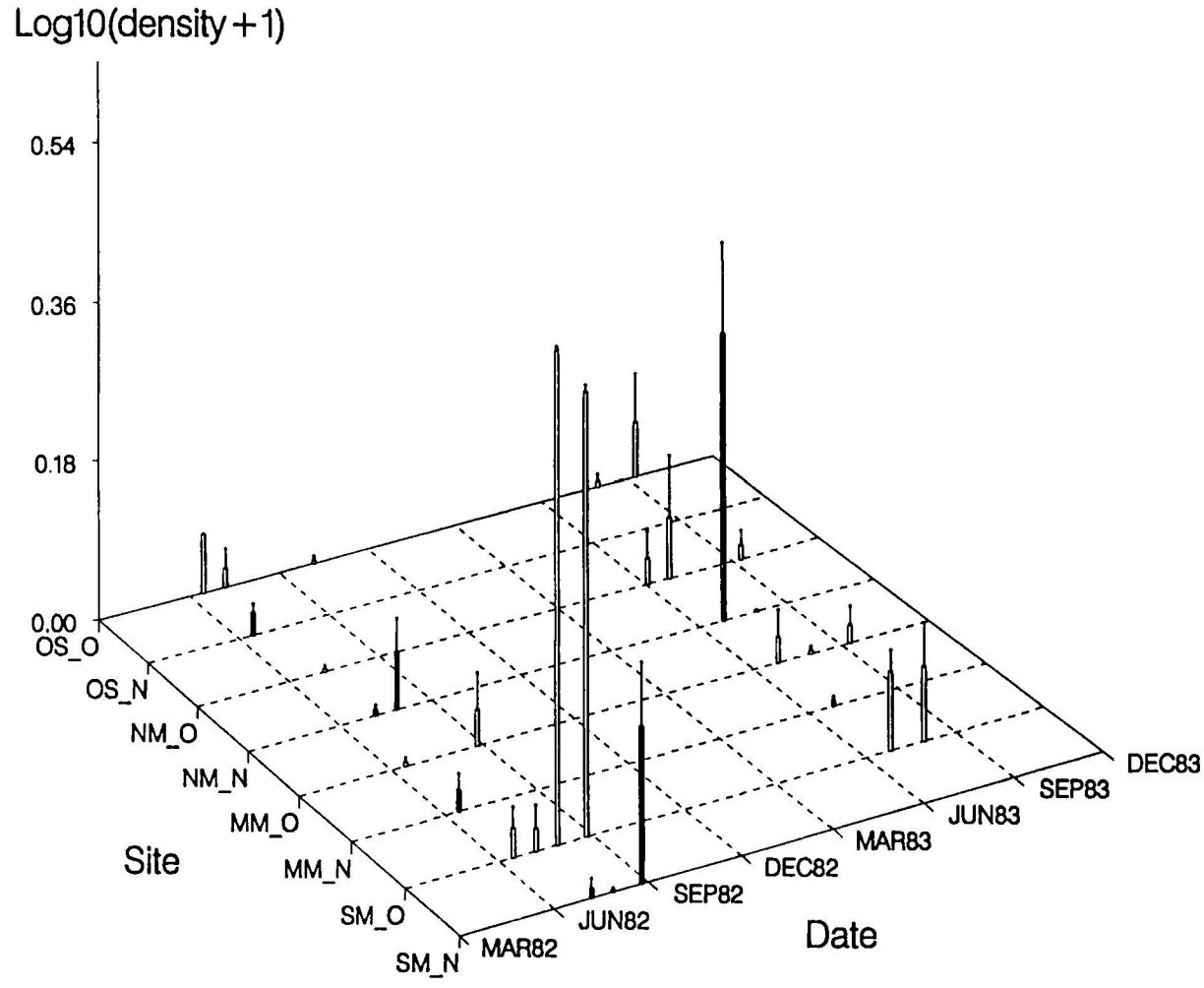
Ovalipes spp. zoea



Acetes americanus carolinae



Libinia spp. zoea



Ovalipes oscellatus have been found by Sandifer (1973), Goy (1976), Johnson (1982), and Maris (1986). Sandifer found it infrequently at his lower bay and bay mouth stations, but with a pattern of seasonal abundance similar to that found for *Ovalipes* spp. in this study - in the summer (June) through the fall (October), and most commonly in September.

Ovalipes oscellatus, the lady crab, has a polyhaline to euhaline distribution in the Chesapeake Bay region (Wass, 1972). It and its congener, *Ovalipes quadulpensis*, are found on the Atlantic shelf at depths of up to 95 m and 227m, respectively (Williams, 1984). The even distribution of larvae between the bay mouth and the offshore sites in this study is consistent with an adult distribution extending onto the shelf. This study's results also allow that the species sampled may be either or both of these congeners.

Acetes americanus carolinae Postlarvae and larvae of this species were found from July-August to September-October (Figure 9b). They, like other members of this cluster, were primarily in the oblique sites, with similar numbers in the bay mouth and offshore.

Earlier reports of this plankter are consistent with this late summer to early fall seasonal pattern. Larvae and postlarvae of *Acetes americanus carolinae* were previously collected in the Chesapeake Bay by Goy (1976). He found peaks in abundance from July to November in the bay mouth area.

Acetes adults are found in estuarine and in oceanic waters to a depth of 42m (Williams, 1984), and have been found year round in Bogue Sound North

Carolina. In the Chesapeake Bay, individuals have been collected in polyhaline and euhaline waters (Wass, 1972).

***Libinia* spp. zoea** These larvae were found from June-July to August-September, primarily in the oblique tow samples. (Figure 9c). There were more in the mouth oblique samples than in the offshore oblique samples.

Libinia spp. larvae have been found by numerous investigators in the Chesapeake Bay (Sandifer, 1973; Goy, 1976; Johnson, 1982; Maris, 1986). Sandifer and Goy found larvae in the lower bay, occurring from May to November with peaks in July to September. There are two species of *Libinia* in the Chesapeake Bay area: *L. dubia* and *L. emarginata* (Wass, 1972), both known commonly as spider crabs. Adults of *L. dubia* are found in the most saline reaches of estuaries and onto the shelf to depths of 46m (Williams, 1984), and in the bay area, the adults are found in polyhaline and euhaline habitats throughout the bay and on the shelf (Wass, 1972). *Libinia emarginata* is also polyhaline, but primarily euhaline, and is found to depths of up to 124m along the Atlantic coast (Williams, 1984). *L. emarginata* is occasionally found in the Chesapeake Bay, but is found most often on the adjacent continental shelf (Wass, 1972). In contrast to the bay mouth predominance reflected by the results of this study, Johnson and Maris found these larvae primarily in offshore waters, leading both to conclude that this species is retained offshore.

Cluster Summary

This cluster had a similar spatial pattern to VC1 and VC2, with its predominance in the mouth oblique tows, however, it was somewhat more abundant offshore and it peaked in the month of September while VC1 and VC2 peaked in July and August (Figure 6c). In contrast to this study, earlier studies of the larvae and juveniles of these three species showed an oceanic distribution more consistent with the distribution of the adults. This study may not be in disagreement, as the single offshore station of this study may have missed the bulk of the larvae which were indeed offshore, and the association in this study, based largely upon the association of larvae taken in the bay mouth, may have been because these larvae were entrained together into the bay from the offshore waters.

VC4

Assemblage:

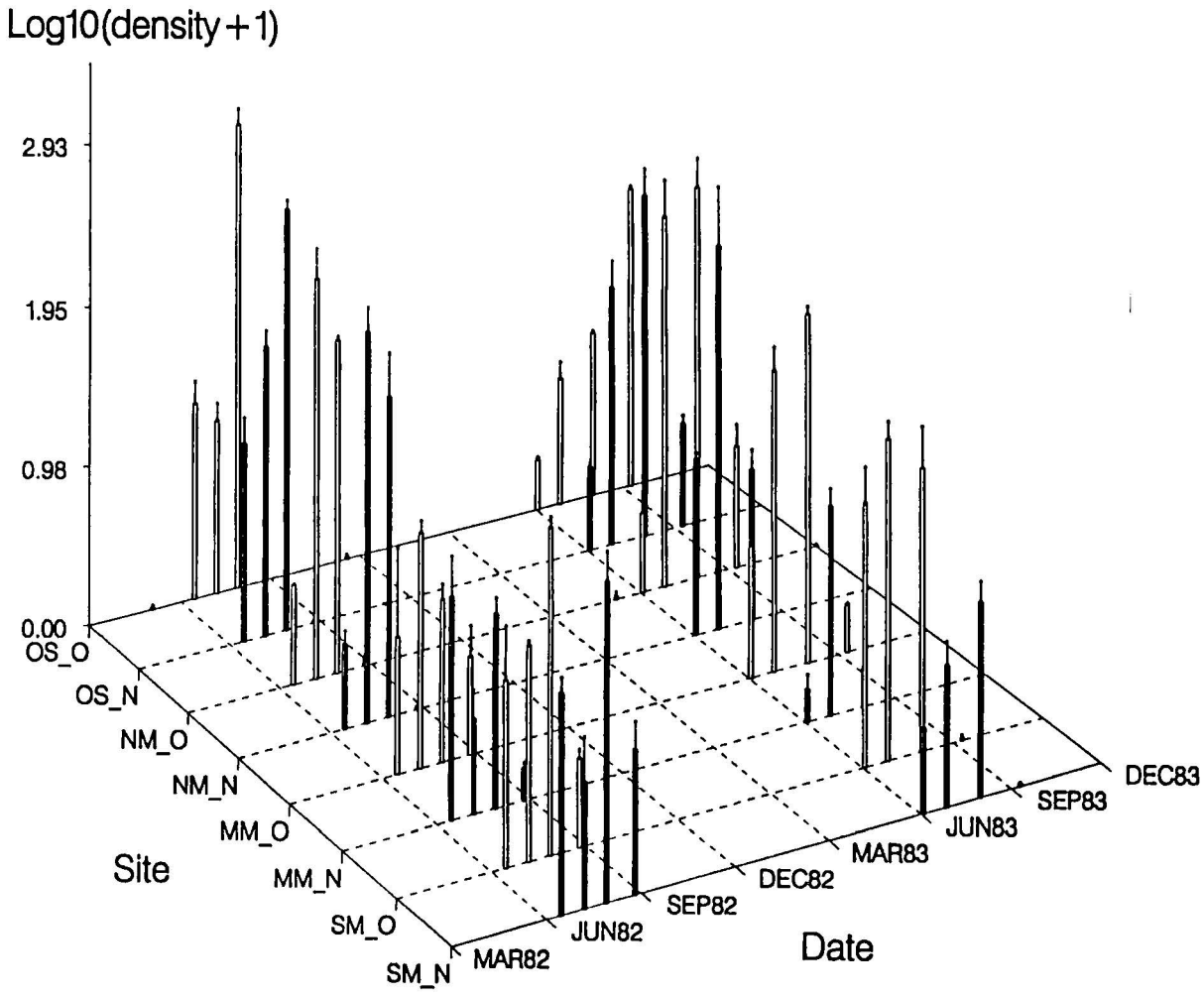
Callinectes spp. zoea (blue crab), Squillid antizoea (mantis shrimp), and *Ocypode* spp. zoea (ghost crab).

Individual Members:

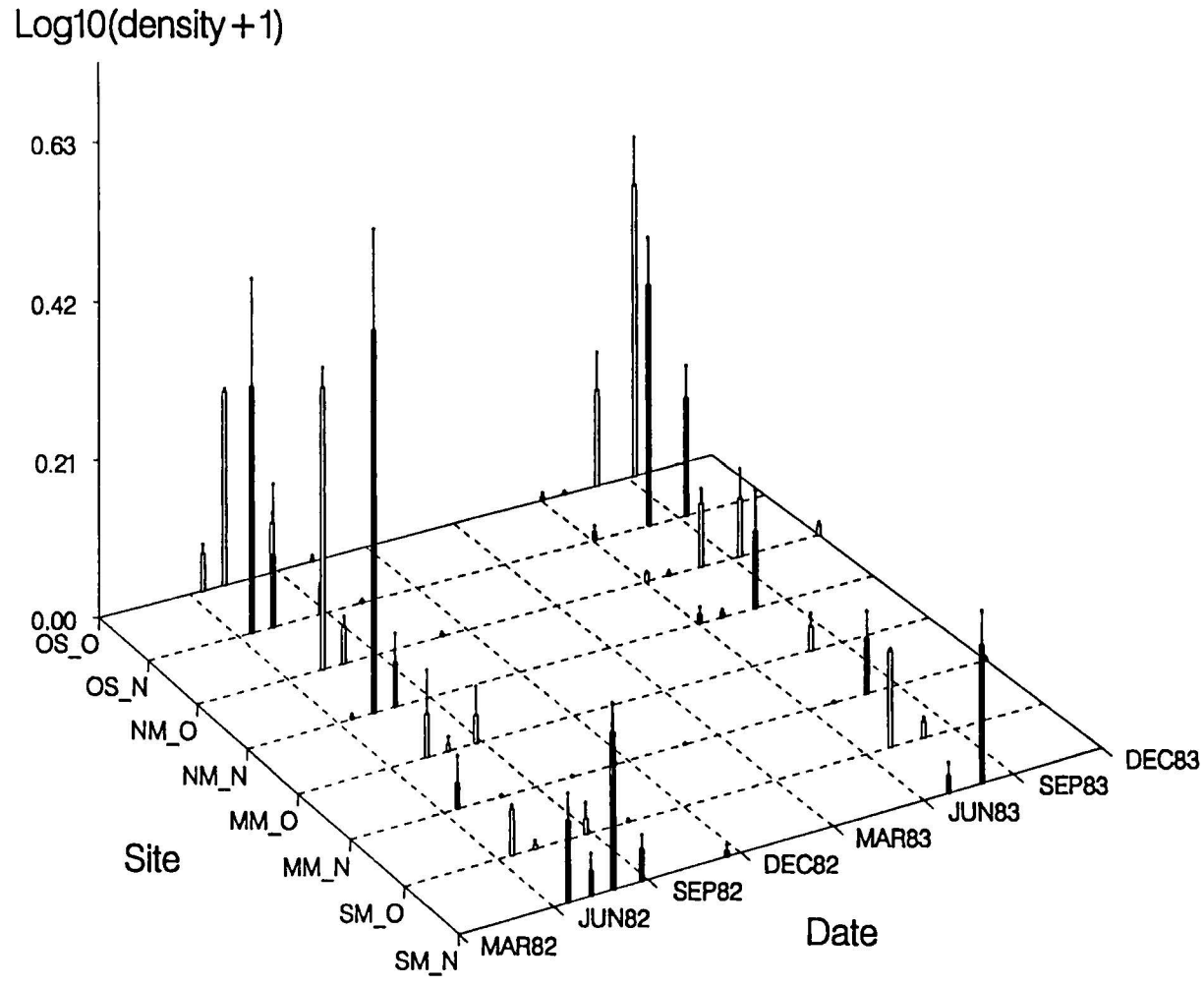
***Callinectes* spp. zoea** The zoeae of the blue crab were the most abundant summer plankters of this study (Figure 10a, Table 2). They were prevalent from June to August-September of both years, with similar

Figure 10. Three-dimensional spatiotemporal plots of log-transformed individual taxon's mean abundance (+ 1 SE) for each member of VC4. Taxa are ordered according to VARCLUS dendrogram (Figure 4): a) *Callinectes* spp. zoea (p.78), b) Squillid antizoea (p.79), c) *Ocypodes* spp. zoea (p.80). Shaded bars are neuston samples, and unshaded bars are oblique samples.

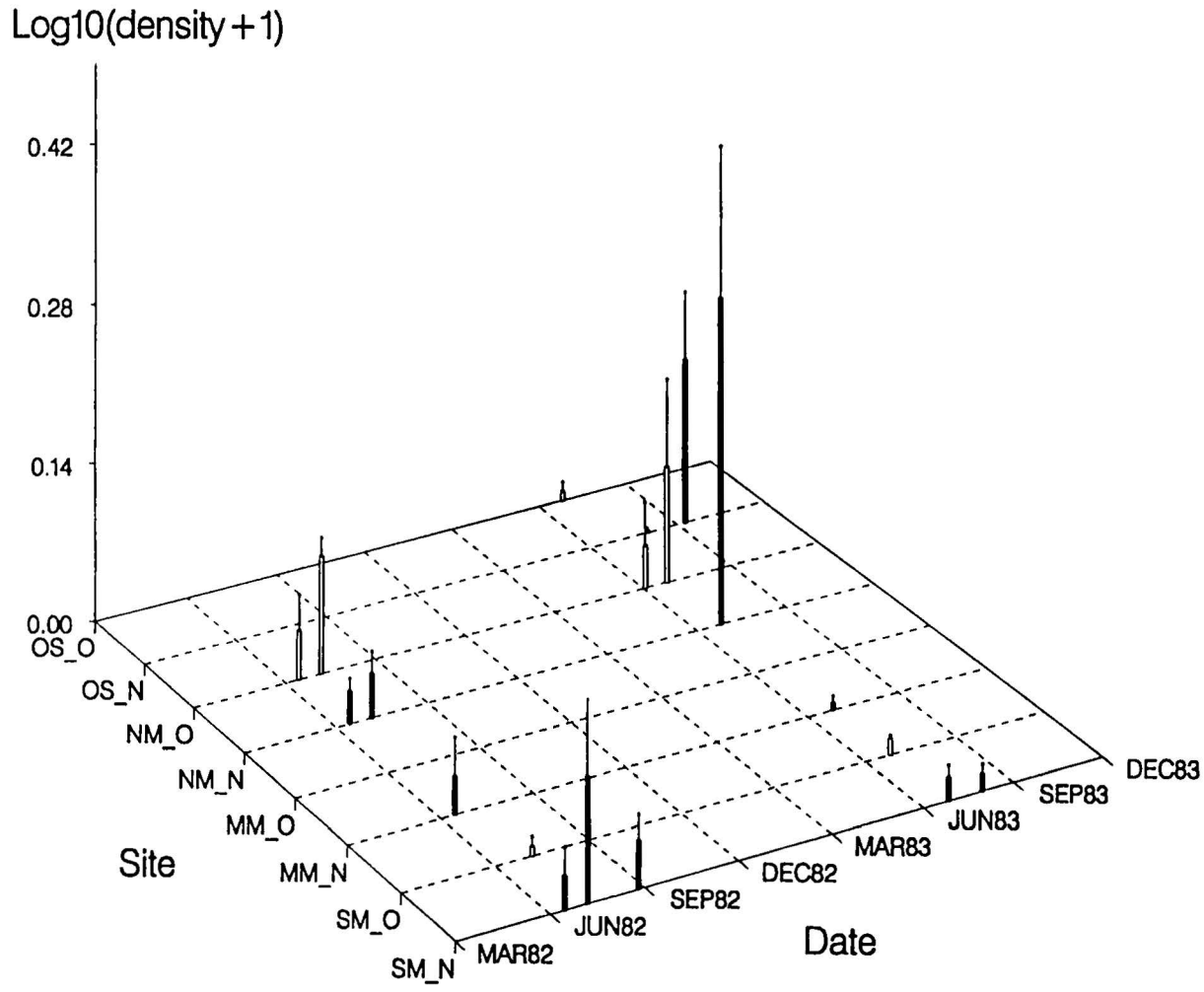
Callinectes spp. zoea



Squillid antizoea



Ocypode spp. zoea



abundances for concurrently collected neuston and oblique samples throughout the sampling area. In general, there were more *Callinectes* zoeae in the samples from the northern mouth and offshore stations, than in samples from the middle and southern mouth stations.

These zoeae were most likely *C. sapidus*, because its adults are very abundant in the bay (Wass, 1972). Zoeae of *Callinectes* have been included in a number of multi-species surveys in the Chesapeake Bay (Sandifer, 1973; Goy, 1976; Maris, 1986). The early life history of *Callinectes* has been studied extensively in the Chesapeake and Delaware bays, and these studies are summarized, along with information concerning the distribution of the adults, in the discussion of *Callinectes* spp. megalopae - found in the VC7 section to follow.

Squillid antizoea Larvae of this species showed an overall pattern similar to its co-member, *Callinectes* spp. zoea. These larvae were also prevalent from June to August-September, with higher abundances in the north mouth and offshore samples (Figure 10c). This species differed from *Callinectes* spp. zoea, in that it was more abundant in the mouth neuston samples than in the corresponding oblique samples.

Larvae of *Squilla empusa* in the Chesapeake Bay were first studied by Morgan (1980). The results of his study, as well as a summary of the adult distribution for *Squilla*, may be found in the *Squilla* (*empusa*?) protozoea discussion in the VC7 section.

***Ocypode* spp. zoea** Larvae of this species were taken sporadically from June to September throughout the study area (Figure 10b). They were generally higher in the neuston samples.

Larvae of the genus *Ocypode*, the ghost crabs, were previously collected by Goy (1976). He found only two larvae in his samples, both in the eastern Chesapeake Bay. Adult ghost crabs are found on sandy beaches in burrows found from the high tide line to up to a quarter mile from the beach (Williams, 1984). In the Chesapeake Bay, the adults are polyhaline to euhaline in distribution (Wass, 1972). Maris (1986) found *Ocypode* only in the night neuston samples from his offshore station, combining this result with the adult distribution, beaches primarily on the ocean, he speculatively concluded that this species has a retained offshore early life history strategy.

Cluster summary

Two members of this group, Squillid antizoea and *Callinectes* spp. zoea, are probably earlier stages of two members of VC7, *Squilla* (*empusa*?) protozoea and *Callinectes* spp megalopa. The association between these larvae is discussed in the VC7 section to follow. *Ocypode* was the weak member of this group, with a weaker correlation with the cluster than the other two members (Table 3), as well as a less similar spatiotemporal pattern (Figure 10b versus Figures 10a and 10c). This cluster has a pattern of predominance from June to late August-early September (Figure 6d), with higher scores (due

to *Squilla* and *Callinectes)* in both the neuston and oblique samples of the north mouth and offshore stations.

VC5

Cancer irroratus zoea (rock crab) and *Crangon septemspinosa* zoea (sand shrimp).

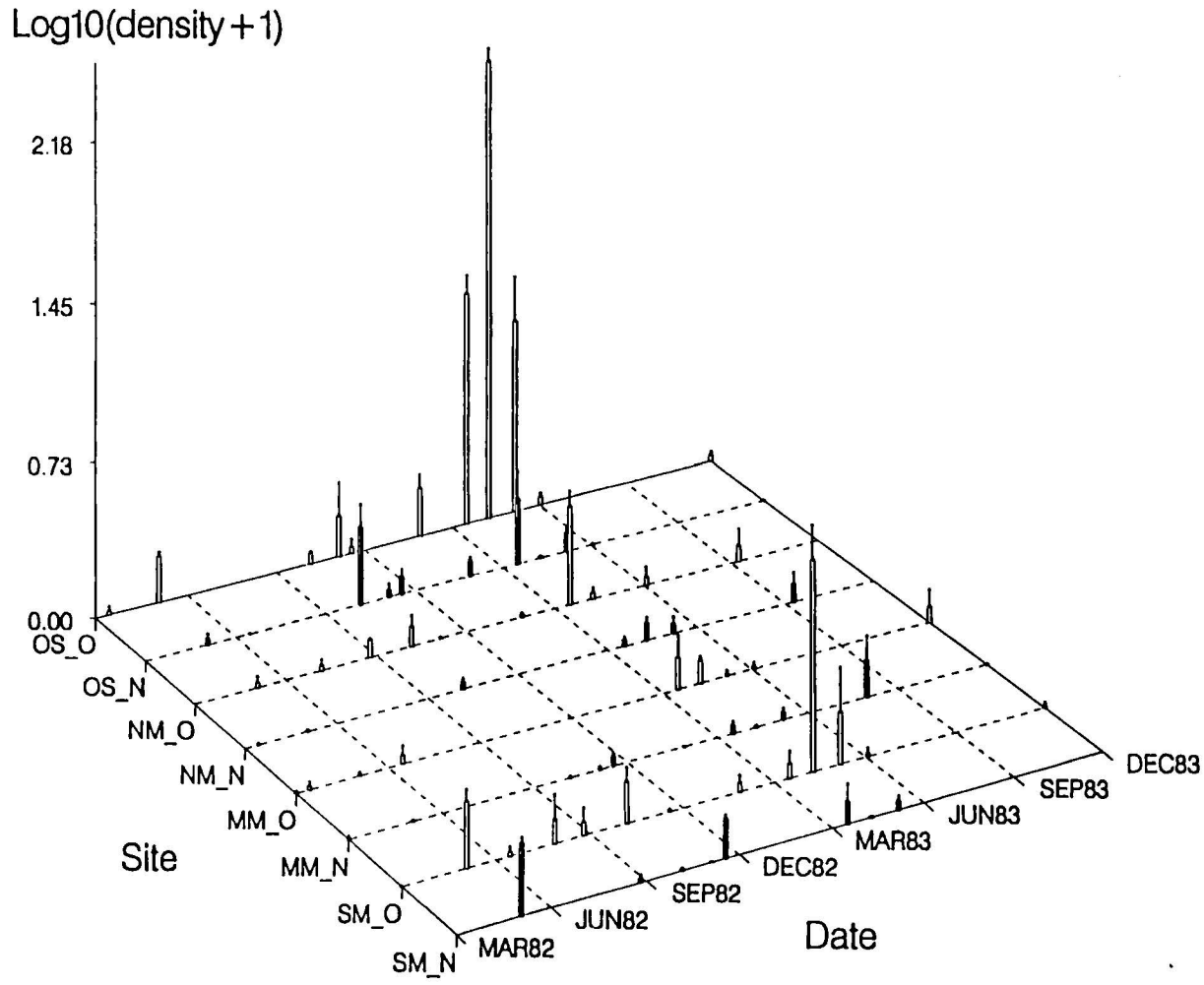
Individual Members:

***Cancer irroratus* zoea** Larvae of this species were found throughout the year at many of the sites (Figure 11a). They were present more often in oblique samples, and had one peak in the two years of the study: during March to May of 1983, primarily at the offshore oblique site.

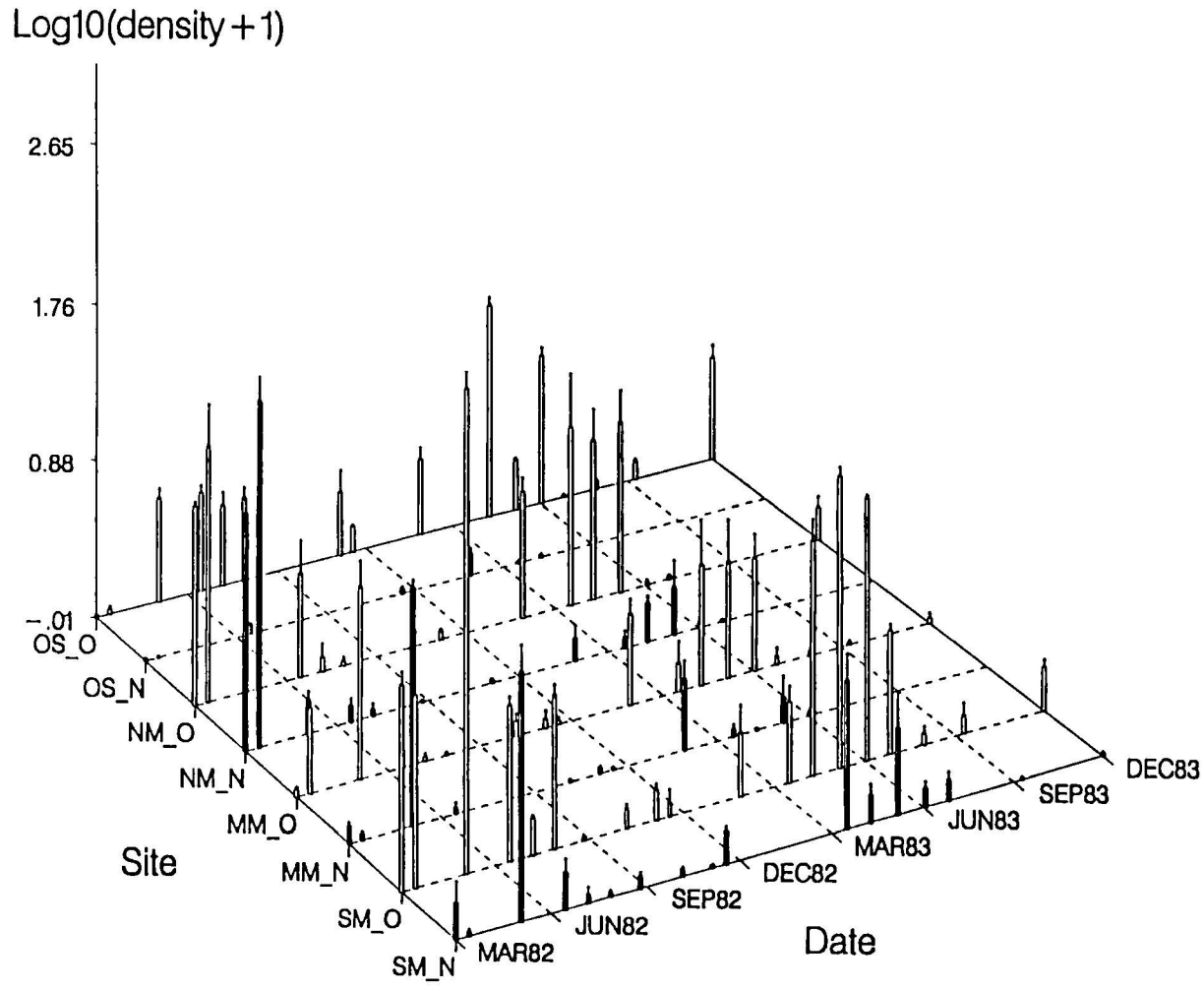
A May peak was also found in earlier published works. Sandifer (1973) found *Cancer* larvae in the lower bay and bay mouth, from May to October, excepting August, with a peak in May. Goy (1976) found the same May peak in abundance, but only found these larvae from April to July. The adults of this species, the rock crab, are primarily oceanic in distribution, reported at depths of up to 575m; they are also occasionally found in the lower reaches of estuaries (Williams, 1984). They are present in the polyhaline waters of the Chesapeake Bay, but are primarily taken from the shelf (Wass, 1972). In Johnson's July to September study, he found *Cancer* megalopae in the nearshore waters off of the bay. Based upon this evidence, he classified it

Figure 11. Three-dimensional spatiotemporal plots of log-transformed individual taxon's mean abundance (+ 1 SE) for each member of VC5. Taxa are ordered according to VARCLUS dendrogram (Figure 4): a) *Cancer irroratus* zoea (p.84), b) *Crangon septemspinosa* zoea (p.85). Shaded bars are neuston samples, and unshaded bars are oblique samples.

Cancer irroratus zoea



Crangon septemspinosa zoea



as retained offshore. Maris classified it with this dispersal-recruitment pattern also, although due to low numbers he did so speculatively. The peak in the offshore waters seen in this study, combined with the known adult distribution, supports the retained offshore hypothesis, although due to the relatively few larvae taken, speculatively.

***Crangon septemspinosa* zoea** Peak abundances of this larva were nearly as high as those of *Callinectes* spp. zoea, and *Crangon* was present to abundant year-round at nearly all the sites (Figure 11b). Its peak abundances were from March to May-June in both years. It was primarily found in the oblique-tow samples throughout the study.

The spring peaks seen in this study were also found in other works. These larvae were the most commonly taken plankter in both Sandifer's (1973) and Goy's (1976) surveys. In both of these surveys, May peaks were noted for this species, with larvae present year round in Goy's survey, and from January to June in Sandifer's study.

Adults of the sand shrimp are most often found near sandy bottoms, from the low water mark to 90 m, with some records from 450m (Williams, 1984). In the Chesapeake Bay, Wass (1972) classified *Crangon septemspinosa* as euryhaline in distribution - found on the inner continental shelf, but more abundant in the lower bay and lower reaches of the major tributaries.

Cluster summary

This cluster was distinguished from the other groups in this study by the predominance of its members in the spring samples (Figure 6e). *Crangon* had a peak in March (Figure 11b), which was not shared by *Cancer* (Figure 11a), and their overall spatiotemporal patterns appear different. However, *Cancer* and *Crangon* had fairly high correlation coefficients with this cluster (Table 3), and they shared a peak in abundance in May of 1983, especially at the offshore oblique site. The lack of more offshore stations, or the long intervals between cruises, may have lead to missing this spring peak in 1982. The patterns observed in this study were in general agreement with the literature.

VC6

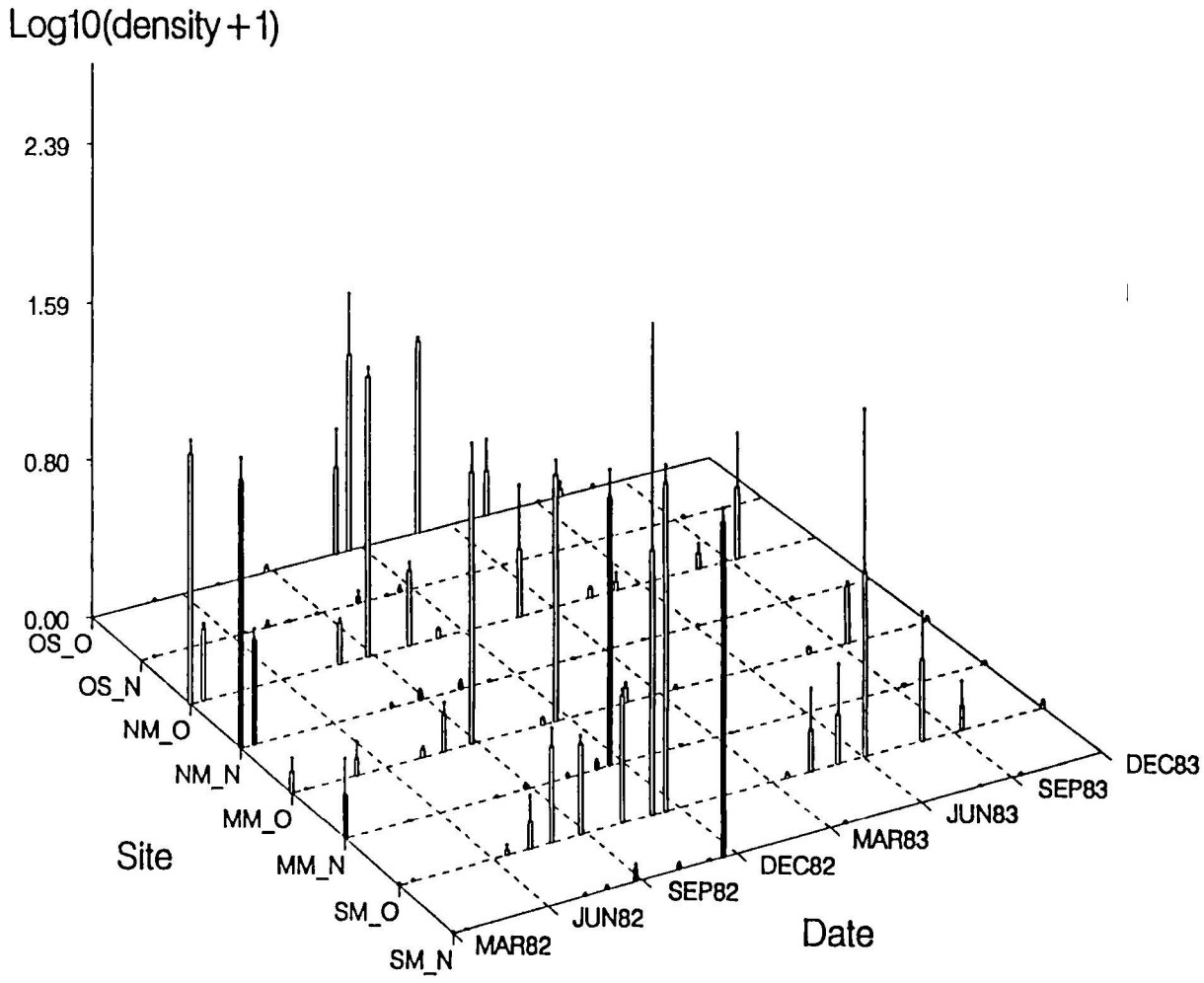
Neomysis americana (opossum shrimp), *Mysidopsis bigelowi* (opossum shrimp), and Megalopa A.

Individual Members:

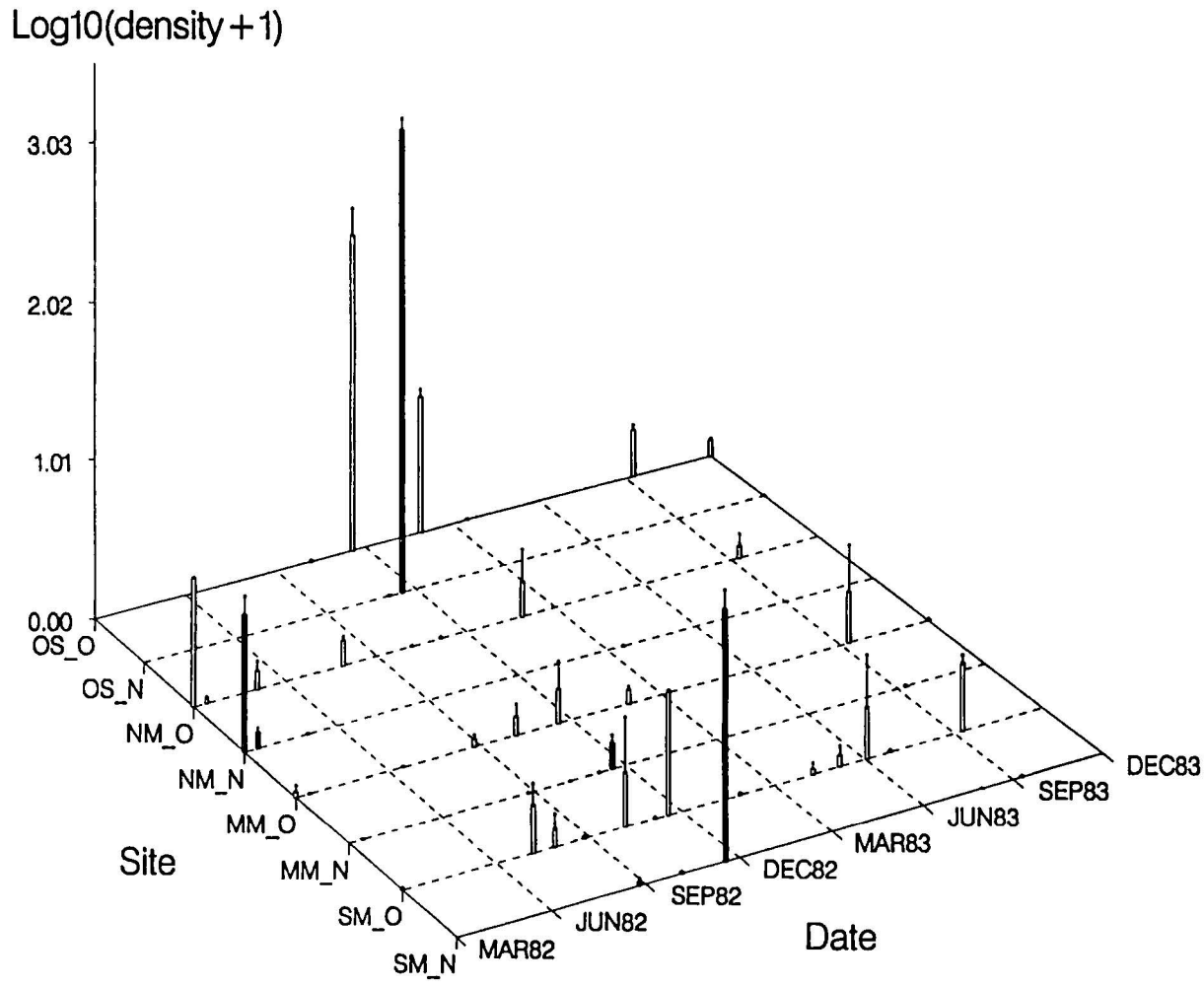
Neomysis americana. Both adults and juveniles of this mysid were taken throughout the study (Figure 12a). There were several samples containing *Neomysis* in high abundance, with some of these samples also containing large numbers of *Mysidopsis* (Figure 12b). The shared peaks of March of 1982 were at the north mouth sites, while the shared peak of 30,

Figure 12. Three-dimensional spatiotemporal plots of log-transformed individual taxon's mean abundance (+ 1 SE) for each member of VC6. Taxa are ordered according to VARCLUS dendrogram (Figure 4): a) *Neomysis americana* (p.88), b) *Mysidopsis bigelowi* (p.89), c) Megalopa A (p.90). Shaded bars are neuston samples, and unshaded bars are oblique samples.

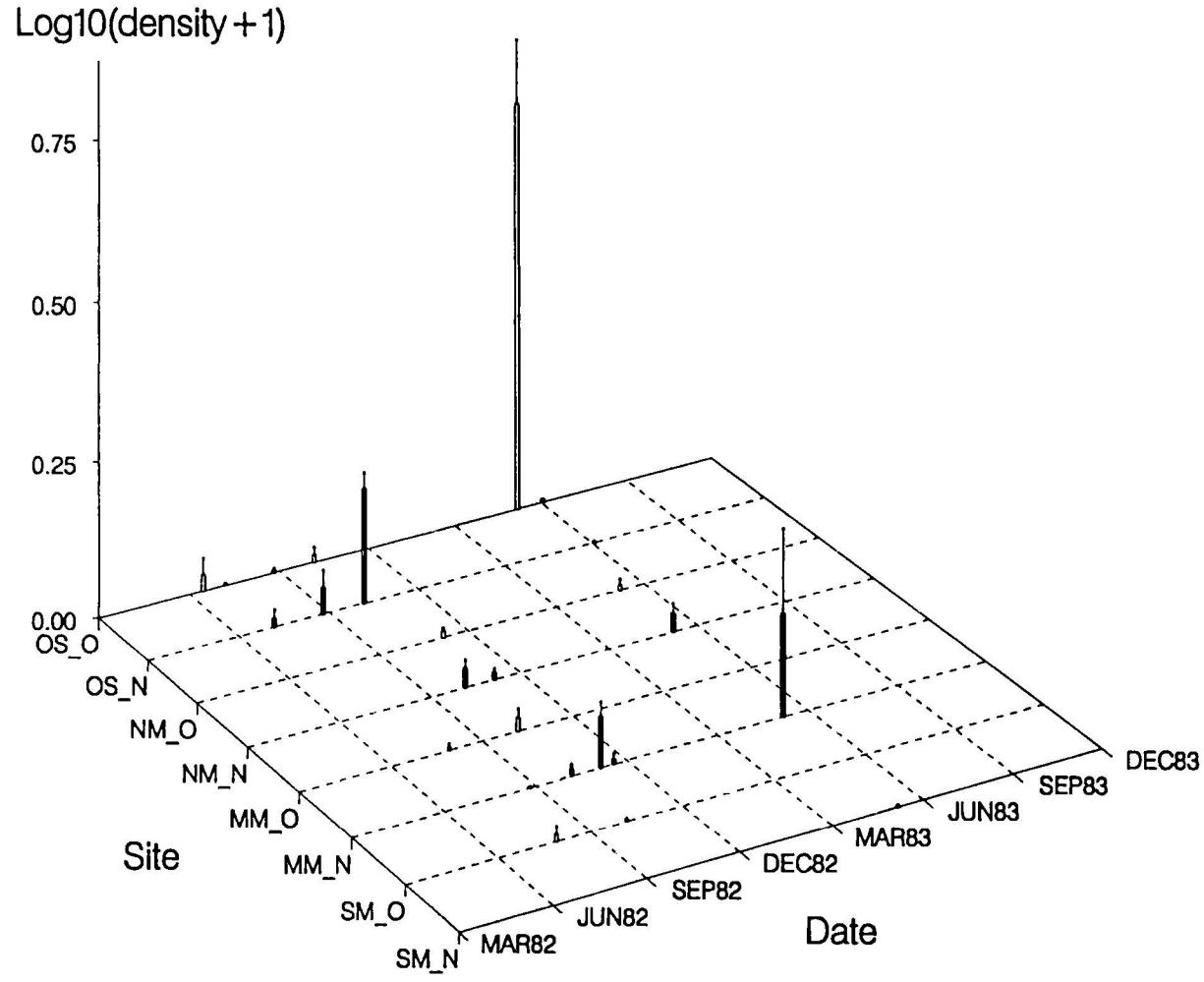
Neomysis americana



Mysidopsis bigelowi



Megalopa A


Log10(density+1)
0.75
0.50
0.25
0.00
OS_O
OS_N
NM_O
NM_N
MM_O
MM_N
SM_O
SM_N
Site
MAR82
JUN82
SEP82
DEC82
MAR83
JUN83
SEP83
DEC83
Date

November 1982 was evident at the southern and middle bay mouth, and offshore sites.

Neomysis americana and other mysids are commonly known as opossum shrimp. *Neomysis* is euryhaline in the Chesapeake Bay, with high numbers in the rivers and lower numbers in the main bay and along the Eastern Shore of Virginia (Wass, 1972). It was the most abundant mysid in Williams's (1972) ten-year survey of meroplankton in coastal North Carolina; it was commonly found in middle to upper reaches of the coastal estuary. It was also the most commonly taken mysid in Allen's (1984) life history study of *Mysidopsis bigelowi* in the Hereford Inlet in southern New Jersey.

Mysidopsis bigelowi Adults and juveniles were found occasionally in this survey (Figure 12b). They were found throughout the area in oblique samples, and had one peak, shared with *Neomysis* (Figure 12a), on November 30th of 1982. During this peak, abundances in the neuston were higher than those in the corresponding oblique samples. On the 17th of March 1982, there was a smaller, also shared, peak with similar oblique and neuston abundances. *Mysidopsis* had a pattern of prevalence in the south mouth oblique samples in 1982 and 1983, which was also found in *Neomysis*.

These opossum shrimp are mesohaline to euhaline in distribution in the Chesapeake Bay, commonly collected in the lower reaches of the Bay's tributaries (Wass, 1972).

Mysidopsis bigelowi was second in abundance in Williams's (1971) ten-year study of meroplankton in the coastal estuaries of North Carolina; its greatest abundance was at the most seaward station.

Megalopa A This megalopal stage was taken many times in 1982, and six times in 1983 (Figure 12c). It was spotty in occurrence, with plankters taken from June-July to November of 1982, and in May and June of 1983. Its pattern of seasonal abundance was inconsistent between years, and its inclusion in VC6 is not explainable.

Cluster summary

Two of the members of this cluster are mysids, the remaining species, Megalopa A, was not positively identified. The association among the mysids was much stronger than that between the mysids and the third member of the group (Table 3). The VARCLUS scores for this group show a broad pattern of occurrence (Figure 6f), as the two mysids are associated with one another apparently because of their shared peaks, not because of similar patterns of overall occurrence (Figures 12a and 12b).

Allen (1984) also found these two mysids to be significantly correlated in abundance in the Hereford Inlet in southern New Jersey. His results also agreed with those of this study, with *Mysidopsis* at its maximum in more oceanic waters and *Neomysis* more commonly taken in the upriver portions of the embayment.

The pattern of high abundance for both mysids in the northern mouth sites in March of 1982 is consistent with an inshore migration in the spring, and high abundance at all of the southern and middle mouth, as well as the offshore sites in November of 1982 is consistent with an offshore migration in the fall: a proposal made by several others, as summarized by Allen (1984). These migrations may have been simply missed in 1983 due to the long intervals between sampling events. However, because of the low intensity and nonspecific sampling design of this study, these conclusions are speculative.

VC7

Squilla (*empusa*?) protozoea (mantis shrimp), *Callinectes* spp. megalopa (blue crab), *Lucifer faxoni*.

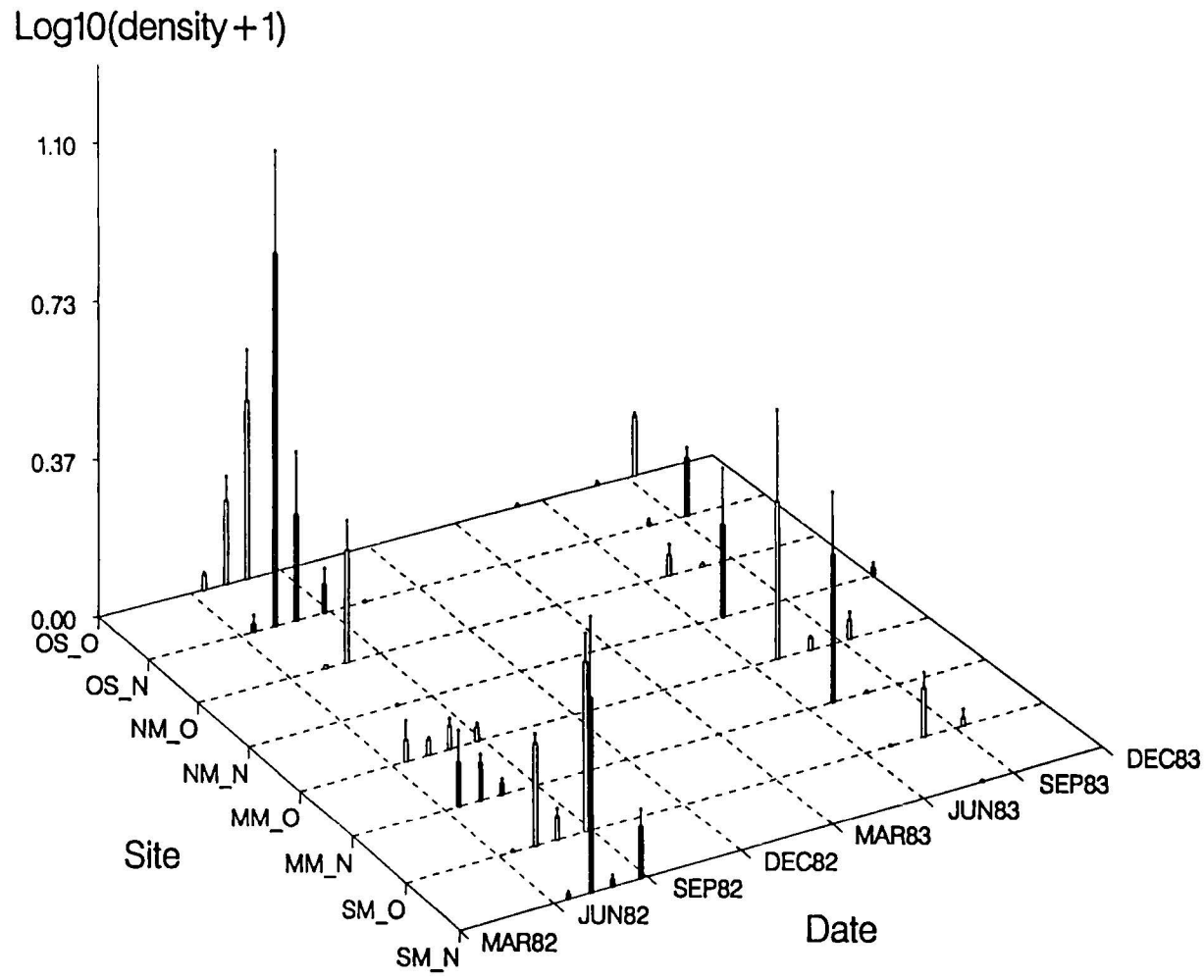
Individual Members:

***Squilla* (*empusa*?) protozoea** These protozoeae are a later larval stage of members of the squillid family, and probably represent later stages of VC4's Squillid antizoea. These protozoeae were taken from June-July to September in both years (Figure 13a). In 1982 they were somewhat more prevalent in the offshore neuston and oblique than in the mouth, while in 1983 no pattern was evident.

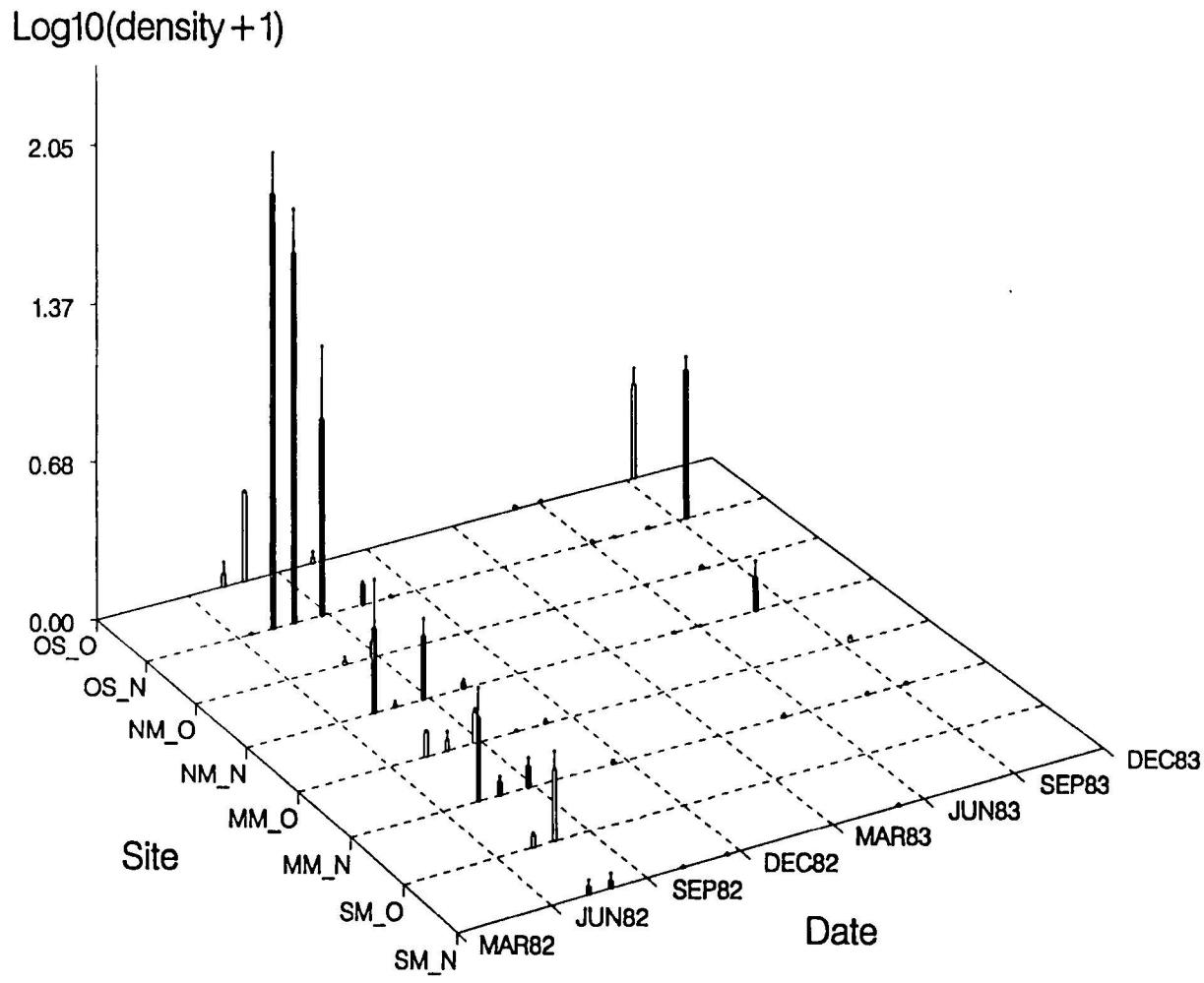
Squillids are commonly known as mantis shrimp. *Squilla empusa* is the only squillid listed by Wass (1972), and the adults are polyhaline and euhaline

Figure 13. Three-dimensional spatiotemporal plots of log-transformed individual taxon's mean abundance (+ 1 SE) for each member of VC7. Taxa are ordered according to VARCLUS dendrogram (Figure 4): a) *Squilla (empusa?)* protozoea (p.94), b) *Callinectes* spp. megalopa (p.95), c) *Lucifer faxoni* postlarva and larva (p.96). Shaded bars are neuston samples, and unshaded bars are oblique samples.

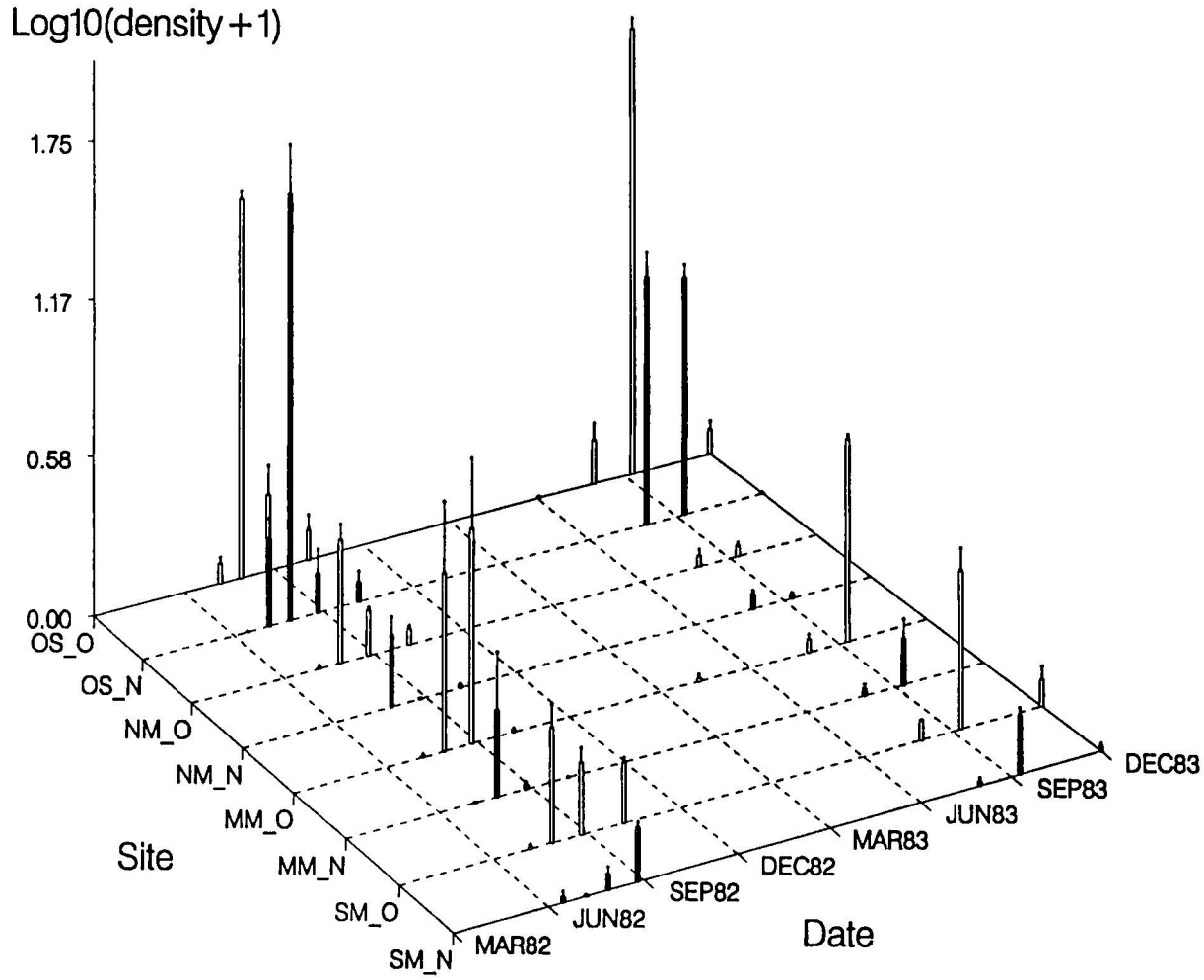
Squilla (empusa?) protozoea



Callinectes spp. megalopa



Lucifer faxoni



in distribution in the Chesapeake Bay. Morgan (1979) found the larvae in the higher salinity waters of the lower bay and along the Eastern Shore of Virginia, with early and late stages found further into the bay than the middle stages. They were present in the plankton from the last week of July until the first week of October, with a peak in the first week of September, similar to the seasonal pattern found in this study. Of the nine larval stages, he found only the first four and the last one within the Chesapeake Bay, the remaining four were found only in bay mouth samples. He took no offshore samples.

***Callinectes* spp. megalopa** These larvae are very likely later stages of the *Callinectes* spp. zoeae which were abundant in this study. Megalopae were found from July to September in 1982, with higher numbers offshore in 1982 than in 1983 (Figure 13b).

Callinectes has been studied by several investigators in the Chesapeake and Delaware Bays. As a result of these inquiries, a paradigm of dispersal and recruitment has emerged. Adult blue crabs are found commonly in estuarine waters on the Atlantic Coast (Williams, 1984), are common in the Chesapeake Bay (Wass, 1972), and are fished commercially. From the time of the late spring until the early fall, gravid females migrate to the mouth of the estuary and spawn (Van Engel, 1958). July and August are typically the months of peak spawning (Dittel and Epifanio, 1982; Epifanio *et al*, 1984). The females release the larvae as a stage I zoeae, and these plankters are most abundant in surface waters, and thus are carried offshore (Provenzano *et al*,

1983; Epifanio, 1988). The larvae develop offshore, with the final larval stage, the megalops, concentrated in the neuston (Epifanio *et al*, 1989; Johnson, 1985; McConaugha *et al*, 1983; Sulkin and Van Heukelen, 1982; Smyth, 1980). These larvae are not swept southward by the prevailing currents due to the predominant south-southeasterly late summer winds (Leming and Johnson 1986; Boicourt, 1982). The megalopae enter the bay, predominantly during storm events, and settle in the shallow reaches of the estuary (Goodrich *et al* 1989). The offshore neustonic abundance of both stages of *Callinectes* in this study fits well with this paradigm.

Lucifer faxoni *Lucifer*, like its fellow group members, had a pattern of mid to late summer abundance at the offshore area (Figure 13c). It was prevalent in the plankton from July-August until September of both years, with maximum abundances offshore. It differed from *Callinectes* megalopae and *Squilla* protozoeae, by having the same pattern of abundance in both 1982 and 1983.

Sandifer (1973) found this species most commonly at the bay mouth and lower bay stations of his transect, suggesting an offshore distribution. He found larvae to postlarvae of these species from September to November, later than this study.

This is a holoplankter, found in estuarine to oceanic waters, from surface waters to depths of 91m (Williams, 1984). Wass (1972) considered it to be polyhaline and euhaline in distribution, with reports primarily from the

top nine meters of the inner shelf waters, although it is found at depths of up to 18 m. The results concerning the larvae from this and Sandifer's study, combined with the adult distribution, indicate a nearshore distribution of the larvae.

Cluster summary

This cluster contains what are most likely the later stages of two of the members of VC4. It shares VC4's pattern of higher abundance in offshore samples in the late summer (Figure 6d), although VC7's peaks are less pronounced (Figure 6g). In these three-dimensional VARCLUS score plots, the VC7 larvae appear to peak later than those in VC4, however, these data were not collected frequently enough during the late summer to be conclusive. The combination of the late stages of *Callinectes* spp. and *Squilla* larvae in this cluster and the combination of their early stages in VC4 suggests that *Squilla* larvae share *Callinectes*'s expelled estuarine recruitment pattern. The results of Morgan (1980) allow for this interpretation: early stages and late stages found in the bay, with middle stages found only further out in the mouth (he took no samples further offshore). The nature of this association may be predatory, as captive *Squilla* can survive on decapod larvae (Morgan, 1980).

VC8

Uca sp. #'s 1 & 3 zoeae (fiddler crabs).

Individual Members:

***Uca* sp. #1 zoea** Larvae in this category were only present in summer of 1982 at the mid mouth and offshore (Figure 14a), a pattern they shared with Uca sp. #3.

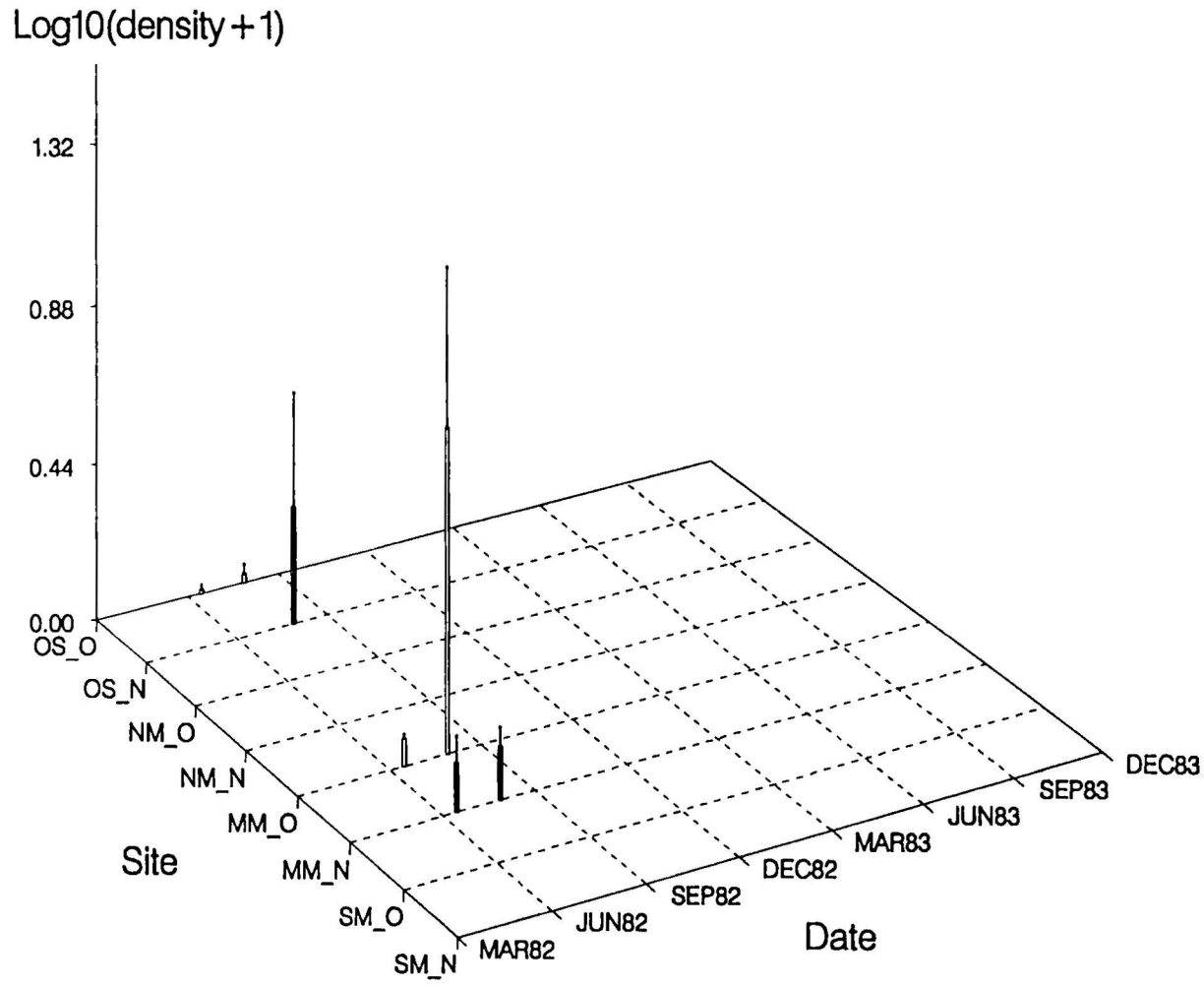
***Uca* sp. #3 zoea** These larvae had the same sparse distribution as Uca #1, with mid mouth and offshore occurrences in the summer of 1982 (Figure 14b).

Cluster summary

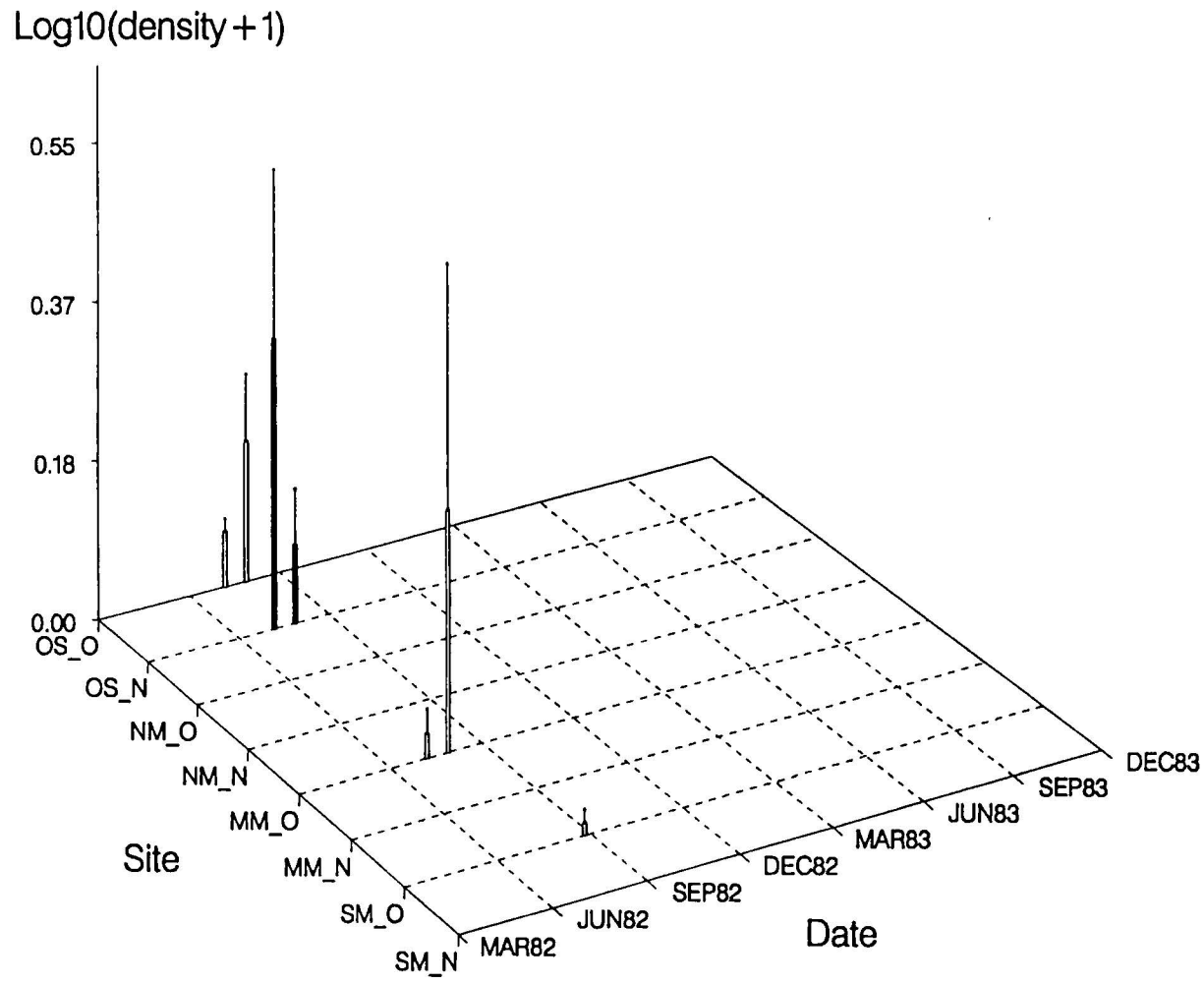
These two species were taken in only eleven samples from June to September of 1982 (Figure 6h): not frequently enough for discussion. Larvae of the genus *Uca* have been studied extensively, and the results of these studies are summarized earlier in the discussion of *Uca* spp. # 2 zoea in the VC1 section.

Figure 14. Three-dimensional spatiotemporal plots of log-transformed individual taxon's mean abundance (+ 1 SE) for each member of VC8. Taxa are ordered according to VARCLUS dendrogram (Figure 4): a) *Uca* sp. #1 zoea (p.101), b) *Uca* sp. #3 zoea (p.102). Shaded bars are neuston samples, and unshaded bars are oblique samples.

Uca sp. #1 zoea


Log10(density+1)
1.32
0.88
0.44
0.00
OS_O
OS_N
NM_O
NM_N
MM_O
MM_N
SM_O
SM_N
Site
MAR82
JUN82
SEP82
DEC82
MAR83
JUN83
SEP83
DEC83
Date

Uca sp. #3 zoea


Log10(density+1)
0.55
0.37
0.18
0.00
OS_O
OS_N
NM_O
NM_N
MM_O
MM_N
SM_O
SM_N
Site
MAR82
JUN82
SEP82
DEC82
MAR83
JUN83
SEP83
DEC83
Date

Williams and Stephenson Analyses

Overall variance structure

In the Williams and Stephenson (W&S) analyses, the majority of the variance was due to temporal differences: the cruise variance was greater than twice the spatial variance, and the interaction was relatively small (Table 4). This is as expected for a study of plankton assemblages dominated by seasonally abundant larval decapods.

Observations on W&S method: inter-taxa patterns

In both the taxa-by-cruise and taxa-by-site dendrograms produced by the Williams and Stephenson (1973) method (Figures 15 and 16), the major split was between abundant and non-abundant species. The twelve species in clusters a2-a6, b, c, d, and e of the taxa-by-cruise dendrogram, and the thirteen species in clusters B-F of the taxa-by-site dendrogram were all ranked in the top 14 by the percent occurrence reduction technique, and highly by the two W&S screens, while those in the large clusters (a1,A1, & A2) were consistently lower ranked (Table 2). It appears that this method has clustered these organisms based upon their overall abundance, as much as upon shared spatial or temporal patterns.

Table 4. Williams and Stephenson mean variance per comparison table. For site and cruise effects, values are mean distances between entities. The value for the interaction is the error variance. Numbers in parentheses are percentages of total variance.

Site	Cruise	Interaction
0.21355 (26%)	0.523613 (65%)	0.0718 (9%)

Figure 15. Williams and Stephenson dendrogram of taxa based upon relative abundances during cruises. Inter-taxa distances due to differences among cruises were calculated using the ANOVA-partioning method of Williams and Stephenson (1973). Dendrogram was formed using these distances and the flexible beta method of Lance and Williams (1967). Beta used for this dendrogram was -0.50. Lower case letters indicate groups, with numbers indicating subdivisions. Validity of groups was evaluated by comparison with diagnostic taxa abundance plots (Figures 7 through 14).

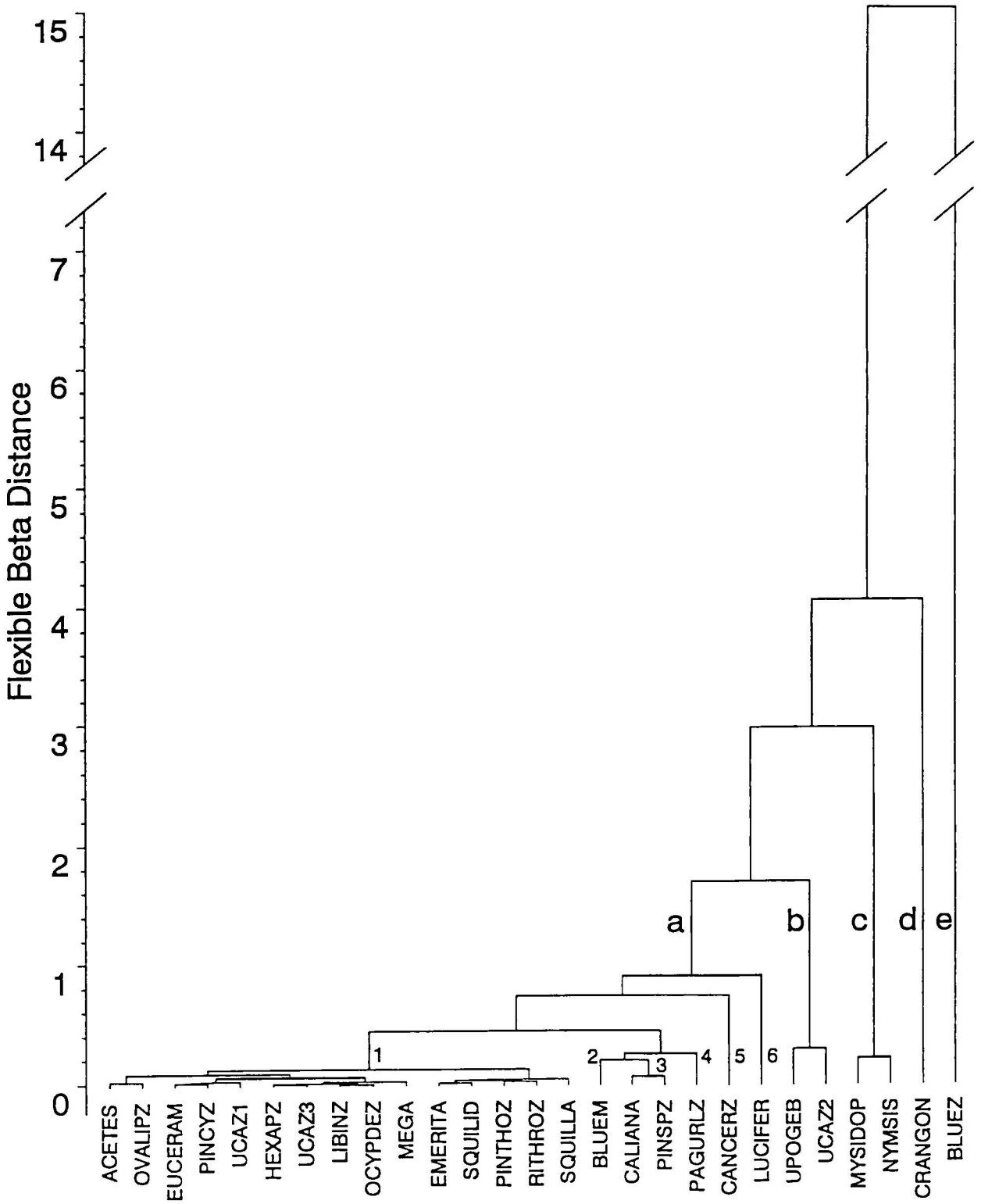
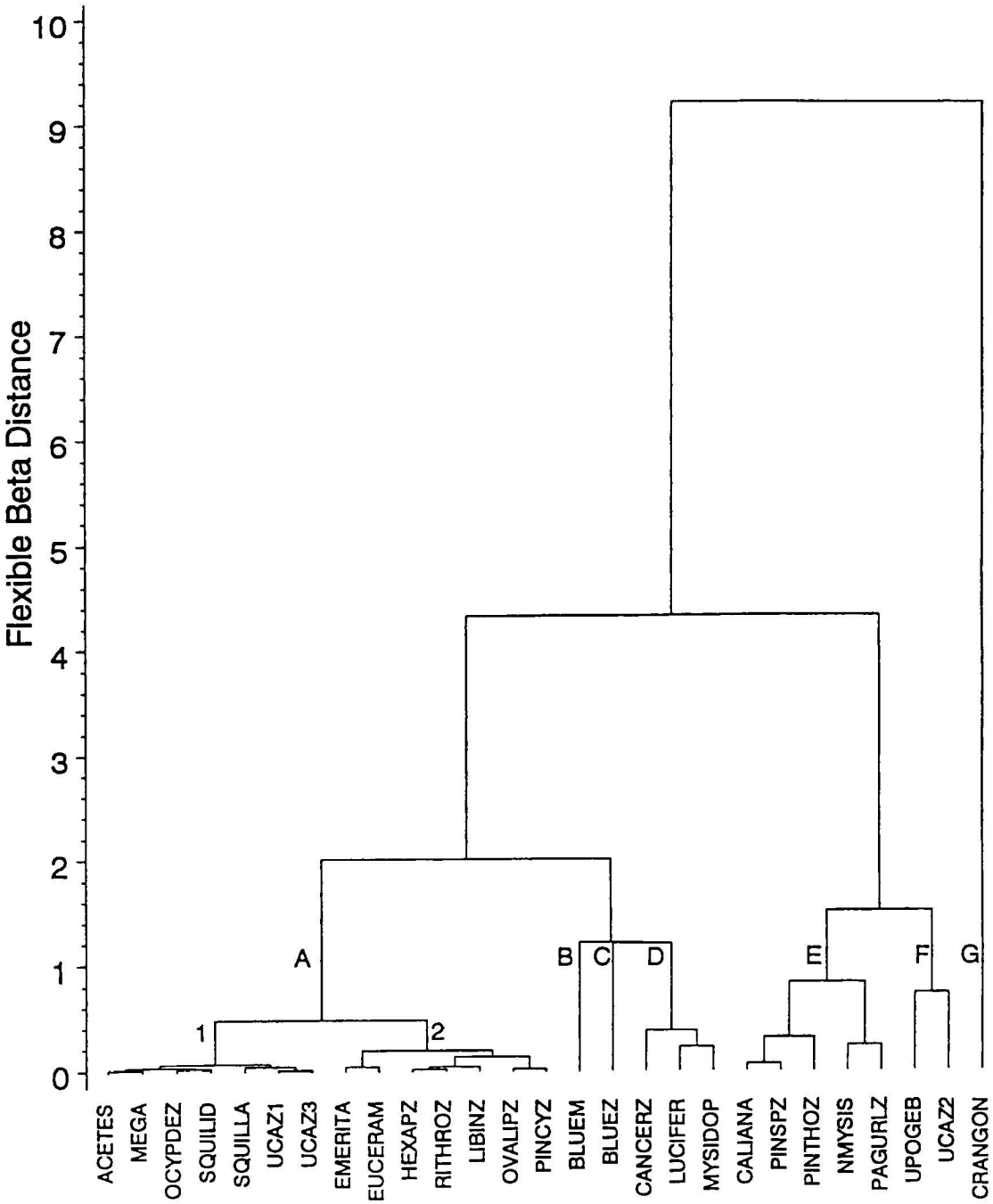

Flexible Beta Distance
15
14
7
6
5
4
3
2
1
0
a
b
c
d
e
1
2
3
4
5
6
ACETES
OVALIPZ
EUCERAM
PINCYZ
UCAZ1
HEXAPZ
UCAZ3
LIBINZ
OCYPDEZ
MEGA
EMERITA
SQUILID
PINTHOZ
RITHROZ
SQUILLA
BLUEM
CALIANA
PINSPZ
PAGURLZ
CANCERZ
LUCIFER
UPOGEB
UCAZ2
MYSIDOP
NYMSIS
CRANGON
BLUEZ

Figure 16. Williams and Stephenson dendrogram of taxa based upon relative abundances at sites. Inter-taxa distances due to differences among sites were calculated using the ANOVA-partioning method of Williams and Stephenson (1973). Dendrogram was formed using these distances and the flexible beta method of Lance and Williams (1967). Beta used for this dendrogram was -0.25. Upper case letters indicate groups, with numbers indicating subdivisions. Validity of groups was evaluated by comparison with diagnostic taxa abundance plots (Figures 7 through 14).


Flexible Beta Distance
10
9
8
7
6
5
4
3
2
1
0
A
B
C
D
E
F
G
1
2
ACETES
MEGA
OCYPDEZ
SQUILID
SQUILLA
UCAZ1
UCAZ3
EMERITA
EUCERAM
HEXAPZ
RITHROZ
LIBINZ
OVALIPZ
PINCYZ
BLUEM
BLUEZ
CANCERZ
LUCIFER
MYSIDOP
CALIANA
PINSPZ
PINTHOZ
NMYSIS
PAGURLZ
UPOGEB
UCAZ2
CRANGON

Temporal patterns

Cruise groups

Dendrogram There were eight cruise groups, divided upon seasonal lines (Figure 17). In all but one case, the 1982 cruise was matched with its 1983 counterpart. In the exceptional case (September), the cruises were paired. However, they were distinct enough that each was considered to be its own group. The November 30th cruise of 1982 had no counterpart in 1983: the 1983 November sample was early in the month, and the December cruise of 1983 was mid-month. These highly seasonal clusters, pairing the same months from the two years, are as expected for seasonally reproducing organisms. This dendrogram was made using a beta value of -0.25.

Discriminant analysis of cruise groups by taxa The cruise groups were not well separated, however, *Callinectes* spp. zoea and both squillid larvae could be seen to be higher in July and August (Figure 18, group 5), also five species could be seen to be higher in September. The September cruises of 1982 and 1983 overlapped considerably, bringing into question my initial separation of them into two groups. The large overlapping mass composed of the remaining groups indicates only their low numbers with respect to the July, August, and September cruises.

Discriminant analysis of cruise groups by physico-chemical measures The histograms for the W&S cruise groups are presented in Figure 19. Dissolved oxygen and temperature loaded heavily on canonical discriminant function 1, in opposite

Figure 17. Dendrogram of cruises from Williams and Stephenson clustering method. Inter-cruise distances due to differences among taxa were calculated using the ANOVA-partioning method of Williams and Stephenson (1973). Dendrogram was formed using these distances and the flexible beta method of Lance and Williams (1967). Beta used for this dendrogram was -0.25. Arabic numerals indicate groups, with lower-case letters indicating subdivisions.

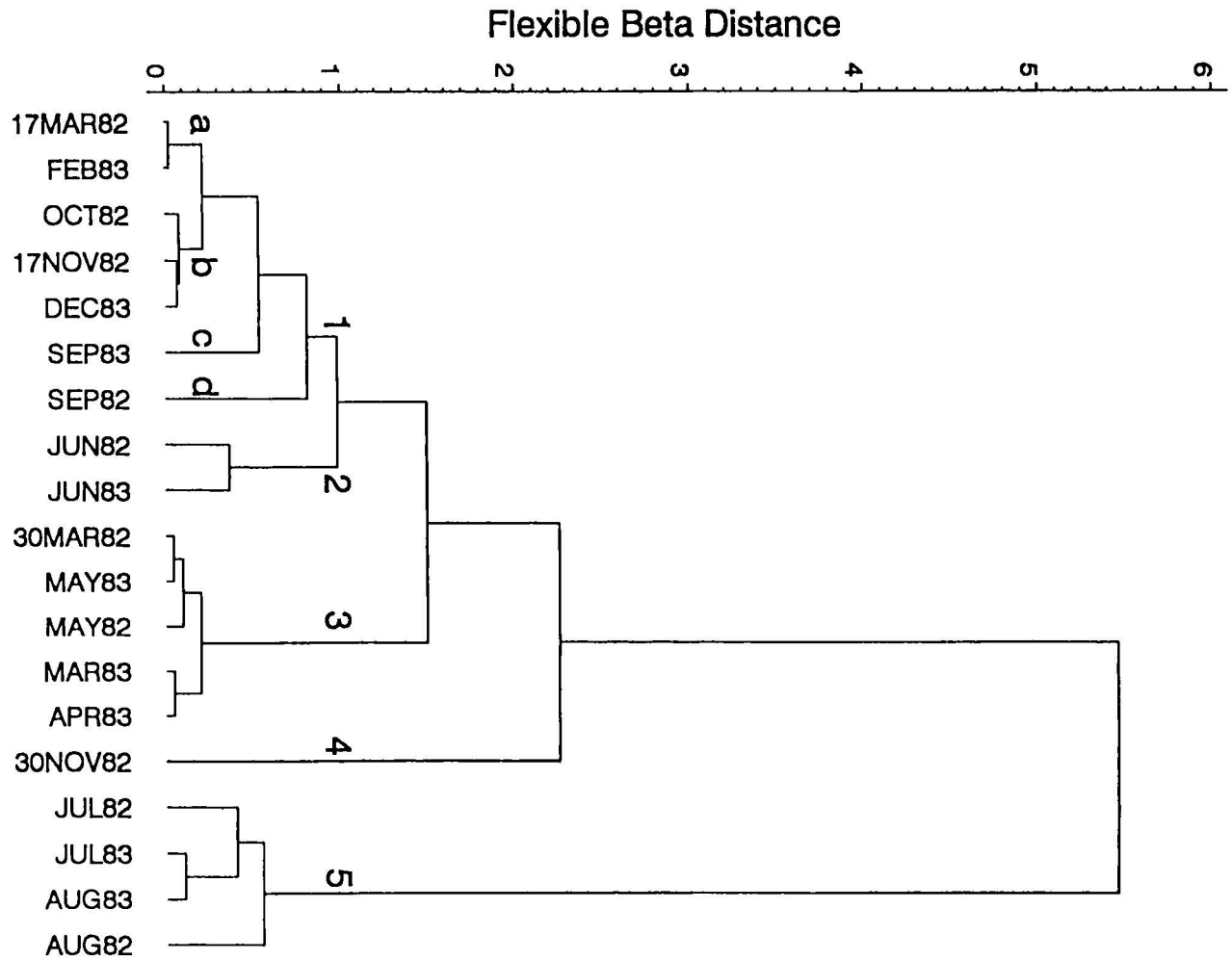

Flexible Beta Distance
0
1
2
3
4
5
6
17MAR82
FEB83
OCT82
17NOV82
DEC83
SEP83
SEP82
JUN82
JUN83
30MAR82
MAY83
MAY82
MAR83
APR83
30NOV82
JUL82
JUL83
AUG83
AUG82
a
b
c
d
1
2
3
4
5

Figure 18. Cruise group confidence ellipses of canonical discriminant scores for plankton data. Scores were calculated using the plankton data (log-transformed mean abundances of replicate samples), and the first two discriminant functions from the canonical discriminant analysis of the plankton data, between cruise groups. Taxa listed were both significantly different between cruise groups (P=0.05), and had a large coefficient for that function (see Methods text for details). Direction of arrows indicates signs of coefficients.

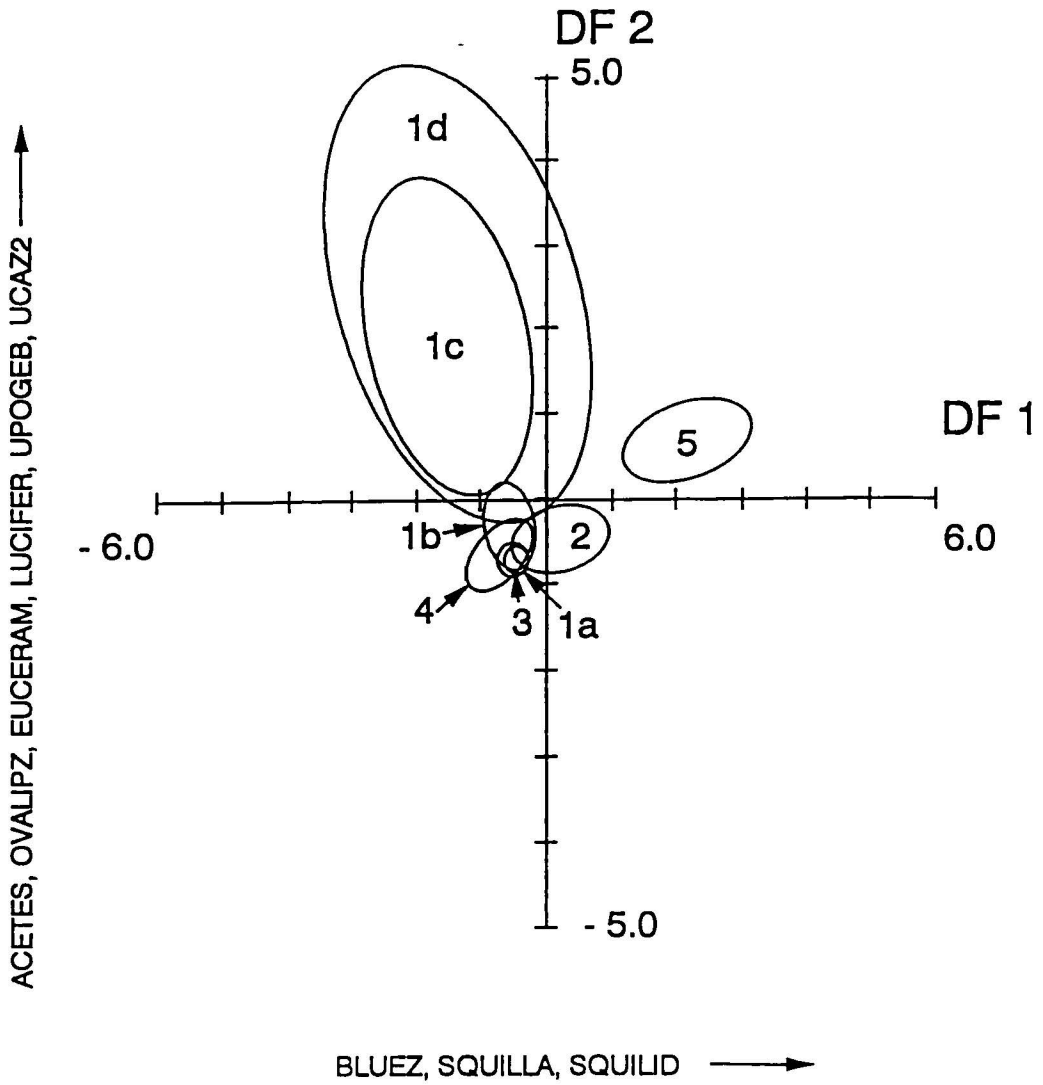
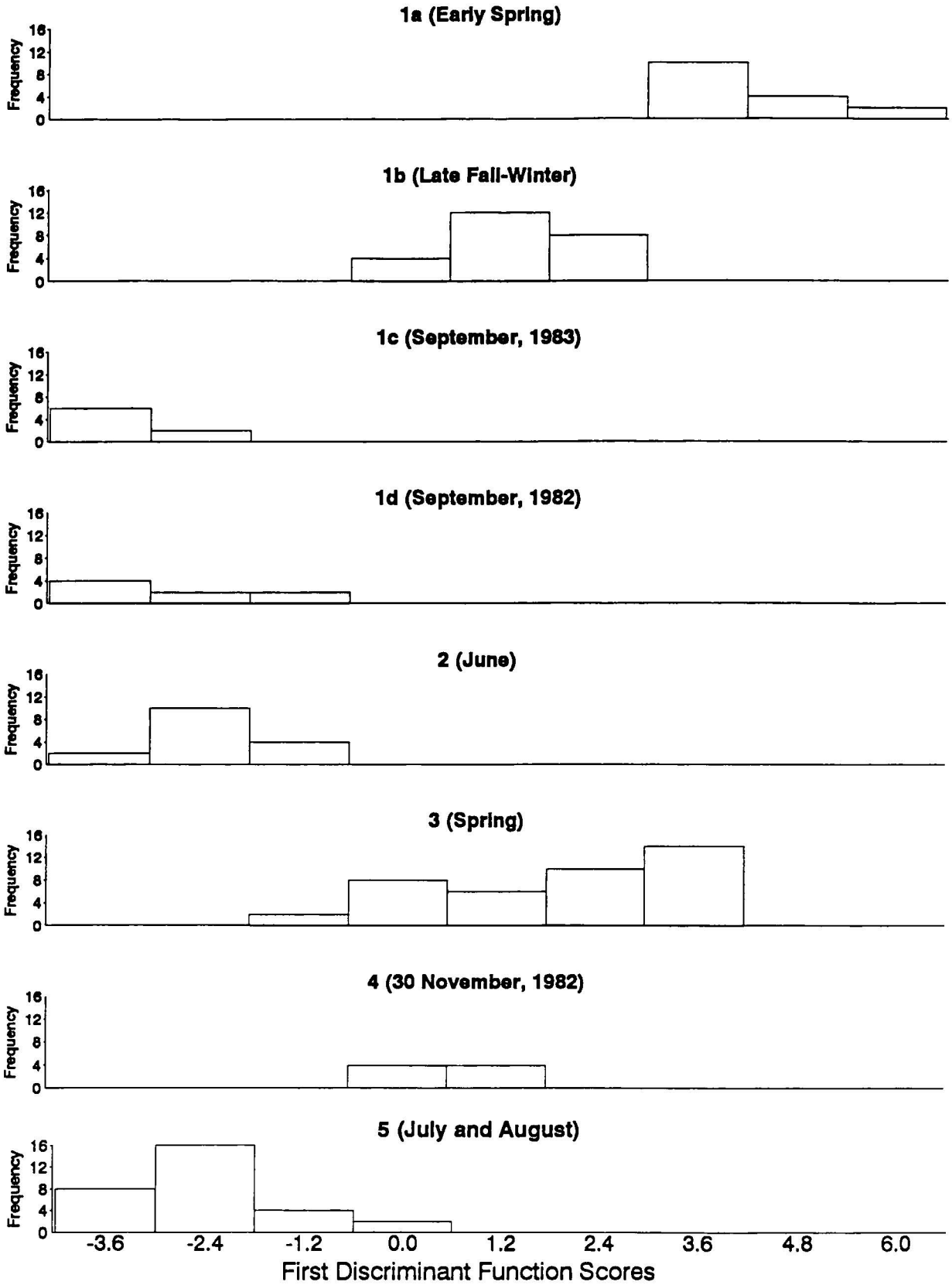

DF 2
5.0
1d
1c
5
DF 1
- 6.0
1b
2
6.0
4
3
1a
- 5.0
ACETES, OVALIPZ, EUCERAM, LUCIFER, UPOGEB, UCAZ2
BLUEZ, SQUILLA, SQUILID

Figure 19. Frequency histograms of cruise group physico-chemical canonical discriminant scores: one histogram for each cruise group. Scores were calculated using the physico-chemical measurements (surface and bottom temperature, salinity, and dissolved oxygen), and the first discriminant function from the canonical discriminant analysis of the physico-chemical data, between cruise groups. Measures listed were significantly different between cruise groups ($p=0.05$), and had large coefficients for the first discriminant function (see Methods text for details). Direction of arrows indicates the signs of the coefficients.


1a (Early Spring)
1b (Late Fall-Winter)
1c (September, 1983)
1d (September, 1982)
2 (June)
3 (Spring)
4 (30 November, 1982)
5 (July and August)
Frequency
16
12
8
4
0
-3.6
-2.4
-1.2
0.0
1.2
2.4
3.6
4.8
6.0
First Discriminant Function Scores
Surface and Bottom DO, Bottom Salinity
Bottom and Surface Temperature

directions. Along this function, it can be seen that temperature was high and dissolved oxygen low in the summer groups (5, 1c, 1d, and 2), and vice versa in the winter and spring samples (groups 3 and 1a). This is simply a reflection of temperature changes from season to season, and is very much expected.

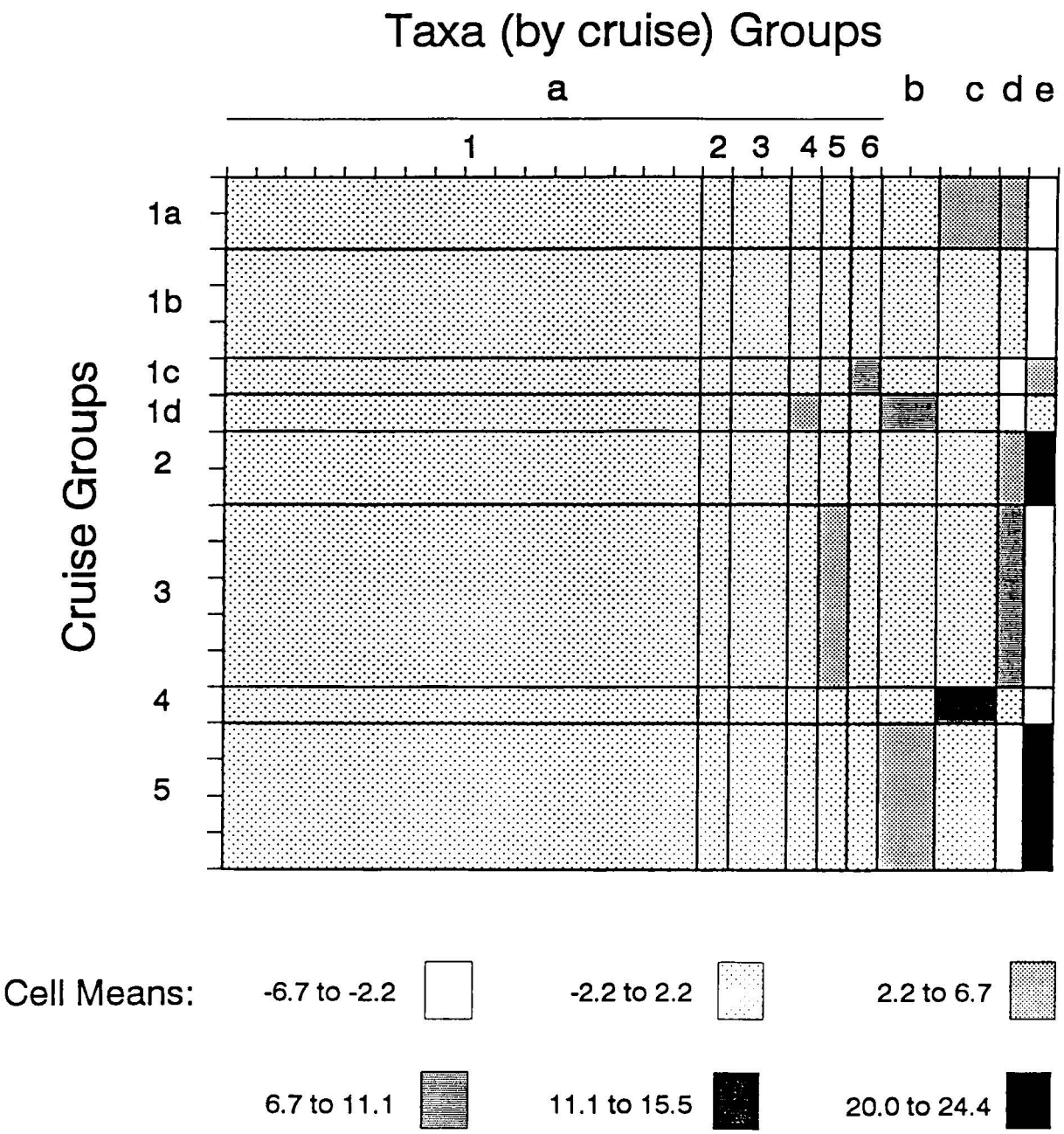
Taxa groups based upon cruises

A beta of -0.50 resulted in ten clusters, one of which had 15 members, with the remaining groups consisting of one or two members (Figure 15). Following is a group-by-group discussion.

W&S Cruise a1 The composition of this cluster of the temporal taxa dendrogram (Figure 15) was internally consistent based upon examination of the three-dimensional plots of individual species (Figures 9b, 9a, 7i, 8b, 14a, 8a, 14b, 9c, 10c, 12c, 7e, 10b, 7a, 7b, 13a). It contained fifteen taxa, all of which were at their most abundant during the summer. However, the distinction of this group of species from others sharing similar late summer abundances (*eg Callinectes* spp. zoea) is questionable.

This group of taxa showed no distinct patterns in the B-table (Figure 20). This is likely because these species were in low abundance relative to other species with late summer peaks, such as *Callinectes* spp. zoea.

Figure 20. Nodal plot representation of Williams and Stephenson B-table showing taxa groups's patterns among cruise groups. Taxa groups were taken from Figure 15, and cruise groups were taken from Figure 17. The B-table values represent the temporal patterns of the taxa: the higher the number (darker the shade), the more often the taxa group's members were taken in the samples from the cruises in the cruise group. These values were calculated using the method of Williams and Stephenson (1973). The horizontal dimension of each rectangle is proportional to the number of taxa in the taxa group (indicated by tick marks), and the vertical dimension is proportional to the number of cruises in the cruise group.


Taxa (by cruise) Groups
a
b
c
d
e
1
2
3
4
5
6
Cruise Groups
1a
1b
1c
1d
2
3
4
5
Cell Means:
-6.7 to -2.2
-2.2 to 2.2
2.2 to 6.7
6.7 to 11.1
11.1 to 15.5
20.0 to 24.4

W&S Cruise a2 This cluster was composed of a single larval type: *Callinectes* megalopa. No temporal trends were apparent in the B-table (Figure 20), even though this species is highly seasonal (Figure 13b). This is probably because peak numbers for these larvae were not high relative to the other plankters also peaking during this time of year.

W&S Cruise a3 Like a1 and a2, the members of this group, *Callianassa* sp.A and *Pinnixa* spp., also had highly seasonal patterns of abundance (Figures 7c and 7d, respectively), without this being reflected in the B-table (Figure 20). Again the poor performance of the B-table may be attributable to low numbers of these larvae relative to larvae such as *Callinectes* zoea.

W&S Cruise a4 *Pagurus longicarpus*, the sole member of this cluster, had a somewhat elevated period of abundance in September of 1982 (cruise group d: Figure 20).

W&S Cruise a5 This group, made up of *Cancer irroratus*, was most prevalent in the spring of 1982 and 1983 (Figure 20). This was also reflected in its individual species plot (Figure 11a).

W&S Cruise a6 *Lucifer faxoni*, the sole member of this group, was found in high number in September of 1982 and 1983 (Figure 13c). The nodal diagram

(Figure 20) only shows the September 1983 peak, probably because the 1982 numbers for *Lucifer* were not high relative to the other taxa during September of 1982.

W&S Cruise b This temporal two species cluster, composed of *Uca* spp zoea #2 and *Upogebia affinis* zoea, was at its most abundant in the late summer and early fall (Figures 7f and 7g), a pattern reflected in their common abundance in temporal clusters **1d** and **5** (Figure 20).

W&S Cruise c The mysids comprising this group were *Neomysis americana* and *Mysidopsis bigelowi*, and these two species had very high abundance during the 30 November, 1982 sampling cruise (Figure 20). These two species also shared a peak during the 17 March, 1982 cruise. As speculated earlier in the discussion of the VARCLUS results, these peaks may be indicative of seasonal migration or spawning.

W&S Cruise d *Crangon septemspinosa* was highest during spring (group 3) and was elevated during late winter (1a) and early summer (2) sampling events (Figure 20). This pattern was also evident in its individual taxa plot (Figure 11b), as discussed in the VARCLUS section.

W&S Cruise e *Callinectes* zoea was extremely abundant during the middle to late summer (5), and in high numbers during the early summer (2) and September of 1983 (1c) (Figure 20).

Summary of W&S temporal analyses

The temporal groups found by the W&S clustering are consistent with what is known about the general seasonal patterns of eumalacostracan plankton. Nearly all of the plankters taken in this study were larval stages or juveniles of seasonally reproducing organisms. The separation of July and August cruises (cluster 5) from the rest, probably reflects the fact that most of the plankters of this study are larval eumalacostracans, and these plankters typically have July and August peaks in abundance within the Chesapeake Bay (Sandifer, 1973; Goy, 1976). Most of these species, including the dominant *Callinectes* larvae, first appear in number in the plankton during June and are last observed in September, probably resulting in the June (2) and September (**1c&d**) clusters found in this study. The March to May date group (3) is likely due to the prevalence of *Crangon* and *Cancer* zoeae during the spring, a seasonal pattern also found by Sandifer (1973). Clusters **1a** and **1b** were probably formed due to low overall abundance of larvae during the late fall and early winter, a pattern observed in earlier studies (Sandifer,1973; Goy,1976), and the separation of the November 30, 1982 cruise from the rest in group 4, was due to the peak observed for the mysids at nearly every station in the sampling area. The abundance of the mysids in November corresponds to the time of the maximum observed by Allen (1984), and may also reflect his hypothesized migration of mysids to oceanic waters in the fall.

Spatial patterns

Site groups

Dendrogram The majority of sites were different enough from one another to merit each being its own cluster: only the bay mouth neuston sites were grouped (Figure 21). The bay mouth neuston sites had relatively low numbers of plankton, as compared to the bay mouth oblique sites and the offshore neuston and oblique sites (Figures 7a through 14b). A beta of -0.25 was required to produce this dendrogram.

Discriminant analysis of site groups by taxa This analysis showed six species to be highest at the south mouth oblique site: *Crangon septemspinosa*, *Pinnotheres ostreum*, *Emerita talpoida*, *Euceramus praelongus*, *Pagurus longicarpus*, and *Callianassa* sp. A. (Figure 22). These species were shown to be prevalent in the mouth oblique samples by the individual species three-dimensional plots (Figures 11b,7a, 7e,7i,7h, and 7c, respectively), but did not appear to be noticeably more abundant at the south oblique site with respect to the other mouth oblique sites, nor, in the case of *Pagurus longicarpus* zoea to be more prevalent in the mouth in general as compared with offshore samples (Figure 7h).

Discriminant analysis of site groups by physicochemical measures Analysis of the seasonally-corrected residuals showed only that the salinity was higher offshore, and that bottom temperature was elevated in the bay mouth (Figure 23). The elevated temperature indicated for the bay mouth sites is likely due to

Figure 21. Dendrogram of sites from Williams and Stephenson clustering method. Inter-site distances due to differences among taxa were calculated using the ANOVA-partioning method of Williams and Stephenson (1973). Dendrogram was formed using these distances and the flexible beta method of Lance and Williams (1967). Beta used for this dendrogram was -0.25. Roman numerals indicate groups, with lower-case letters indicating subdivisions.

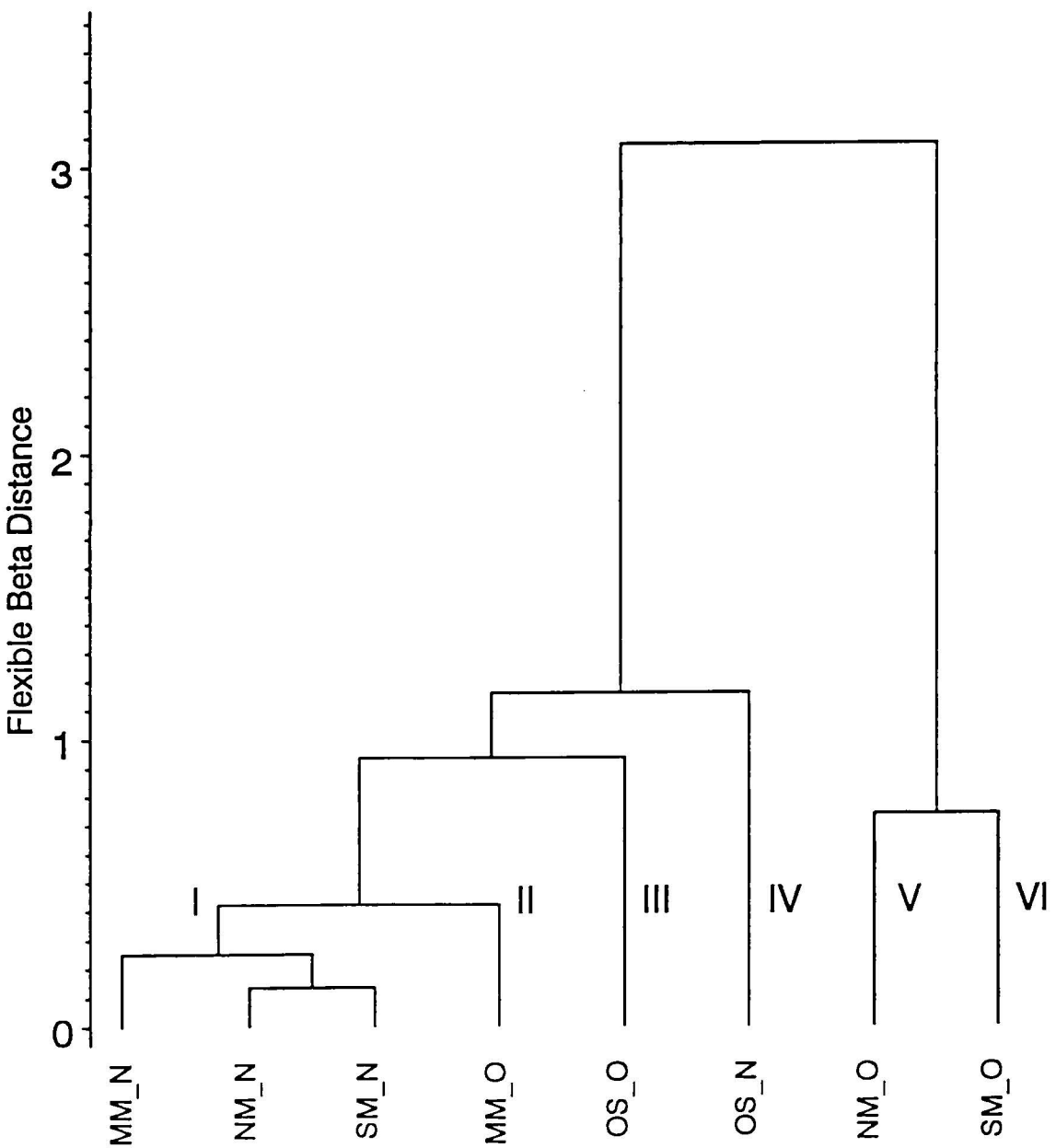

Flexible Beta Distance
0
1
2
3
I
II
III
IV
V
VI
MM_N
NM_N
SM_N
MM_O
OS_O
OS_N
NM_O
SM_O

Figure 22. Frequency histograms of site group canonical discriminant scores for plankton data: one histogram for each site group. Scores were calculated using the plankton data (log-transformed mean abundances of replicate samples), and the first discriminant function from the canonical discriminant analysis of the plankton data, between site groups. Taxa listed were significantly different between site groups ($p=0.05$), and had large coefficients for the first discriminant function (see Methods text for details). Direction of arrows indicates the signs of the coefficients.

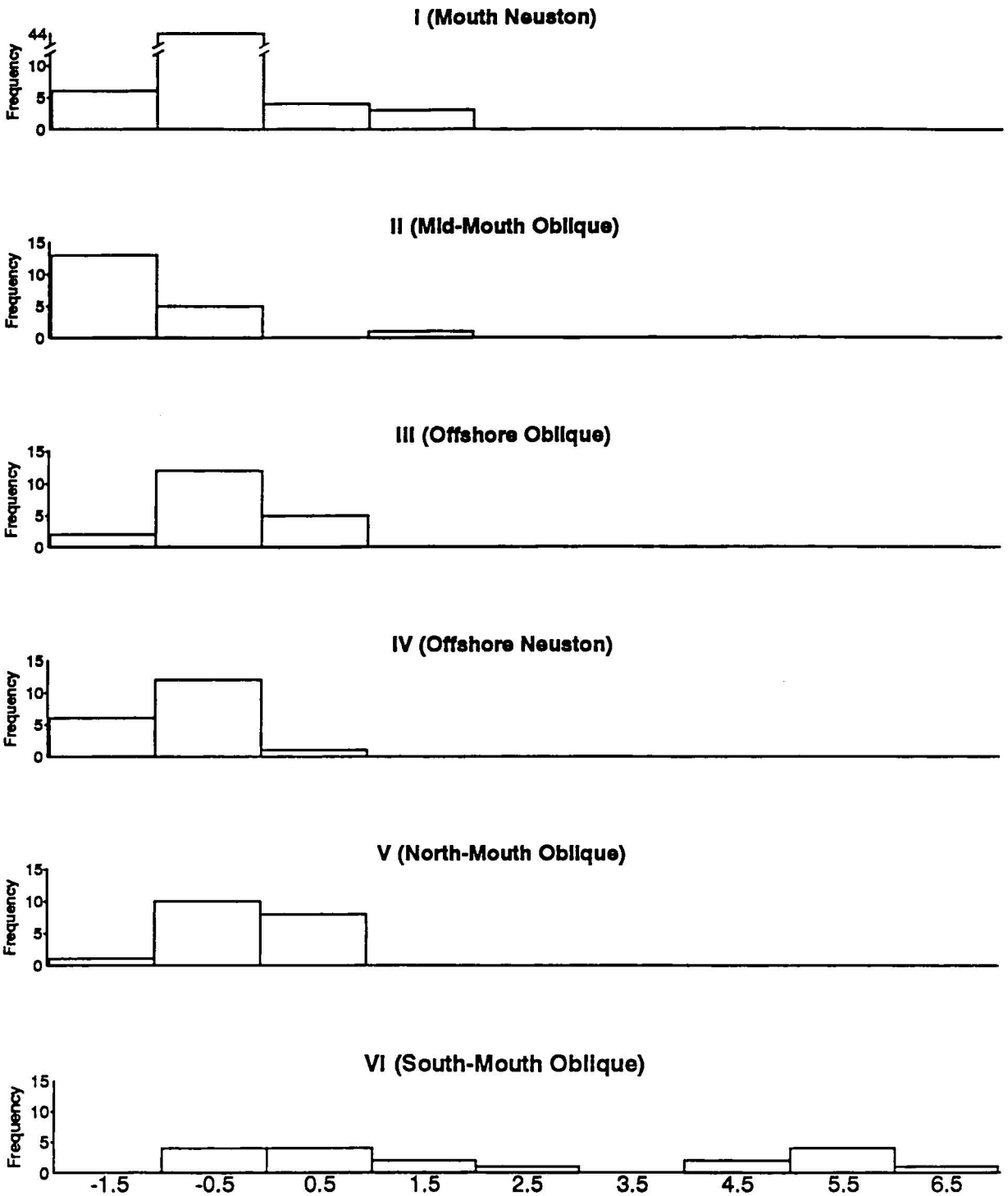
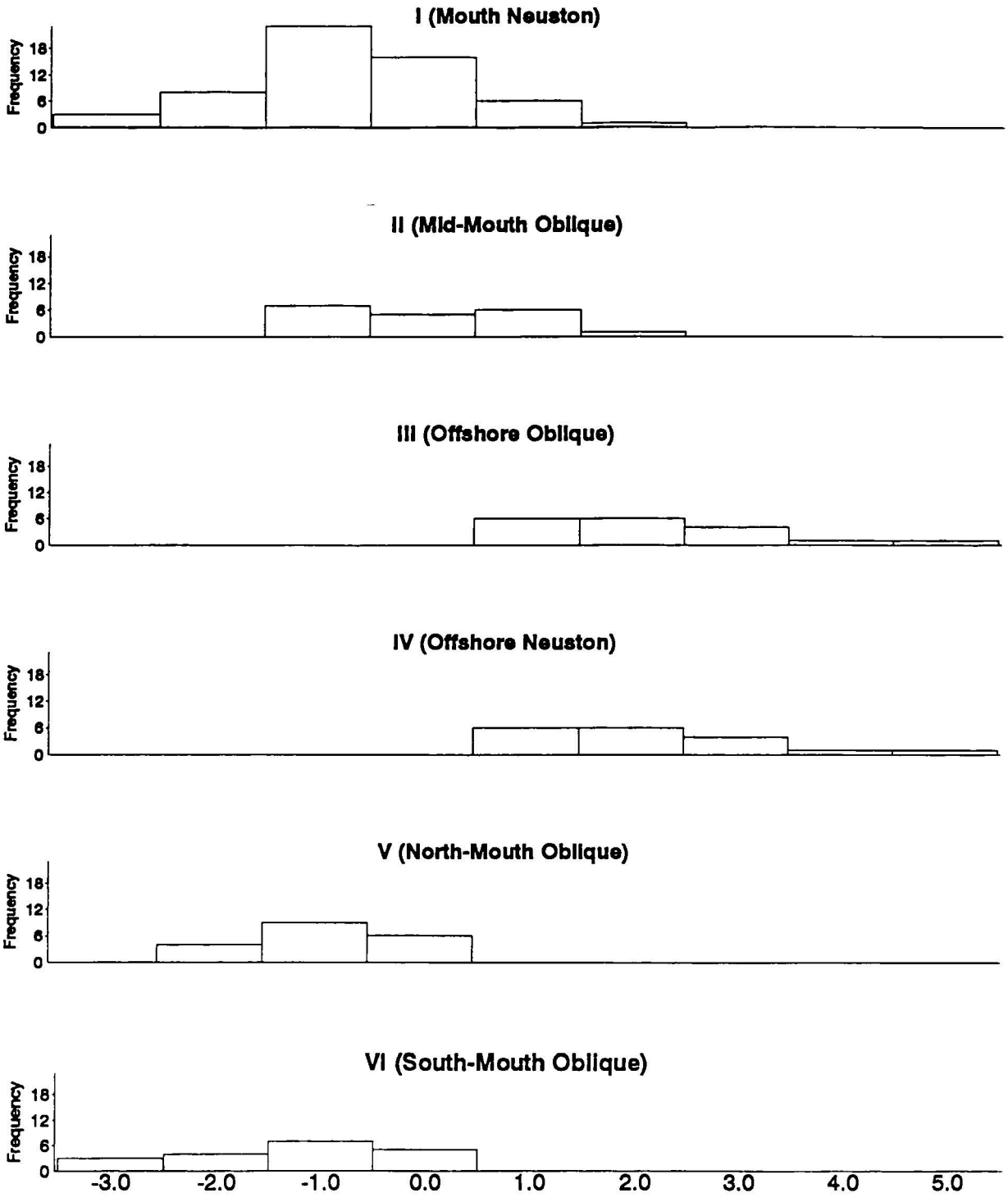

I (Mouth Neuston)
II (Mid-Mouth Oblique)
III (Offshore Oblique)
IV (Offshore Neuston)
V (North-Mouth Oblique)
VI (South-Mouth Oblique)
Frequency
44
10
5
0
15
-1.5
-0.5
0.5
1.5
2.5
3.5
4.5
5.5
6.5
First Discriminant Function Scores
CRANGON, PINTHOZ, EMERITA, EUCERAM, PAGURLZ, CALIANA

Figure 23. Frequency histograms of site group physico-chemical canonical discriminant scores: one histogram for each site group. Scores were calculated using the physico-chemical measurements (surface and bottom temperature, salinity, and dissolved oxygen), and the first discriminant function from the canonical discriminant analysis of the physico-chemical data, between site groups. Measures listed were significantly different between site groups ($p=0.05$), and had large coefficients for the first discriminant function (see Methods text for explanation). Direction of arrows indicates the signs of the coefficients.


I (Mouth Neuston)
II (Mid-Mouth Oblique)
III (Offshore Oblique)
IV (Offshore Neuston)
V (North-Mouth Oblique)
VI (South-Mouth Oblique)
Frequency
18
12
6
0
-3.0
-2.0
-1.0
0.0
1.0
2.0
3.0
4.0
5.0
First Discriminant Function Scores
Surface and Bottom Salinity
Bottom Temperature

temperature patterns in the summer months, when the bottom waters of the bay are able to warm up more than the bottom waters offshore.

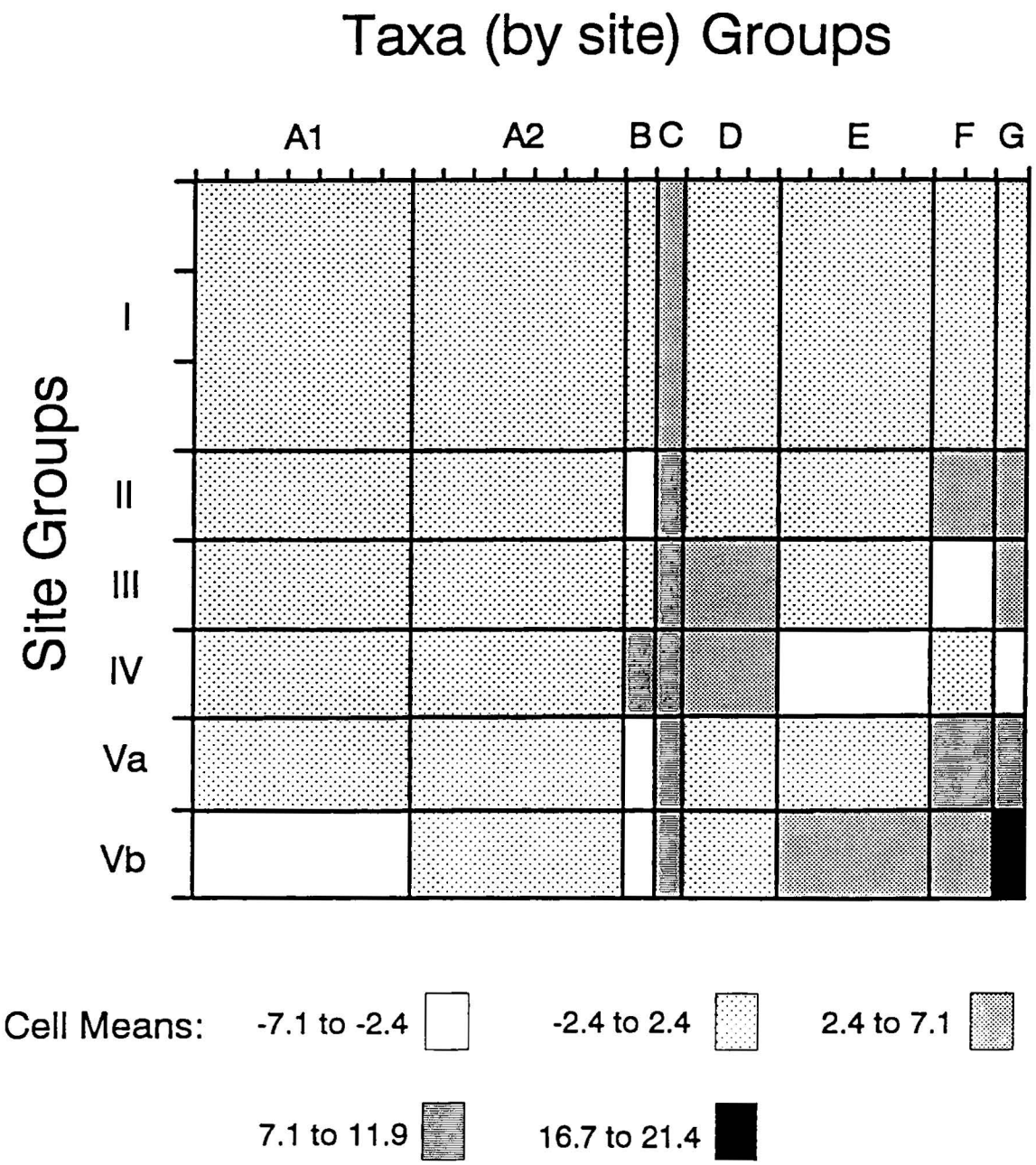
Taxa groups based upon sites

Eight groups resulted from a flexible sorting scheme with a beta value of -0.25 (Figure 16). Similar to the taxa groups based upon cruises dendrogram, some groups were large, with the remaining groups composed of one or two taxa each. The groups are discussed individually below.

W&S Site A1 The validity of cluster A1 (Figure 16) was generally supported by a comparison of the three-dimensional single taxa plots with one another. The taxa in cluster **A1** were found primarily in the mouth oblique samples (Figures 9b,12c,10c,13a,14a,and 14b). However, why the taxa of this cluster were not associated with *Crangon septemspinosa* zoea (Figure 11b), which also was found at its highest in mouth oblique samples is questionable. In the B-table (Figure 24), this group showed only a low value for site group **Vb**, because of the low abundance of the members of A1 as compared to *Crangon* (group G) and other plankters abundant at this site.

W&S Site A2 Similar to A1, cluster A2 was not placed with cluster **G** (*Crangon*), which was also more prevalent in the mouth oblique samples. This cluster also failed to show any pattern in the B-table (Figure 24), again due to the low abundances of its members.

Figure 24. Nodal plot representation of Williams and Stephenson B-table, showing taxa groups's patterns among site groups. Taxa groups were taken from Figure 16, and site groups were taken from Figure 21. The B-table values represent the spatial patterns of the taxa: the higher the number (darker the shade), the more often the taxa group's members were taken in the samples from the sites in the site group. These values were calculated using the method of Williams and Stephenson (1973). The horizontal dimension of each rectangle is proportional to the number of taxa in the taxa group (indicated by tick marks), and the vertical dimension is proportional to the number of sites in the site group.


Taxa (by site) Groups
A1
A2
B C
D
E
F
G
Site Groups
I
II
III
IV
Va
Vb
Cell Means:
-7.1 to -2.4
-2.4 to 2.4
2.4 to 7.1
7.1 to 11.9
16.7 to 21.4

W&S Site B *Callinectes* spp. megalopa, the sole member of this group, was found at its highest at the offshore neuston site (Figures 24 and 13b). This is consistent with the offshore development of *Callinectes* spp., as discussed in the VARCLUS section.

W&S Site C The zoeal stages of *Callinectes* spp., the earlier stages of the member of W&S Site group B, was the only member of this group. Like the megalopal stage it was in high numbers in the offshore neuston samples, however, it also was in high numbers at all the other sites (Figure 24), and was also dominant when present at any site (Figure 10a).

W&S Site D The members of this group (*Cancer irroratus* zoea, *Lucifer faxoni*, and *Mysidopsis bigelowi*) were abundant as a whole at the offshore oblique and neuston sites (Figure 24). Consultation with their individual plots shows that this was true for *Lucifer* (Figure 13c) and somewhat true for *Mysidopsis* (Figure 12b), while *Cancer* (Figure 11a) was found in high concentrations only at the offshore oblique site. This general offshore abundance is in keeping with what is known about their early life histories (*cf* VARCLUS section).

W&S Site E Cluster E was composed of taxa which were most consistently abundant in the oblique samples taken at the south mouth station (Figure 24), and in other bay mouth oblique collections (Figures 7c,7d,7a,12a and 7h). While this group

is internally consistent, I find it puzzling that this group was not more closely associated with groups A1 and A2.

W&S Site F Cluster F was comprised of the same two species as the taxa-by-cruise cluster b: *Upogebia affinis* and *Uca* spp. #2, both of which were found primarily in the mouth oblique sites (Figure 24 and Figures 7g and 7f).

W&S Site G The single-taxa cluster G was *Crangon septemspinosa* which was highest in the mouth oblique samples, especially in the southern mouth area (Figures 24, 22 and 11b). By examination of the dendrogram, it appears very different from most of the other taxa in its spatial distribution, when it is in reality very similar.

Summary of W&S spatial analyses

The spatial groups found by the W&S clustering (Figure 21) are generally consistent with earlier studies. The offshore neuston has been established as important for *Callinectes* (Smyth,1980; Johnson,1982), and this site was distinguished from the rest of the sites in this study, apparently due to *Callinectes* spp zoea and megalopae (Figures 10a and 13b). The abundance of *Callinectes* spp. zoea and megalopa, *Cancer irroratus* zoea, and others in the offshore oblique collections, and the lack of the larvae in mouth oblique samples helped establish this site as its own

group. Apparently the mouth neuston collections were lumped together because they had low abundances of most organisms throughout the study. However, this study was done in daylight, and the mouth neuston is preferentially inhabited by many species during the night (Maris, 1986).

Canberra Analyses

Sample groups.

With the commonly used beta value of -0.25 (Boesch, 1977), clusters were not evident, and a beta value of -0.50 was necessary to produce distinct sample groups with the Canberra metric distances. The samples, combinations of site and cruise, were best divided into six groups (Figure 25). Table 5 contains information summarizing the makeup of these six clusters. The three categories in Table 5 were chosen based upon the results of the VARCLUS and Williams and Stephenson analyses, which showed most species at their highest from July through September, and distinguishable from one another by their prevalence, or lack thereof, in the either the mouth neuston or the offshore sites. Sample group 1 was somewhat weighted towards the peak abundance months of July through September, and towards neuston samples. Group 2 was heavily weighted towards the peak abundance months, and somewhat higher in its proportion of offshore and oblique samples when compared with the study as a whole. In contrast, group 3, while small, was composed of all neuston samples. Group 4 was made up of mostly mouth samples from the non-peak months. Three of the five members of group 5 were neuston samples from the offshore station, though during non-peak months. During peak abundance months, *Callinectes* spp. larvae are found in the shelf neuston waters (Leming and Johnson,

Figure 25. Dendrogram of samples from Canberra clustering method. Inter-sample distances, due to differences among taxa, were calculated using the Canberra Metric (Boesch, 1977). Dendrogram was formed using these distances and the flexible beta method of Lance and Williams (1967). Beta used for this dendrogram was -0.50. Numbers indicate groups, and members of each group are listed below.

Group 1
AUG82MM_N
JUL83OS_O
JUN83NM_N
JUN83NM_O
MAY83MM_N
MAY82OS_N
SEP83MM_N
JUN83SM_N
NOV82aSM_N
AUG83OS_O
JUL83MM_N
SEP83NM_O
JUN82MM_N
AUG83NM_N
JUN82SM_N
AUG83SM_N
OCT82MM_N
DEC83OS_N
NOV82aMM_N
JUN83OS_N
OCT82NM_N
JUN83OS_O
OCT82SM_N
SEP82SM_O
NOV82aNM_O
MAR82bMM_N
OCT82OS_O
NOV82bNM_O
SEP83SM_N
SEP83OS_N
MAY82aOS_O
AUG82OS_N
AUG82OS_O
NOV82bNM_N
NOV82aNM_N
JUL83SM_O
MAR82aSM_O
NOV82bSM_N
FEB83MM_N
DEC83MM_N
AUG83MM_O
AUG82SM_N
AUG83NM_O
JUL82MM_O
NOV82bMM_O
JUL82NM_O
JUL82SM_N
JUL82NM_N
AUG82NM_N
JUL83NM_O
NOV82aOS_N
DEC83MM_O
MAR83SM_O
JUL82OS_N
NOV82aMM_O
NOV82bMM_N
DEC83SM_O
DEC83OS_O

Group 2
SEP82MM_N
JUL82OS_O
SEP82OS_O
MAR83MM_O
SEP83NM_N
NOV82aOS_O
FEB83SM_N
JUN82NM_N
NOV82OS_O
JUL83NM_N
OCT82OS_N
DEC83NM_O
AUG83MM_N
MAY83OS_O
OCT82MM_O
SEP82NM_N
SEP82OS_N
JUN82OS_O
AUG83OS_N
JUN82OS_N
NOV82OS_N
SEP83MM_O
DEC83SM_N
APR83MM_O
SEP83OS_O
JUL83MM_O
JUL82MM_N
JUN83MM_O
OCT82NM_O
AUG82MM_O
AUG82NM_O
SEP82MM_O
JUL82SM_O
AUG83SM_O
JUL83OS_N
JUL83SM_N
SEP82SM_N
JUN82MM_O
MAR83NM_N
FEB83SM_O
MAR82bMM_O
MAY82NM_N
MAR83OS_O
NOV82SM_O

Group 3
MAR83MM_N
APR83NM_N
FEB83OS_N
FEB83NM_N
MAR82aSM_N
MAR82bSM_N
MAR82bOS_N

Group 4
SEP83SM_O
DEC83NM_N
JUN83MM_N
OCT82SM_O
APR83OS_O
MAY82SM_N
APR83SM_O
MAR83NM_O
MAY83SM_O
MAR82bNM_O
MAY82SM_O
MAY83NM_N
MAY83SM_N
AUG82SM_O
JUN82NM_O
JUN82SM_O
MAY83MM_O
MAY83NM_O
MAY82NM_O
JUN83SM_O
FEB83MM_O
MAY82MM_N
MAR82bNM_N
MAY82MM_O
FEB83NM_O
APR83NM_O
MAR82aNM_N
FEB83OS_O
MAR82aNM_O
MAR83SM_N
MAR82bSM_O

Group 5
SEP82NM_O
MAR82aOS_O
MAR83OS_N
MAR82aOS_N
MAY83OS_N

Group 6
MAR82aMM_N
APR83SM_N
NOV82aSM_O
APR83MM_N
MAR82bOS_O
MAR82aMM_O
APR83OS_N

HEIGHT
10
9
8
7
6
5
4
3
2
1
0
1
2
3
4
5
6

Table 5. Composition of Canberra sample groups. In parentheses beside the name of each group are the total number of samples contained within that group. The "neuston" column presents the observed percentage of neuston samples, as compared to the total number of samples (152 = 8 sites x 19 cruises). Since an equal number (following calculation of replicates's mean) of neuston and oblique samples were taken, the expected value for the number of neuston samples within any group is 50%. The expected value for the "July-Sept." column is 32%, and this should be compared to the observed percentages in the "July-Sept." column. In the offshore column the observed percentages of offshore samples in each cluster is presented, and these values should be compared to the expected value of 25% (two of the eight sites were offshore).

Canberra Sample Cluster (n)	Neuston Percentage (50%)	July-Sept. Percentage (32%)	Offshore Percentage (25%)
1 (58)	59%	41%	24%
2 (44)	43%	48%	32%
3 (7)	100%	0%	29%
4 (31)	33%	6%	6%
5 (5)	60%	20%	80%
6 (7)	57%	0%	29%

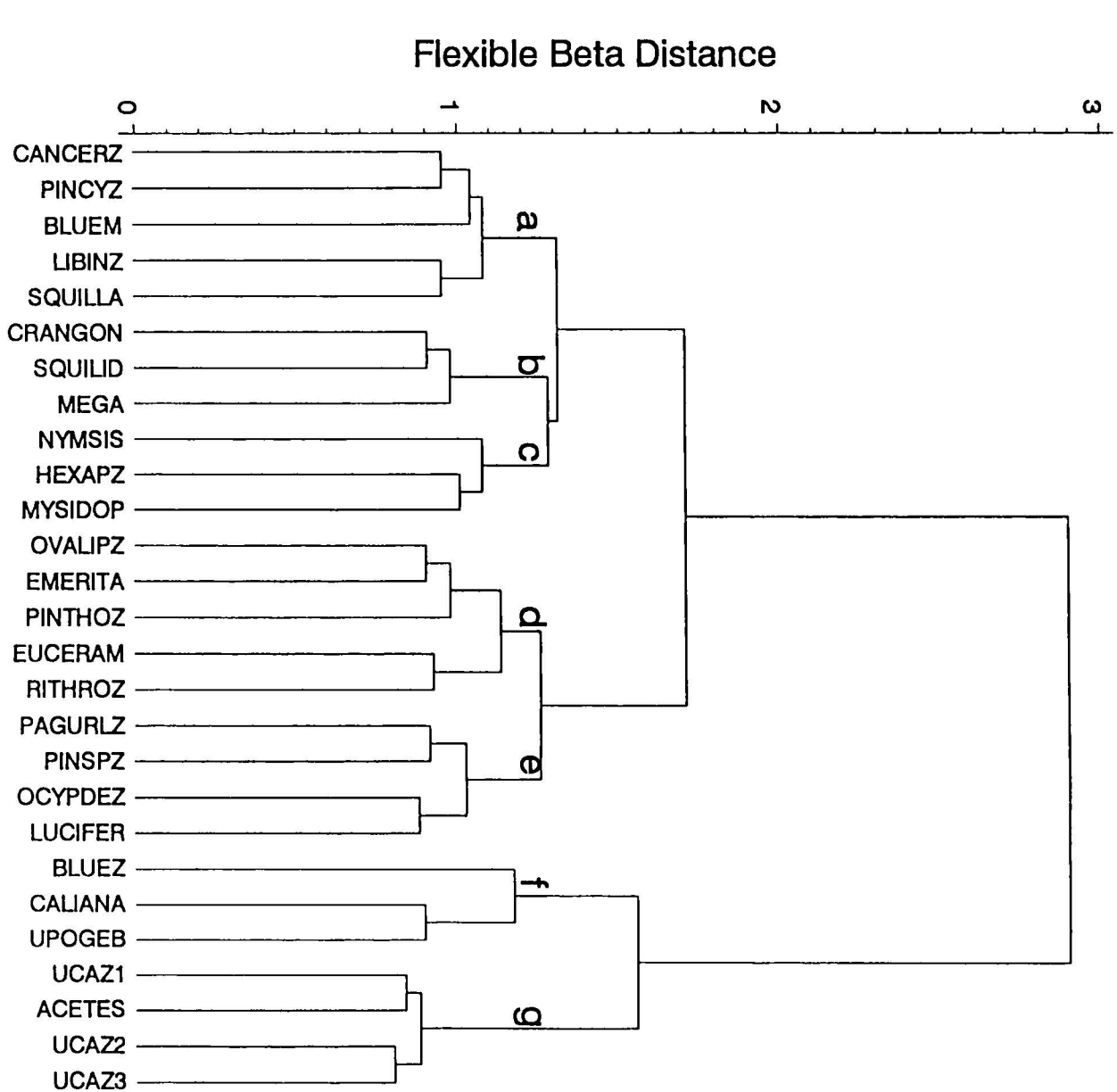
1986). And finally, group 6 contains seven samples, none of which were found in July through September.

Taxa groups.

There were seven species groups, labeled a through g (Figure 26), resulting from a beta value of -0.75. Following the format of the previous two sections, each species cluster is reviewed individually.

Canberra a This cluster is of questionable validity, as it contains *Cancer irroratus* which was at its highest in the spring of 1983 (Figure 11a), and larval stages of four other crustacean meroplankters which reached their respective peaks in the late summer and early fall (Figures 8b,13b,9c,and 13a). In addition, the summer species of this group, although alike in seasonal abundance, differed in their spatial distribution: *Callinectes* spp. megalopae peaked in the samples from the offshore neuston in 1982, *Pinnixa cylindrica* was at its most abundant in mouth oblique samples, *Squilla (empusa?)* protozoeae were most abundant in the mouth neuston samples, and *Libinia* spp. zoeae were scattered throughout the both the oblique and neuston bay mouth collections. In contrast to the cluster as a whole, the pairing of *Squilla* and *Libinia* has some validity as they do share peaks at the south oblique site during the summer of 1982, however, few *Libinia* were present at the offshore site in 1982, when *Squilla* was at its highest.

Figure 26. Dendrogram of taxa from Canberra clustering method. Inter-taxa distances, due to differences among samples, were calculated using the Canberra Metric (Boesch, 1977). Dendrogram was formed using these distances and the flexible beta method of Lance and Williams (1967). Beta used for this dendrogram was -0.75. Letters indicate groups, with numbers indicating subdivisions. Validity of groups was evaluated by comparison with diagnostic taxa abundance plots (Figures 7 through 14).


Flexible Beta Distance
0
1
2
3
CANCERZ
PINCYZ
BLUEM
LIBINZ
SQUILLA
CRANGON
SQUILID
MEGA
NYMSIS
HEXAPZ
MYSIDOP
OVALIPZ
EMERITA
PINTHOZ
EUCERAM
RITHROZ
PAGURLZ
PINSPZ
OCYPDEZ
LUCIFER
BLUEZ
CALIANA
UPOGEB
UCAZ1
ACETES
UCAZ2
UCAZ3
a
b
c
d
e
f
g

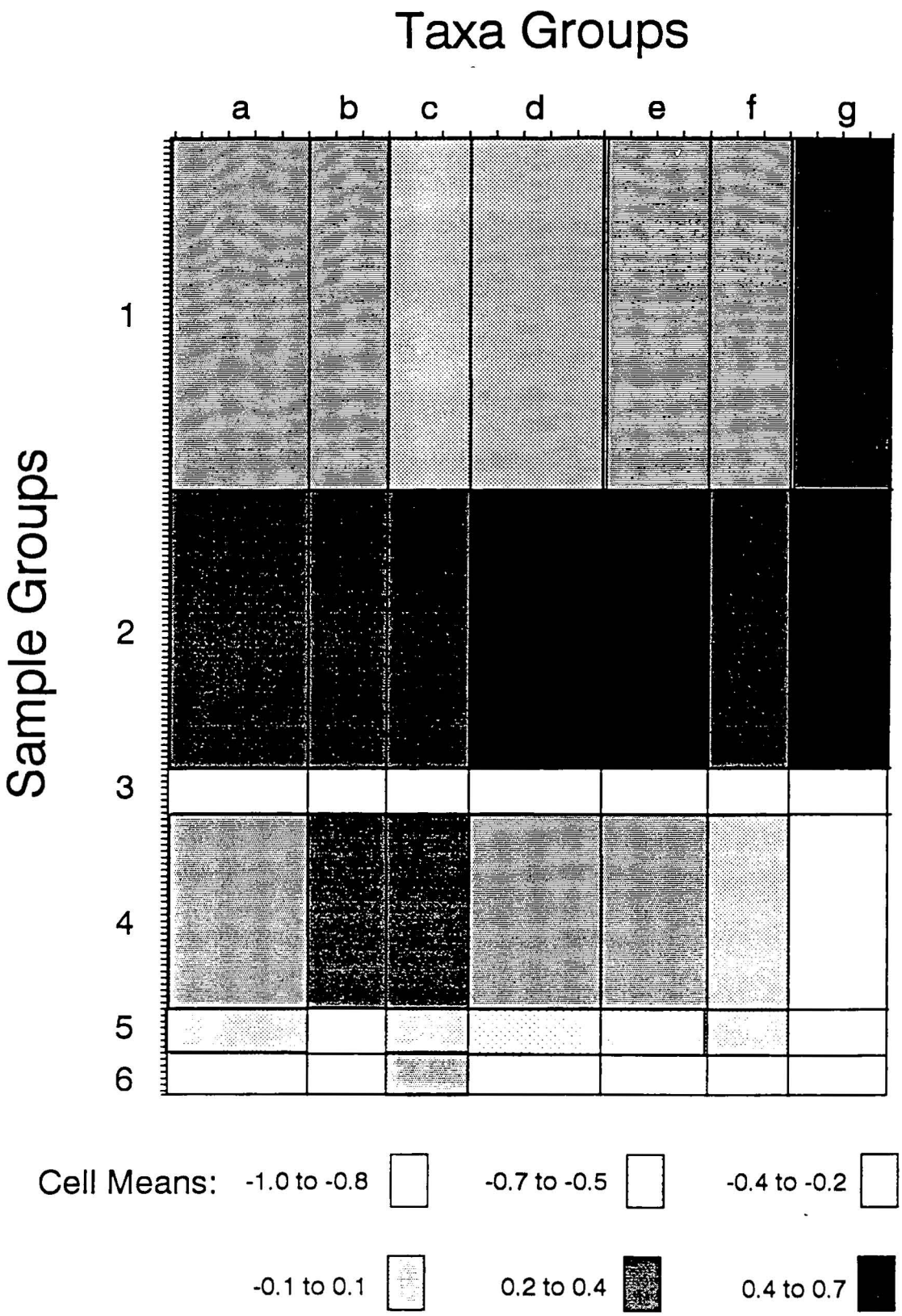
Looking at these larvae as a group in the quantitative nodal analysis, these larvae were at their highest in groups 2 and 1, showing a peak in the summer months of July to September (Figure 27). This summer peak is most likely due to the presence of the four late summer peaking species: *Pinnixa cylindrica* zoea, *Callinectes* spp. megalopa, *Libinia emarginata* zoea, and *Squilla* (*empusa*?) protozoea.

Canberra b The association of *Crangon septemspinosa* and Squillid antizoea in this cluster is very questionable. While *Crangon* was present in samples which also contained squillid larvae (Figures 11b and 10c), the squillid peak was in the late summer, and *Crangon* peaked in the spring when no squillid larvae were present. Megalopa A spp. overlapped little with either of these species (Figure 12c).

The dual nature of this group is reflected in the results of the quantitative nodal analysis (Figure 27). It has its two highest values in groups 2 and 4, showing the presence of Squillid antizoea and *Crangon septemspinosa* zoea, respectively.

Canberra c The association between *Hexapanopeus angustifrons* and *Mysidopsis bigelowi* in this cluster is marginal, while the association between *Mysidopsis* and *Neomysis* has merit. *Mysidopsis bigelowi* and *Hexapanopeus angustifrons* do co-occur during *Hexapanopeus*'s summer peak (Figures 12b and 8a), however *Mysidopsis* peaked in abundance in March and November of 1982. The association of *Neomysis* and *Mysidopsis* has merit because they had samples in common which had peak abundances, observed during the sampling events in March and November, 1982 (Figures 12a and 12b). The March peaks were possibly

Figure 27. Quantitative nodal plot, formed using the method of Boesch (1977). Plot shows the paterns of abundance of the taxa groups's among the sample groups. Taxa groups were taken from Figure 26, and sample groups were taken from Figure 25. The nodal values represent the spatio-temporal patterns of the taxa: the higher the number (darker the shade), the more often the taxa group's members were taken in the samples from the sample group. The horizontal dimension of each rectangle is proportional to the number of taxa in the taxa group (indicated by tick marks), and the vertical dimension is proportional to the number of samples in the sample group.


Taxa Groups
a
b
c
d
e
f
g
Sample Groups
1
2
3
4
5
6
Cell Means:
-1.0 to -0.8
-0.7 to -0.5
-0.4 to -0.2
-0.1 to 0.1
0.2 to 0.4
0.4 to 0.7

represented in the quantitative nodal analysis by the high values in sample group 4; group 4 contains all four of the north mouth samples for the month of March, 1982 (Figure 27). The stronger late November peaks of 1982 were not represented, probably because the November samples were included in the large site group 1, which also contained a number of summer samples, having few if any mysids. A potential explanation of the nature of the association between *Neomysis* and *Mysidopsis* was recounted in the earlier discussion of VC 6.

Canberra d This cluster is basically valid, as all of the members were most abundant in the oblique bay mouth sites during the late summer (Figures 9a,7e,7a,7i, and 7b). This pattern of late summer abundance was also seen in the results of the quantitative nodal analysis, where this group showed its highest numbers in cluster 2: a sample group with high numbers of late summer samples (Figure 27 and Table 5).

Canberra e This cluster has some merit. *Pagurus longicarpus* and *Pinnixa* spp. zoeae were both most common at the bay mouth oblique sites during the late summer and early fall (Figure 7h and 7d). The quantitative nodal analysis reflected this late summer/early fall pattern, as this species group, like Canberra d, had its highest values for sample clusters 1 and 2.

Canberra f *Callinectes* spp. zoea did have a lot of temporal overlap with *Callianassa* sp. A zoea and *Upogebia affinis* zoea. However, it temporally overlapped most of the species in this study. The placing of *Callinectes* spp. zoea

with these other two, above all others, is questionable, as *Callinectes* had a significant presence offshore while the other two did not. These species did share a pattern of late summer to early fall abundance (Figures 10a, 7c, and 7g); a pattern also seen in the results of the quantitative nodal analysis, where they had high values for the summer sample groups 1 and 2.

Canberra g This group contains two pairings of species which have some merit. *Uca* sp. 1 zoeae and *Uca* sp. 3 zoeae were encountered rarely, although generally in the same samples. The association of *Acetes americanus* with *Uca* sp. 2 zoeae seems reasonable, as these larval stages overlap in some early September summer samples (Figures 9b and 9f); however, this is the time of the onset and peak of *Acetes* abundance, whereas *Uca* sp. 2 zoea peaked earlier. The general pattern of late summer abundance, primarily evident for *Acetes* and *Uca* sp. 2 zoea, was reflected by the high value for groups 1 and 2 (Figure 27).

Summary of Canberra-based Analyses At best, the Canberra-based analyses confirmed the results of the VARCLUS and W&S methods. At worst, questionable species associations were made. The results of the quantitative nodal analysis did reflect the high relative abundance of larval decapods in sample groups 1 and 2, the two groups containing the bulk of the July through September samples (Figure 27 and Table 5).

SUMMARY AND CONCLUSIONS

This section is designed to directly address the purposes of this study, with a subsection for each of my two original objectives. In the "Assemblage Characterization" subsection, I focus upon a) the most strongly suggested species assemblages; b) the major temporal and spatial patterns of these assemblages, and of the plankters in general; and c) the physico-chemical preferences of these eumalacostracan plankters. In the second subsection, "Methods Evaluation", I summarize the evidence for the superiority of the VARCLUS method, citing evidence for a) greater accuracy, as supported by confirmation with the individual species plots; and b) easier interpretation and use of the results. However, in this subsection, I also summarize the benefits of the other two methods, and the benefit of taking several approaches in general.

1) Assemblage Characterization

a) Species Assemblages

In general, there were no strong multiple species assemblages found; the strongest associations were between pairs of species. Pairings which were most strongly supported by these data were: *Uca* sp. 2 zoea and *Upogebia affinis* zoea, paired by the VARCLUS and both the temporal and spatial W&S analyses; *Mysidopsis bigelowi* and *Neomysis americana*, which were paired by

both the VARCLUS and temporal W&S analyses; and *Callinectes* and the squillids, both with early and late larval stages that were paired with one another by the VARCLUS analysis.

Uca sp. #2 zoeae and *Upogebia affinis* zoeae were found together in the mouth oblique samples. As they do not share the same dispersal-recruitment strategy, their pairing points out that, while the assignment of these strategies is important to understanding the early life history of a species and also serves as a summary of the spatiotemporal distribution of their larvae, the assignment of a strategy does not dictate the species's association with other species. In this case, the *Uca* sp. #2 larvae were likely carried down into the lower Chesapeake Bay, where they intermingled with the resident *Upogebia affinis* zoeae.

Mysidopsis bigelowi and *Neomysis americana* were found together in the spring and fall of 1982. This result was made most apparent by the temporal W&S nodal analysis, which showed the high abundance of both of these species during the cruise of 30 November, 1982. These two were also found together in VC6 and species group c of the Canberra analysis, and this result supported the hypothesis put forward by Allen (1984) of spring and fall migrations of adults for breeding.

Both the early and late stages of *Callinectes* and squillid larvae were found in greatest abundance offshore in the late summer. These shared patterns of abundance resulting in the formation of VC4 and VC7, and matched the temporal patterns described in the literature for both species:

matching the overall spatial distribution for *Callinectes*, as well as matching the lower bay distribution for *Squilla*. The offshore spatial distribution in this study for the squillid larvae did not contradict the earlier work by Morgan (1980), however, as his study did not include any offshore sampling. The results of this study for squillid larvae, lead me to propose that it shares *Callinectes* expelled-estuarine early life history strategy, and that *Squilla* larvae may be feeding on *Callinectes* larvae.

Aside from inter-taxa patterns discussed above for VARCLUS groups 4,6, and 7, the VARCLUS taxa clusters served as an outline of the many species's patterns of temporal and spatial abundance. The various members of VARCLUS 1 and 2, *Pinnotheres ostreum* zoea, *Rhithropanopeus harrisii* zoea, *Callianassa* sp. A zoea, *Pinnixa* spp. zoea, *Emerita talpoida* zoea, *Pagurus longicarpus* zoea, *Euceramus praelongus* zoea, *Hexapanopeus angustifrons* zoea and *Pinnixa cylindrica* zoea., as well as *Uca* and *Upogebia*, discussed above, were found in the late summer oblique tows taken in the bay mouth, indicating a late summer spawn and a lower bay or nearshore distribution.

VC3 had three members whose larvae were previously found during the late summer, and earlier identified as having an offshore larval and adult distribution. This study showed the same seasonal pattern; however, the spatial pattern was not the same. Two of the members of VC3, *Ovalipes* and *Acetes* were found offshore; however, they were found in similar numbers inshore. The third member, *Libinia*, was found in highest number inshore. I postulate that the lack of offshore abundance for *Libinia* may be due to having

only one station, and that it may have been associated with the other two members of VC3 because they all came into the bay in the same water mass.

The two decapods which had the temporal distributions which differed the most from the rest of the decapod larvae were the zoeae of *Crangon septemspinosa* and *Cancer irroratus*, paired in VC5. *Cancer* and *Crangon* had their peaks in the spring months of March and May, respectively. It should also be noted that a member of VC1, *Pagurus longicarpus* zoea, was found into the late fall, after most of the other species of decapod larvae were gone, although *Pagurus* had its peak in the late summer as did the majority of the other zoeae.

b) Major Temporal and Spatial Patterns

In addition to identifying the major fall of 1982 peak shared by the mysids, the Williams and Stephenson (1973) clustering analyses summarized the major temporal and spatial patterns.

The major temporal pattern observed was the high degree of seasonality, as expected for seasonally reproducing organisms. This was reflected in the individual species plots, the VARCLUS score plots, in the W&S cruise groups, and in the nodal plots from the temporal W&S-based analyses and, to a lesser degree, the nodal plots from the Canberra-based analyses. In general, the plankters were present in highest numbers in the late summer months, reflecting the prevalence of the decapod larvae in the eumalacostracan plankton. This pattern of late summer abundance was also

seen for the sergestids, as both *Acetes americanus* and *Lucifer faxoni* zoeae were most prevalent in late August and September.

The major spatial pattern was the prevalence of species in the bay mouth oblique samples. This was reflected by VC1, the largest group of the VARCLUS analysis (containing a third of the total species), being found in highest number in the bay mouth oblique samples. This was also reflected in the discriminant analysis of the W&S site groups, where the only site group singled-out was the south-mouth oblique group with several species higher at that site. However, this pattern may be an artifact of the data analysis, because 75% of the observations in the data set were from mouth sites. This unbalanced spatial sampling regime very likely influenced the selection of species in the data reduction.

The other spatial pattern was the prevalence of the larvae in the oblique samples. This is probably because the samples were taken during the day, as many of these species are at their most abundant in the neuston at night (Maris, 1986).

c) Physicochemical preferences

The canonical discriminant analysis of the W&S site and cruise groups, the best summary of the overall spatial and temporal affinities of these organisms, offered no unexpected results. Temperature and dissolved oxygen were both highly seasonal, and inversely related to one another. Salinity was shown to be higher offshore.

2) Methods Evaluation

a) Accuracy

VARCLUS was the most accurate overall of the three methods. With the exception of *Pagurus longicarpus* zoea, VC1 was an accurate compilation of species whose spatiotemporal distribution in this study was primarily in the mouth oblique samples during the late summer. The same was true for VC2. VC3 was a reasonable association of three species whose temporal distribution was a little later in the summer, and had more numbers offshore. VC4 and VC7 accurately associated the early and late stages of *Callinectes* spp. and *Squilla* spp. *Cancer irroratus* and *Crangon septemspinosa* were correctly identified as having similarly timed peaks of zoeae in the spring, and were put together in VC5. And the mysids were appropriately clustered in VC6, based upon their shared peaks in the spring and fall of 1982.

The Williams and Stephenson analyses weren't as accurate, although they accurately and conclusively indicated the major shared peak of the mysids in late November of 1982. The formation of the large groups of both the temporal and spatial clusters appeared to be as much due to shared overall low abundances, as to shared peaks. Additional circumstantial evidence for the overall abundances of species overwhelming the analysis were the single species clusters for *Callinectes* spp. zoea in the temporal W&S clustering, and *Crangon septemspinosa* zoea in the spatial partition. Both of these species were very abundant, and *Callinectes* spp. zoeae should have been associated with the other decapods also abundant in the months of July and August, while

Crangon septemspinosa's spatial distribution was very similar to many of the other larvae: abundant in the mouth oblique tows.

The Canberra analyses were weak. The Canberra taxa dendrogram did contain a few reasonable pairings; however, many were nonsensical and most of the reasonable associations were already evident in the the results of the VARCLUS and W&S analyses.

b) Ease of Interpretation

While clustering methods offer an objective way to delineate species assemblages, the decision of what level of distance to use to define the clusters is often both difficult and subjective. The VARCLUS method offered several distinct advantages in making this decision. The analysis could be run with and without protecting the hierarchical structure, to look for distances below which the clusters are not maintained. Random runs could be used to show how strong the clusters were, at the chosen distance. Finally, the strength of association table (Table 3), allowed me to assess both the overall strength of a cluster, as well as which combinations of species are best represented by the cluster.

It is also important to have accurate and useful auxiliary or supporting plots. These plots are used to both help interpret and to assess the validity of clustering analyses. The three-dimensional plots produced from the scores of the VARCLUS analysis, provided a summary of the overall spatiotemporal pattern of each of the VARCLUS groups. These plots were initially somewhat

difficult to grasp because they were three-dimensional, but following familiarization they generally provided a good and interpretable summary of the VARCLUS's spatiotemporal pattern. The ellipse plots, used to present the results of the W&S discriminant analyses for both taxa and physicochemical data were also relatively easy to interpret. In contrast, the nodal plots of both the Canberra and W&S analyses were quite difficult to interpret. In both applications of nodal analysis, stronger patterns were most likely to be seen for small species groups, especially when they intersected with small sample or site or cruise groups. The intersection of larger species or sample/site/cruise groups with one another lead to less extreme values, because the large number of samples involved diluted any strong patterns. In the W&S analyses, the calculation of the B-table values further muddled the interpretation, because to have a high score, a group of species would have to be both abundant with respect to their own mean abundance, and abundant with respect to other samples of plankton in that site or cruise group. For example, in the temporal W&S nodal analysis, it was difficult to decide in summer cruise group nodes whether species were at a low relative to their own average abundance, or were just overshadowed by the very abundant *Callinectes* spp. zoeae.

Finally, there is the question of the general utility of multivariate analyses. This is a valid question because of the potential for misinterpretation of results. This question may be made even more apparent by my reliance upon the individual species three-dimensional plots throughout this study. Objectively finding assemblages of species is a very complicated procedure.

Multivariate analyses can serve as an objective first step, reproducible by anyone given the same data and analytical approach. These analyses can also provide a framework of association which can be evaluated, and maybe even subjectively modified (providing this is acknowledged by the data analyst, and the results considered exploratory). In this study, I could not have simply started with three-dimensional plots of all 91 eumalacostracan plankters, and then compared them to one another to characterize the associations between them. However, plots of the reduced subset of species, selected by objective multivariate methods and grouped by same, were very useful in both evaluating the results of the multivariate statistical analyses and in making apparent the spatiotemporal patterns of individual eumalacostracan plankton. Finally, while multivariate analyses do not always offer concise answers, they do provide a framework for comparisons when the data are too complex to be understood otherwise. It is more useful to have unclear or incomplete answers, than none at all.

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