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Quantitative studies of the macrofauna associated with the Mesohaline oyster reefs of the James River, Virginia

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QUANTITATIVE STUDIES OF THE MACROFAUNA ASSOCIATED WITH THE MESOHALINE OYSTER REEFS OF THE JAMES RIVER, VIRGINIA

A Dissertation
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Doctor of Philosophy

By

Peter Foster Larsen

1974

APPROVAL SHEET

This dissertation is submitted in partial fulfillment of
the requirements for the degree of

Doctor of Philosophy

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Approved, July 1974

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TABLE OF CONTENTS

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LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The present study was made to investigate the community structure and dynamics of the benthic macrofauna associated with the oyster reefs of the James River, Virginia. Attention was focused on the mesohaline region (5-18^{o}/oo salinity) of the estuary and was primarily limited to one substrate type. The sampling program was designed to produce a list of associated species and data on variation in species abundances over an annual cycle. The normal yearly cycle was modified in June 1972 by a severe freshet caused by the passage of Tropical Storm Agnes over the Chesapeake Bay drainage basin which permitted an evaluation of faunal response to sudden reductions in salinity.

Eight sites in the lower James River, representing the range of productive natural oyster reefs, were selected for sampling. Sampling was accomplished with a suction sampler which allowed the quantitative collection of all components of the benthic macrofauna. The sites were sampled quarterly for one year.

The 192 samples yielded 142 species from 11 phyla. The number of species collected was at a higher in December 1971 and declined through the remainder of the study. Twelve species were found to be important oyster associates based on both abundance and frequency of occurrence. They are: Peloscolex spp., Nerets succinea, Heteromastus filiformis, Boccardia hamata, Polydora ligni, Polydora websteri, Cassidinidea lunifrons, Melita nitida, Corophium lacustre, Balanus improvisus and Electra crustulenta.

Density varied from 2,395 to 125,573 individuals/m^{2}. Spring was the season of greatest abundance. The amount of shell surface available was important in determining density per unit area of bottom. The number of species decreased monotonically upestuary with decreasing salinity. Informational diversity also decreased in an upestuary direction with variations in the trend caused by secondary substrate changes. Evenness was more important than species richness in determining diversity levels. The high spatial heterogeneity of the reefs permitted the maintenance of higher informational diversity levels than are found in estuarine soft-bottom habitats. Most sites responded to the Tropical Storm Agnes freshet with an increase in diversity reflecting increased evenness.

Computer classification clearly separated the upestuary from the downestuary sites and the pre-Agnes for post-Agnes stations. Possible reasons for the spatial discontinuity are discussed.

Consideration of the distribution of individuals by feeding, purchase (relationship to the substrate) and larval dispersal type indicated an increase in the abundance of suspension feeding epifauna in an upestuary direction. This phenomenon is largely due to two species, Balanus improvisus and Corophium lacustre. Possible reasons for this distribution are discussed.

Only ten of the species found are commonly considered to be faithful or obligate oyster associates. They are: *Cliona truitti*, *Stylochus ellipticus*, *Nereiphylla fragilis*, *Boccardia hamata*, *Polydora websteri*, *Crepidula convexa*, *Eupleura caudata*, *Urosalpinx cinerea*, *Odostomia impressa* and *Pinnotheres ostreum*. For several reasons most of these species can be considered unimportant in the present situation.

Comparison of species lists from several recent estuarine studies shows that the oyster assemblages are qualitatively no more similar to each other than they are to estuarine soft-bottom assemblages.

The oyster reef assemblage appears to be one manifestation of a larger estuarine assemblage. It differs from soft-bottom assemblages principally in quantitative aspects. The controlling feature of the assemblage's character is the increased spatial heterogeneity provided by the shell surfaces, which allows the development of dense populations and relatively high diversities. The assemblage is not spatially or temporally homogeneous but undergoes significant changes in community structure both seasonality and along the estuarine gradient.

QUANTITATIVE STUDIES OF THE MACROFAUNA ASSOCIATED WITH THE MESOHALINE OYSTER REEFS OF THE JAMES RIVER, VIRGINIA

INTRODUCTION

The formation of reefs or beds by the accumulation of shell and debris from living and dead generations of oysters and their associated fauna is a common estuarine phenomenon on a wide geographic range. Due to their economic importance, the biology of the various oyster species, and their real or potential competitors and predators, have been studied extensively (cf. Joyce 1972, Galtsoff 1964, others). The difficulty of sampling these hard bottoms, however, has greatly limited the number of quantitative macrofaunal studies of this major brackish-water biotope. Published accounts of oyster assemblage investigations have involved derelict or semi-derelict grounds (Hagmeier and Kandler 1927, Caspers 1950, Mistakidis 1951, Thomas 1970, and Maurer and Watling 1973).

Quantitative gradient studies of the macrobenthos of North American estuaries are few and limited to soft-bottoms (Burbanck, Pierce and Whiteley 1956, Sanders, Mangelsdorf and Hampson 1965, Boesch 1971 and Tenore 1972). The only study to address itself to the fauna of hard bottoms is the qualitative work of Wells (1961). The advent of suction samplers (Brett, 1964) has greatly expanded the range of sediments which can be sampled reliably and has made it feasible to undertake a quantitative study of the macrofauna associated with productive oyster grounds.

The present study was made to investigate the community structure and dynamics of the benthic macrofauna associated with the shell reefs of the James River, Virginia. Attention was focused on the mesohaline region (5-18o/oo salinity) of the estuary and was primarily limited to one substrate type. The sampling program was designed to produce a list of associated species and data on variation in species abundances over an annual cycle. The normal yearly cycle was modified in June 1972 by a severe freshet caused by the passage of Tropical Storm Agnes over the Chesapeake Bay drainage basin, which permitted an evaluation of faunal response to sudden reductions in salinity. The numerical techniques of classification and informational diversity were used to establish the spatial and temporal relationships between the sampling sites. Consideration was given to the distribution of higher taxonomic and life form categories in an attempt to form generalizations about the influence of the estuarine gradient on the faunal assemblage. The information generated by the above analyses is used to characterize the nature of the James River oyster assemblage.

THE JAMES RIVER ESTUARY

The James River is one of the best known estuaries in the world (cf. Barrick, Dow, Tennyson, Wojcik, Norcross and Hargis, 1971). It is the southernmost tributary of the Chesapeake Bay system (Fig. 1) and it contributes about 16% of the Bay's yearly freshwater input. It is shallow (average depth 3.7 m) and is moderately well mixed vertically.

The normal longitudinal salinity distribution for each season is shown in Fig. 2. The years of sampling, 1971 and 1972, were wetter than normal, so these "normal" values must be considered slightly higher than those present in the immediate presampling period. In late June of 1972 a severe freshet was caused by the passage of Tropical

Figure 1. The lower Chesapeake Bay region.

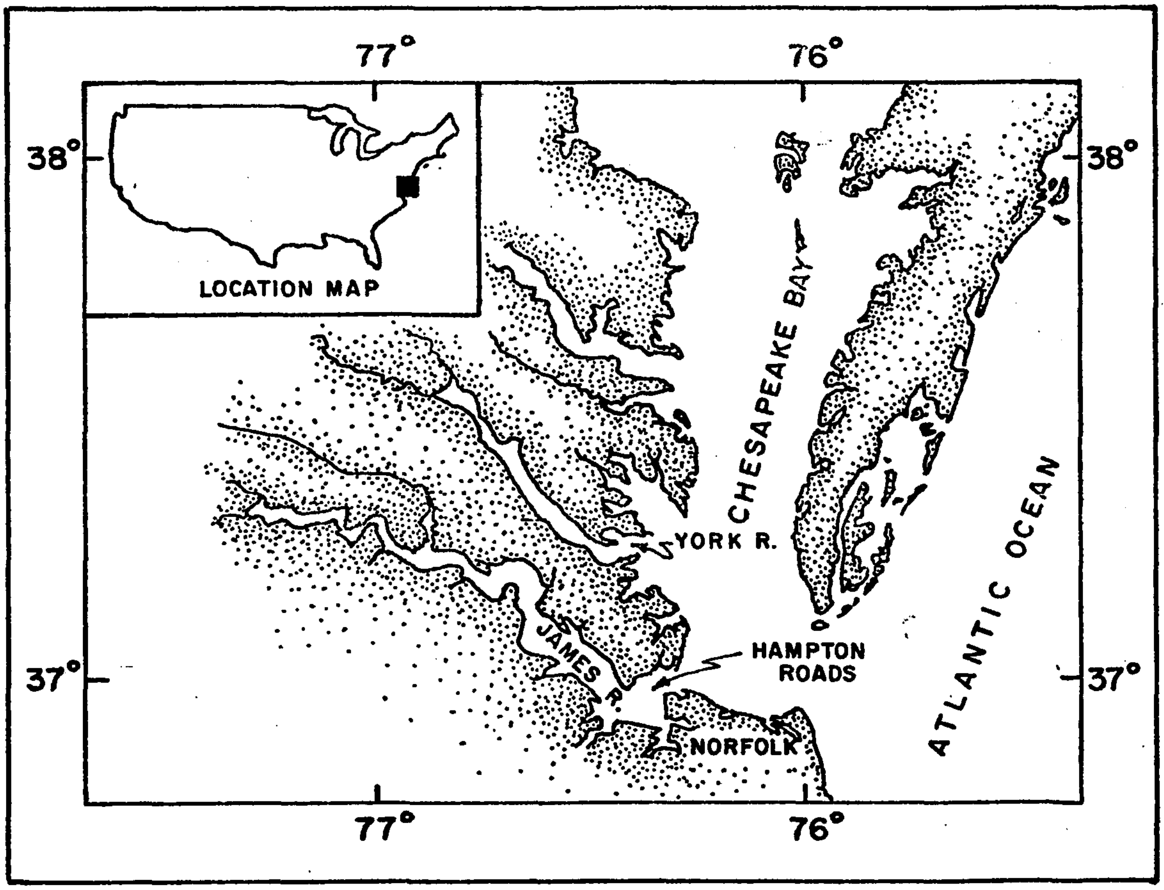
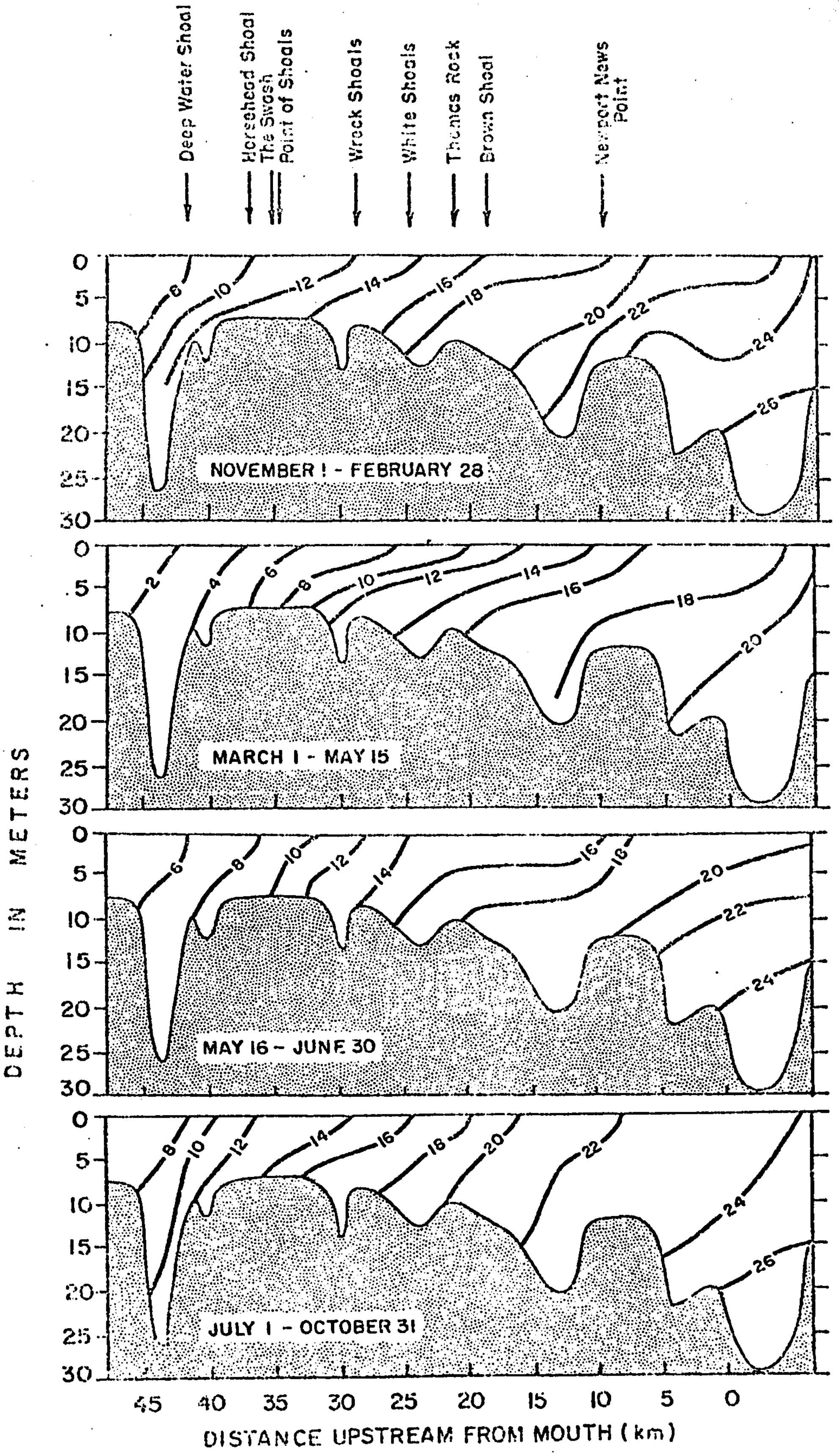

77°
76°
38°
38°
37°
37°
77°
76°
LOCATION MAP
CHESAPEAKE BAY
YORK R.
JAMES R.
HAMPTON ROADS
NORFOLK
ATLANTIC OCEAN

Figure 2. Normal seasonal salinity distribution of the James River Estuary. Average from 1944 to 1965. Modified from Nichols (1972).


Deep Water Shoal
Horsehead Shoal
The Swash
Point of Shoals
Wreck Shoals
White Shoals
Thomas Rock
Brown Shoal
Newport News Point
NOVEMBER 1 - FEBRUARY 28
6
10
12
14
16
18
20
22
24
26
MARCH 1 - MAY 15
2
4
6
8
10
12
14
16
18
20
MAY 16 - JUNE 30
6
8
10
12
14
16
18
20
22
24
JULY 1 - OCTOBER 31
8
10
12
14
16
18
20
22
24
26
DEPTH IN METERS
0
5
10
15
20
25
30
45
40
35
30
25
20
15
10
5
0
DISTANCE UPSTREAM FROM MOUTH (km)

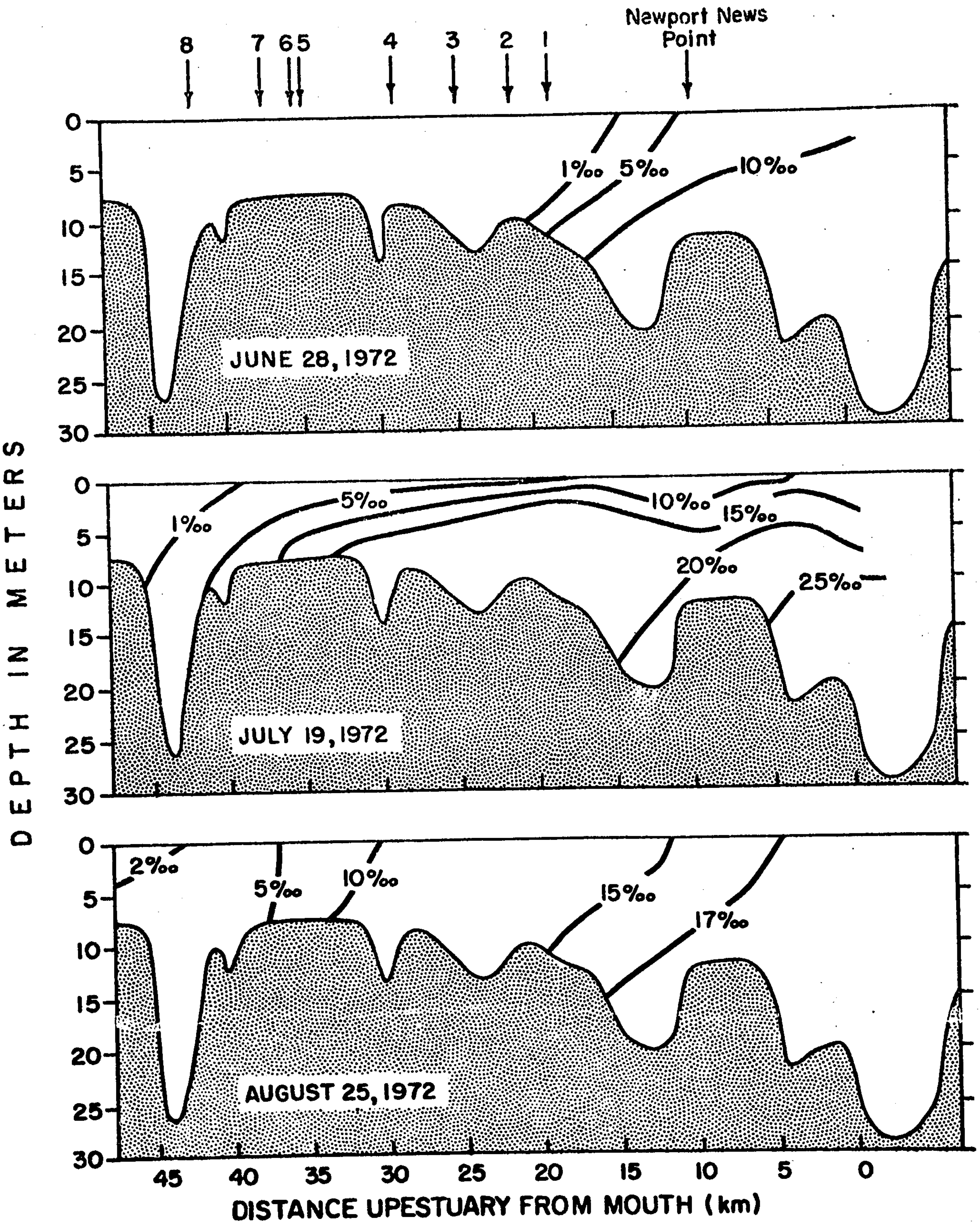
Storm Agnes over the watershed and this significantly altered the salinity pattern for over two months (Fig. 3). Salinity varies about $4^{o}/oo$ between low and high water throughout the middle reaches of the estuary. Tidal currents seldom exceed 1 m/sec. The annual temperature range is about 25°C. Detailed information on the hydrography and geology of the James River estuary can be found in Pritchard (1952) and Nichols (1972).

The estuary is subjected to various forms of pollution related to the surrounding high population and industrial density and its use as a transportation corridor and terminus.

THE OYSTER INDUSTRY

The James River oyster beds are natural structures of geological prominence that have kept pace with sedimentation and the rise in sea level for the last several thousand years. Since the advent of intensive tonging, however, there has been a recession in the height of several of the reefs (Marshall, 1953). The dense areas in Fig. 4 represent shell layers over 3 m thick and the surrounding areas have thin layers of shells, often concentrated in patches 10 to 30 cm thick (Nichols, 1972). These public seed beds are the largest seed beds on the east coast of North America and are the basis for the Virginia oyster fishery. The 1971 harvest of 439,000 bushels of seed was valued at about 1.1 million dollars and accounted for 76% of the seed production in Virginia. Approximately 150 tong boats were engaged in this effort. This level of production represents a substantial decline from the production of a decade ago and only a fraction of the 2,000,000 bushels of seed produced annually during the height of the Chesapeake Bay oyster industry.

Figure 3. Alteration of salinity distribution as a result of Hurrican Agnes. Modified from Andersen, et al. (1973).



Newport News Point
8
7
6
5
4
3
2
1
1‰
5‰
10‰
JUNE 28, 1972
1‰
5‰
10‰
15‰
20‰
25‰
JULY 19, 1972
2‰
5‰
10‰
15‰
17‰
AUGUST 25, 1972
DEPTH IN METERS
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5
10
15
20
25
30
45
40
35
30
25
20
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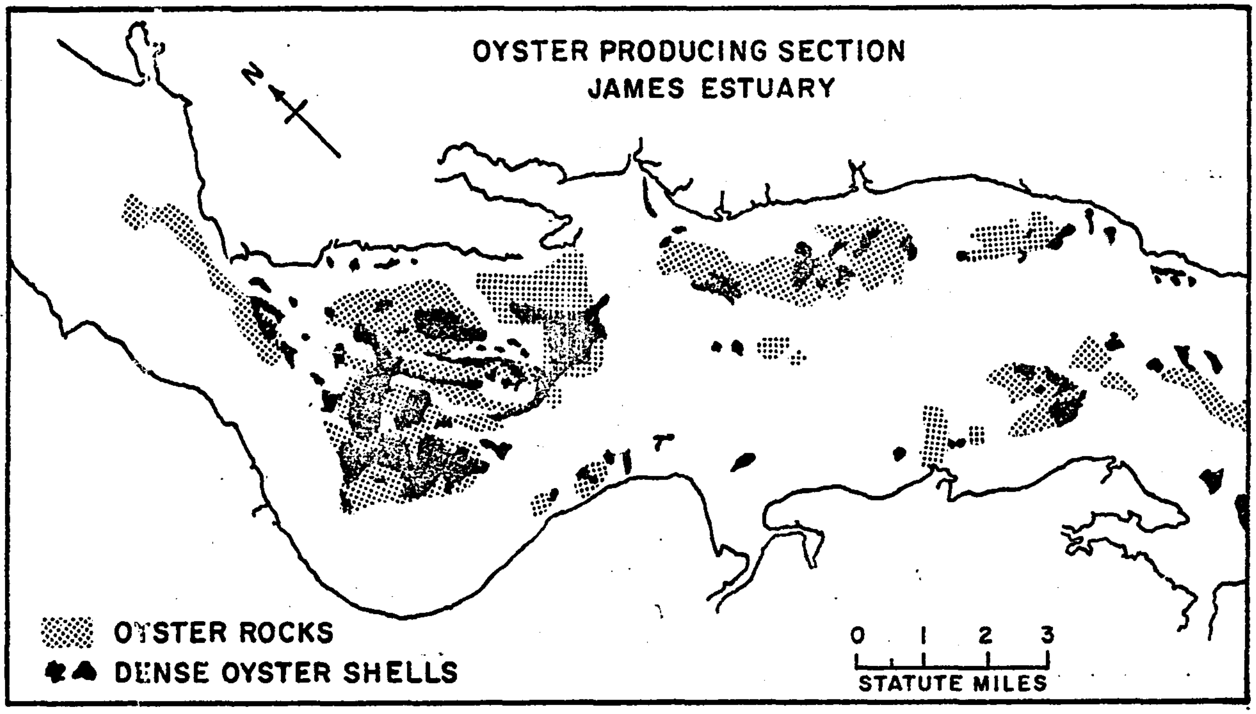
10
5
0
DISTANCE UPESTUARY FROM MOUTH (km)

Figure 4. The oyster producing section of the James River Estuary.


OYSTER PRODUCING SECTION
JAMES ESTUARY

Presently the producing reefs are located between 18 and 43 kilometers above the mouth of the James River whereas, historically, oystering also occurred below kilometer 18. This contraction of the range of productive reefs was caused by the decimation of the higher salinity populations in the early 1960's by the sporozoan disease MSX (Andrews and Wood, 1967). Much of the preceding account was based on personal communication with D. S. Haven.

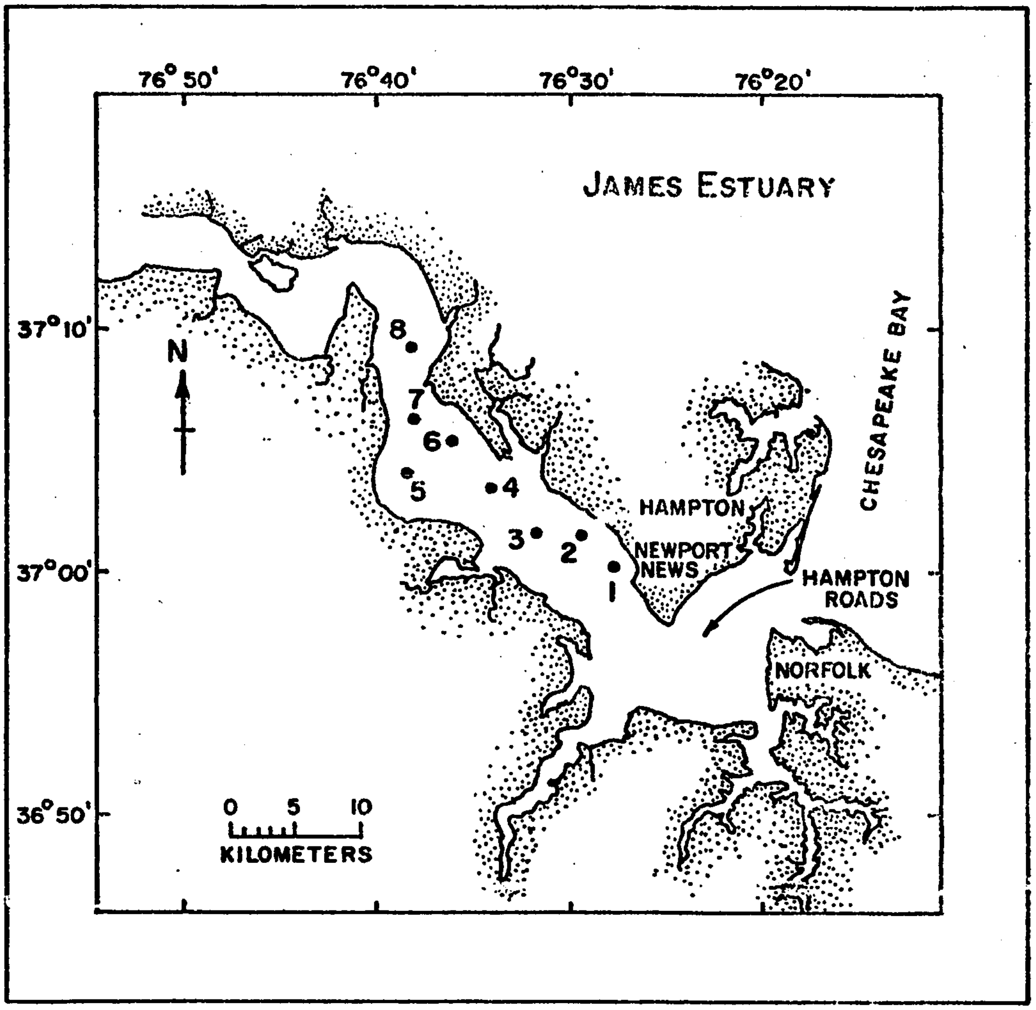
METHODS AND MATERIALS

FIELD METHODS

Between Brown Shoal and Deep Water Shoal in the lower James River, eight sampling sites, representing the range of productive natural oyster reefs, were selected (Fig. 5). Each site was sampled in December 1971 (Fall), March-April (Winter), June (Spring) and September (Summer) 1972, with a surface operated suction sampler (Larsen, 1974). The June sampling period ended five days before the passage of Tropical Storm Agnes and the September samples were collected 10 to 12 weeks after it. All components of the benthic macrofauna were considered quantitatively collected due to the excellent penetration of this type of sampler into even the coarsest substrates.

Selection of a representative sampling site on each reef was based on prior knowledge of the reef and on test dredgings and hand tong samples. Care was taken to locate the sampling site on the highest, best defined portion of the reef, while allowing about 100 m radius around the site for the random location of sampling points. Stakes were implanted to mark the sampling area and angles to fixed points on land,

Figure 5. The location of sampling sites in the James River Estuary. Common names of sites are: 1) Brown Shoal; 2) Thomas' Rock; 3) White Shoal; 4) Wreck Shoal; 5) Point of Shoals; 6) The Swash; 7) Horsehead Shoal; 8) Deep Water Shoal.


76° 50'
76°40'
76°30'
76°20'
JAMES ESTUARY
37°10'
37°00'
36°50'
N
8
7
6
5
4
3
2
1
HAMPTON
NEWPORT NEWS
HAMPTON ROADS
NORFOLK
CHESAPEAKE BAY
0
5
10
KILOMETERS

or navigational aids, were determined by sextant so that the positions could be relocated should the stakes be lost.

Six samples of $0.0126m^2$ each were taken from an anchored boat at predetermined points around a given stake. Points were chosen by the "spoked-wheel" technique used by Orth (1971a). In application, a hypothetical wheel with numbered spokes, each having six nodes, was placed over the site, with the first spoke pointing north. The nodes defined potential sampling points. The actual nodes to be sampled were determined by the use of a random number table, e.g. if the number picked from the table was 23, the third node of the second spoke was sampled. Sampling points were thus chosen for every site before the start of each quarter's sampling.

The boat was held in place over a sampling point by an oyster dredge, filled outside of the sampling area and so positioned that wind and tide caused the boat to drift to the desired point. Two replicate samples were taken at each of three points at a site.

Samples obtained with the suction sampler were retained in a 505 micron mesh bag. The bags were removed from the sampler, labeled, and placed in a $MgSO_4$-sea water solution to relax the organisms. Full strength formalin was added after a few hours to produce approximately a five-percent solution. The volume of each sample was determined by displacement of water. The sample volume cannot be considered a function of the volume of the substrate sampled because most fine material was lost during the sampling process; nevertheless, it is a useful measure of coarse material present, which was predominantly mollusc shells. This relationship does not hold for all samples, however, because the few samples taken in a clayey substrate included large balls of clay resistant to breakdown by the water jet.

Samples of bottom water were taken at each site and returned to the laboratory for determination of salinity and dissolved oxygen levels. The temperature of the bottom water was noted in the field and qualitative observations were made on current speed and direction. The depth of water at each sampling point, as measured on the shaft of the sampler, was recorded.

LABORATORY PROCEDURES

Samples were sieved into four size fractions (9.5, 4.0, 1.0 and 0.5 mm) to facilitate handling. The coarsest fraction included oyster shells, larger bivalves and decapod crustaceans. Each shell was examined under an illuminated magnifying lens to identify any encrusting forms and to enumerate the noncolonial individuals. The shells were then fragmented with pliers and the light fraction was removed by decantation into a 0.5 mm sieve. The fraction was made up principally of shellboring annelids and individuals in deep crevices missed during examination of the whole shells. The heavier fragments remaining after decantation were examined under a dissecting microscope to insure complete recovery of the shell-infesting organisms. Live oysters were opened and checked for symbionts. The 4 mm fraction was examined under an illuminated magnifying glass. The fraction contained the larger motile forms but only a few encrusting species, because of the small size of the shell fragments. The 1.0 mm fraction was separated by decantation into a light fraction of unshelled fauna and detritus, and a residual of fine shell cinder and heavy-bodied fauna. Both fractions were picked, sorted, and the individuals enumerated and identified with the use of a dissecting microscope. Preliminary analysis of the 0.5 mm fraction showed that it added very little in the way of individuals or addition species. It was decided that the inordinate expenditure of time necessary to process this fraction was not justified by the slight information gain.

CLASSIFICATORY METHODS

Classificatory methods are helpful in seeking the generalities of patterns of distribution often masked in a complex data set. Recently, benthic community investigators have used one of two classificatory approaches in their analyses. The first proceeds in the tradition of Petersen and Thorson (Thorson, 1957) to characterize communities or associations based on the distributions of a few numerically dominant, "characteristic" and/or visually obvious species, consequently disregarding the majority of the information collected. The utility of this method, however, has been challenged (Thorson 1966, Mills 1969) because of its questionable validity in many situations.

The second approach to classification involves numerical analysis of all, or most, of the sample data. Computer programs have been developed to cope with the higher degree of complexity of these classifactory methods and marine examples are presented by Stephenson, Williams and Lance (1970), Day, Field and Montgomery (1971), Hughes and Thomas (1971 a,b) and Boesch (1973). The latter approach was considered the most rewarding with respect to gaining a meaningful insight into the distributional patterns of the macrofauna associated with oyster reefs.

There are several types of classificatory systems to choose from, but hierarchical agglomerative systems are presently the most refined

(Williams, 1971). A combination of two similarity indices and two hierarchical clustering strategies were used in the present study.

Similarity Indices

The first similarity index chosen was that of Sorensen (1948). This is a qualitative index (presence-absence), the type recommended by Lambert and Dale (1964) for analysis of survey data. It is calculated as: $S = 2c/(a+b)$, where S = similarity coefficient, a = number of species in sample a, b = number of species in sample b, and c = number of species shared by the samples. The value of the index can range from 0, for no species in common, to 1, for identical species lists. The use of binary data can be considered an extreme transformation to correct for numerical dominance.

Greig-Smith (1964) advocated the use of quantitative data in survey situations and Williams, Lance, Webb, Tracey and Connell (1969) showed that qualitative data can be unsatisfactory, if based on relatively small samples from a complex environment such as a rain forest or marine benthic situation. An index with proven success in this type of situation and employed in this study was the Canberra metric dissimilarity coefficient (Stephenson, Williams and Cook 1972). The index takes the form of

$$d_{1,2} = (1/n) \sum_{i}^{n} |x_{1i} - x_{2i}| \quad /(x_{1i} + x_{2i})$$

where $d_{1,2}$ is the dissimilarity between the entities 1 and 2, and x_1 and x_2 are the values of the ith attribute of the entities. A principal advantage of this measure over other popular indices such as Bray-Curtis and Euclidean distance is that it is self-standardized over individual comparisons and is therefore relatively insensitive to large outlying values (Williams, Lance, Webb and Tracey 1973). The data were, however, log-transformed before use as an added precaution against being overwhelmed by outlying values.

Clustering Strategies

Dendrograms were constructed from the intersample similarity matrices using the group averaging (Sokal and Smeath, 1963) and flexible sorting (Lance and Williams, 1967) strategies. They have been used in combination previously (Stephenson et al. 1972, and Boesch 1973).

Clustering strategies may be space-distorting or space-conserving, i.e. as groups are formed it may appear that a space between groups is contracted, dilated or unchanged (Lance and Williams, 1967). In the case of space contraction, a group will appear to move closer to another element as it grows and the chances are increased that an individual will add to a pre-existing group rather than become the nucleus of a new group. An individual is defined as the smallest or basic classifiable unit and an element is a group of one or more individuals. A space contracting strategy, by its nature, will result in the chaining of elements, i.e. the successive formation of groups by the addition of a single individual to a pre-existing group. Space dilation effectively moves a forming group away from other elements and hence makes that group more difficult to join. The larger a group becomes the more difficult it is to join, forcing the formation of many small groups. While groupings of this type are usually the most meaningful ecologically, non-conformist groups can and do result. Non-conformist groups are the result of misclassifications which occur when a group withdraws so far from one of its own natural members that this member finds it easier to join another group. It is possible for a non-conformist group to contain only elements which are dissimilar to everything else, including other members of this group (Williams, 1971). All intensely, i.e. space-dilating, clustering strategies exhibit this group size dependence, although it can be reduced in flexible sorting (Williams, Clifford and Lance, 1971). In a space-conserving strategy, interelement distances remain unchanged by group formation.

Flexible sorting is a space-distorting strategy with the nature and degree of the distortion a function of the cluster intensity coefficient (β). If h, i, j are elements with d_{hi}, d_{hj} and d_{ij} the distances between them, and i and j are fused into a group k, then the distance between h and k is defined by the equation:

$$d_{hk} = \alpha\,(d_{hi} + d_{hj}) + \beta d_{ij}$$

with the limitations that $2\alpha + \beta = 1$ and $\beta < 1$ (Williams et al., 1971). There is then a unique value for α for each value of β. The space-contracting properties are highest as β approaches unity and the intensity of clustering increases as β decreases. Tests were made with β set at -0.50, the conventional -0.25, and 0.0 to find the most appropriate value for this set of data.

The group averaging clustering strategy is a space-conserving method with the similarity of a group to another element being the mean similarity of its members. This relatively weak clustering strategy, while often not very powerful when used singularly in an ecological context, is valuable as a check for misclassifications when used in conjunction with an intensely clustering strategy.

COMMUNITY STRUCTURE ANALYSES

Shannon's formula for informational diversity (Pielou, 1966) was used as a measure of the degree of organization in the assemblages of organisms collected. This was calculated as: $H' = -\Sigma p_i \log p_i$, where H' is the estimated population value of the average diversity, s is the number of species in the collection, and p_i is the proportion of the ith species in the collection. The evenness and species richness components of diversity were computed as: $J' = H'/\log s$ for evenness (Pielou, 1970) and $SR = (s-1)/\ln N$ for species richness (Margalef, 1958), where N is the number of individuals and s the number of species in the collection.

Rank analysis of dominants was employed using a 5-point system, where the most abundant species in a sample was awarded 5 points, the second most abundant 4 points, and so on to the species ranked fifth.

In addition, all species were placed into one of five feeding types, one of five purchase (relationship to the substrate) types, and one of three reproductive types, based on published accounts and consultation with experts.

All data were coded and punched onto computer cards using the standard format described by Swartz (1972). A formal taxonomic code was used for the fauna (Swartz, et al. 1972). Structural analyses were performed on the IBM Model 1130 computer located at the Virginia Institute of Marine Science, while the classificatory programs were run on the IBM Model 360-50 operated by the Computer Center at the College of William and Mary.

RESULTS

THE FAUNA

The 192 samples yielded 142 recognizable taxa, 121 of which could be identified to the species level. The 124 noncolonial species included 80,629 individuals. Appendix I gives a phylogenetic listing of all taxa found and their stations of occurrence. Colonial species, sponges, hydroids and bryozoans, while included in all species lists, were excluded from analyses involving numbers of individuals. _Peloscolex heterochaetus_ and _P. gabriellae_ were treated as a single species for the purposes of this study because of the special techniques necessary to separate them accurately.

Of the 11 phyla represented in the collections, the richest were Arthropoda, Annelida and Mollusca, in that order (Table 1). These three phyla accounted for 76.7% of all species and 87.9% of noncolonial species.

SEASONALITY

The distribution of species by the number of seasons of occurrence is described in Table 2. A large proportion, 34.8%, of the total number of species were taken during only one sampling period, but most of these species were rare rather than seasonally cyclic.

There were three distinct temporal patterns exhibited by the 14.2% and 17.0% of the species which had occurrences limited to two or three seasons respectively. One small group, exemplified by the urochordate _Molgula manhattensis_ and the estuarine endemic bivalve _Congeria leucophaeta_, consisted of species which had a definite seasonal pulse in their abundances, but were present in such small numbers at other times that they

Table I. Distribution of species among the higher taxa.

Phylum or Higher Taxon	Number of Species	
Porifera	3	
Cnidaria	10	
Platyhelminthes	2	
Rhynchocoela	7	
Ectoprocta	5	
Entoprocta	1	
Phoronidea	1	
Annelida	36	
Mollusca	32	
Pelecypoda		14
Gastropoda		18
Arthropoda	41	
Copepoda		3
Cirripedia		2
Mysidacea		1
Cumacea		3
Isopoda		4
Amphipoda		14
Decapoda		9
Insecta		5
Chordata	4	
Urochordata		1
Vertebrata		3

Table 2. Seasonality of species by number and percentage.

Number of Seasons of Occurrence	No. of Species	Percentage of Species
1	49	34.8
2	20	14.2
3	24	17.0
4	48	34.0

were subject to random exclusion from the samples. A second group included species which were probably constant members of the assemblage under investigation, but were present in low enough densities to be subject to the same type of sampling error. Members of this group included the nemertean Amphiporus bioculatus, the decapod Upogebia affinis, and the amphipod Pleusymtes glaber. The third pattern of temporal distribution of species with occurrences in two or three seasons was undoubtedly a response to Tropical Storm Agnes. Of the 24 species present in three seasons, 15 were present in all sampling periods before Agnes but absent in the post-Agnes collections. That this pattern was a normal seasonal effect is unlikely as many of the species involved, such as the polychaetes Sabella microphthalma and Hydroides dianthus and the gastropods Mitrella lunata and Crepidula convexa, are well-documented as being faithful members of the estuarine fauna.

Forty-eight species, 34% of the total, were present throughout the year in moderate to high numbers over a wide range of sites.

The greatest number of species in a season occurred in the fall of 1971, the first sampling period, followed by a continual decline through the remainder of the study period (Table 3). The large decline in the number of species between the fall (December) and winter samples (March-April)was expected, as it is in March and April that the yearly low in salinity is normally experienced. A net loss of five species was registered between the winter and spring (June) samples, but this decline is not large enough to realistically attribute to a real reduction in species richness, especially since some sites showed an increase

Table 3. Occurrence of species by season

Season	Number of Species	Percentage of Species
Fall	106	74.6
Winter	93	65.4
Spring	88	61.9
Summer	71	50.0

during the period. By far the most significant loss of species was noted between the spring and summer (September) collections. Although the highest salinities and water temperatures were observed in September, only 50% of the total number of species recorded were found at that time. This is most likely a reflection of the severe salinity reductions caused by Hurricane Agnes in late June.

CONSTANCY AND ABUNDANCE

It is usual in a multi-species collection to find many rare species and few abundant ones (Pielou, 1970). The present situation conforms to this generalization in that the greatest number of species indeed had very few occurrences (Table 4), however, a surprisingly high number were nearly ubiquitous.

Species were ranked by number of stations of occurrence (maximum 32), number of samples of occurrence (maximum 192), and total number of individuals; the 15 highest ranking species by each criteria are listed in Table 5.

The three lists are similar; 11 species are common to all three. Electra crustulenta, the encrusting bryozoan, is a colonial form hence could not be ranked by abundance. Crassostrea virginica was encountered at 31 of 32 stations but due to a relatively low density was found in only 61% of the replicates and was not ranked by abundance. The two shell-boring polychaetes, Polydora websteri and Boccardia hamata, occurred at fewer stations and in fewer replicates than Crassostrea, a preferred substrate. The nemertean species d and the naked goby Gobiosoma bosci occurred at 26 and 24 stations respectively, but were present in relatively low numbers; hence they are absent from the last

Table 4. Frequency of recording of species in the summated collections.

Frequencies of Recording	Number of Species Recorded
1	40
2	16
3	9
4	5
5	12
6	7
7	4
8	5
9	2
10	3
11	2
12	4
13	4
14	3
15	4
16	2
18	1
19	1
20	2
24	1
26	1
29	3
30	3
31	3
32	4

Table 5. Rankings of species by station constancy, sample constancy, and number.

Rank by Station Constancy	Rank by Sample Constancy	Rank by Number
Peloscolex spp. (32)	*Peloscolex* spp. (177)	*Balanus improvisus* (28,955)
Nereis succinea (32)	*Nereis succinea* (168)	*Peloscolex* spp. (8523)
Heteromastus filiformis (32)	*Electra crustulenta* (164)	*Diadumene leucolena* (4134)
Cassidinidea lunifrons (32)	*Balanus improvisus* (161)	*Polydora ligni* (3872)
Electra crustulenta (31)	*Heteromastus filiformis* (159)	*Brachidontes recurvus* (3566)
Melita nitida (31)	*Cassisinidea lunifrons* (148)	*Streblospio benedicti* (3562)
Crassostrea virginica (31)	*Melita nitida* (141)	*Nereis succinea* (3364)
Balanus improvisus (30)	*Polydora ligni* (136)	*Corophium lacustre* (3304)
Corophium lacustre (30)	*Brachidontes recurvus* (131)	*Melita nitida* (3059)
Boccardia hamata (30)	*Corophium lacustre* (124)	*Cassidinidea lunifrons* (2764)
Polydora ligni (29)	*Crassostrea virginica* (117)	*Heteromastus filiformis* (2361)
Brachidontes recurvus (29)	*Boccardia hamata* (115)	*Boccardia hamata* (1952)
Polydora websteri (29)	*Polydora websteri* (108)	*Odostomia impressa* (1358)
Species d (26)	*Streblospio benedicti* (89)	*Congeria leucophaeta* (1212)
Gobiosoma bosci (24)	*Diadumene leucolena* (85)	*Polydora websteri* (982)

two columns. Low salinity limited the upestuary occurrence of the spionid annelid Streblospio benedicti and the anemone Diadumene leucolena (Appendix I), so they were not ranked among the top fifteen by stations of occurrence. Both the pyramidellid Odostomia impressa and the bivalve Congeria leucophaeta were represented by enough individuals to rank 13th and 14th in total abundance, but their distributions were limited temporally and spatially, precluding a high rating in constancy.

The 11 species ranked on all three lists, i.e. those that form a constant and numerically important part of the oyster's environment over the range of sites studied, are: the annelids Peloscolex spp., Nereis succinea, Heteromastus filiformis, Boccardia hamata, Polydora ligni and P. websteri, the crustaceans Cassidinidea lunifrons, Melita nitida, Corophium lacustre, and Balanus improvisus, and the bivalve Brachidontes recurvus. Together these species represent 77.5% of the individuals sampled. The colonial Electra crustulenta may also be considered a member of this group.

CHARACTERISTICS OF INDIVIDUAL SITES

The physical and biological conditions at each sampling site are described in this section. In Table 6 ranges of tidally uncorrected depth and salinity, observed during sampling, for each site are presented. Species are ranked by abundance at each site in Table 7 a-h with data pertaining to species abundance by season, cumulative number of individuals, percentage each species represents of total individuals and cumulative percentage.

Brown Shoal

Site I is located on Brown Shoal, the second most downestuary site

Table 6. Some physical characteristics of the sampling sites including ranges of depth and salinity observed during sampling.

Site	Depth Range (m)	Mean Depth	Salinity Range (o/oo)	Kilometers From Mouth
1	2.1-4.1	3.12	13.8-17.6	18.9
2	1.8-4.0	2.88	11.5-13.4	21.4
3	1.5-2.7	1.91	10.4-13.7	25.2
4	2.7-3.7	3.24	9.5-12.3	29.2
5	1.2-3.4	2.37	2.0- 9.3	35.0
6	2.7-5.5	3.89	2.1- 9.6	35.3
7	1.8-3.7	2.68	1.6- 8.8	37.1
8	1.4-4.1	2.79	0.7- 6.2	42.4

Table 7. Seasonal and total abundance and derivatives. Seasonal values are per 0.076 m^2. Presence of a colonial species is indicated by "+".

Part A - Site I

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Streblospio benedicti	1	16	242	1087	7	1352	1352	16.8	16.8
Peloscolex spp.	2	203	584	385	25	1197	2549	14.8	31.7
Diadumene leucolena	3	90	431	255	54	830	3379	10.3	42.0
Polydora ligni	4	45	417	330	6	798	4177	9.9	51.9
Heteromastus filiformis	5	86	151	146	100	483	4660	6.0	57.9
Nereis succinea	6	36	252	122	28	438	5098	5.4	63.4
Molgula manhattensis	7		1	1	422	424	5522	5.2	68.6
Odostomia impressa	8	179	23	51	10	263	5785	3.2	71.9
Pseudeurythoe sp.	9	100	66	49	27	242	6027	2.0	74.9
Eteone heteropoda	10	8	25	115	7	155	6182	1.9	76.9
Mya arenaria	11	32	45	62	4	143	6325	1.7	78.6
Mitrella lunata	12	61	28	14		103	6428	1.2	79.9
Edotea triloba	13	35	21	42	3	101	6529	1.2	81.2
Neomysis americana	14	93		2		95	6624	1.1	82.4
Cyathura burbancki	15	16	27	34	17	94	6718	1.1	83.5
Balanus improvisus	16			39	54	93	6811	1.1	84.7
Mulinia lateralis	17			84	7	91	6902	1.1	85.8
Melita nitida	18	12	33	33	11	89	6991	1.1	86.9
Polydora websteri	19	7	28	47		82	7073	1.0	87.9
Scoloplos fragilis	20	32	13	33	4	82	7155	1.0	89.0
Gyptis vittata	21	25	25	25	3	78	7233	0.9	89.9
Tharyx setigera	22	14	30	30		74	7307	0.9	90.9
Lyonsia hyalina	23	3	3	40	14	60	7367	0.7	91.6
Paracaprella tenuis	24	17		31	5	53	7420	0.6	92.3
Glycinde solitaria	25	18	15	16	2	51	7471	0.6	92.9
Zygonemertes virescens	26	11	15	20	2	48	7519	0.5	93.5
Acteocina canaliculata	27	20	4	14		38	7557	0.4	94.0
Boccardia hamata	28		19	11	7	37	7594	0.4	94.4
Cassidinidea lunifrons	29	6	19	5	7	37	7631	0.4	94.9
Crepidula convexa	30	19	4	13		36	7667	0.4	95.3

Table 7. - Part A - Site I (Cont'd.)

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Nassarius vibex	31	5	1	20	9	35	7702	0.4	95.8
Sabellaria vulgaris	32	16	4	8		28	7730	0.3	96.1
Epitonium rupicolum	33	7	15	2	1	25	7755	0.3	96.4
Corophium lacustre	34	1	2	2	17	22	7777	0.2	96.7
Syllid a	35	17	2			19	7796	0.2	96.9
Hydroides dianthus	36	5	2	12		19	7815	0.2	97.2
Sabella microphthalma	37	9	8	1		18	7833	0.2	97.4
Doridella obscura	38		7	10		17	7850	0.2	97.6
Mangelia plicosa	39	7	4	5		16	7866	0.1	97.8
Parahesione luteola	40			10	1	11	7877	0.1	97.9
Pyramidella fusca	41	1	3	5	2	11	7888	0.1	98.1
Stenothoe minuta	42	3		7		10	7898	0.1	98.2
Nemertean sp. d	43	3			5	8	7906	0.0	98.3
Unciola irrorata	44	7				7	7913	0.0	98.4
Anadara transversa	45	1	1	5		7	7920	0.0	98.5
Glycera dibranchiata	46		5	1		6	7926	0.0	98.6
Stylochus ellipticus	47	2		2	2	6	7932	0.0	98.6
Panopeus herbstii	48	2			3	5	7937	0.0	98.7
Ampelisca abdita	49	5				5	7942	0.0	98.8
Crassostrea virginica	50	2		2	1	5	7947	0.0	98.9
Fabricia sabella	51	3	2			5	7952	0.0	98.9
Leucon americanus	52			4		4	7956	0.0	98.9
Cyclaspis varians	53	2	2			4	7960	0.0	99.0
Cratena pilata	54	4				4	7964	0.0	99.0
Skeneopsis planorbis	55	2	1	1		4	7968	0.0	99.1
Scolecolepides viridis	56			3		3	7971	0.0	99.1
Edwardsia elegans	57		2	1		3	7974	0.0	99.2
Gobiosoma bosci	58	1			2	3	7977	0.0	99.2
Upogebia affinis	59	2			1	3	7980	0.0	00.2

Table 7. - Part A - Site I (Cont'd.)

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Pectinaria gouldii	60	2	1			3	7983	0.0	99.3
Paleanotus heteroseta	61	2		1		3	7986	0.0	99.3
Zygeupolia rubens	62	2		1		3	7989	0.0	99.3
Crangon septemspinosa	63			1	1	2	7991	0.0	99.4
Larval shrimp	64			2		2	7993	0.0	99.4
Mercenaria mercenaria	65			2		2	7995	0.0	99.4
Neopanope sayi	66		1	1		2	7997	0.0	99.4
Gammarus mucronatus	67		2			2	7999	0.0	99.5
Urosalpinx cinerea	68		2			2	8001	0.0	99.5
Drilonereis filum	69		2			2	8003	0.0	99.5
Baetidae	70	1	1			2	8005	0.0	99.5
Callinectes sapidus	71	1			1	2	8007	0.0	99.6
Cyclopodia	72	1		1		2	8009	0.0	99.6
Cerithiopsis greeni	73	2				2	8011	0.0	99.6
Clymenella torquata	74	2				2	8013	0.0	99.6
Spiochaetopterus oculatus	75	2				2	8015	0.0	99.7
Tellina agilis	76	1			1	2	8017	0.0	99.7
Glycera americana	77	2				2	8019	0.0	99.7
Sympleustes glaber	78				1	1	8020	0.0	99.7
Cyathura polita	79				1	1	8021	0.0	99.7
Brachidontes recurvus	80				1	1	8022	0.0	99.8
Oxyurostylis smithi	81			1		1	8023	0.0	99.8
Trichoptera	82			1		1	8024	0.0	99.8
Ancistrosyllis jonesi	83			1		1	8025	0.0	99.8
Paraprionospio pinnata	84		1			1	8026	0.0	99.8
Prionospio?	85		1			1	8027	0.0	99.8
Phoronis architecta	86		1			1	8028	0.0	99.8
Centropages hamatus	87		1			1	8029	0.0	99.8
Eupleura caudata	88		1			1	8030	0.0	99.8

Table 7. - Part A - Site 1 (Cont'd.)

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Spio?	89		1			1	8031	0.0	99.9
Pinnotheres ostreum	90	1				1	8032	0.0	99.9
Gammarus daiberi	91	1				1	8033	0.0	99.9
Tetrastemma jeani	92	1				1	8034	0.0	99.9
Acartia sp.	93	1				1	8035	0.0	99.9
Odostomia dux	94	1				1	8036	0.0	99.9
Terebellid?	95	1				1	8037	0.0	99.9
Spionid a	96	1				1	8038	0.0	99.9
Microciona prolifera		+	+	+					
Cliona truitti		+							
Cordylophora caspia				+					
Garveia franciscana					+				
Clytia hemisphaerica					+				
Obelia bicuspidata			+		+				
Gonothyraea loveni		+	+						
Victorella pavida		+							
Anguinella palmata		+	+	+					
Aeverrillia armata		+	+	+	+				
Membranipora tenuis			+		+				
Electra crustulenta			+	+	+				
#species		73	61	64	47	108			
#individuals		1316	2597	3249	876	8038			

Table 7. - Part B - Site 2

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Streblospio benedicti	1	24	256	799	12	1091	1091	11.5	11.5
Polydora ligni	2	80	238	588	117	1023	2114	10.8	22.3
Diadumene leucolena	3	516	219	205		940	3054	9.9	32.3
Peloscolex spp.	4	100	280	408	62	850	3904	8.9	41.2
Heteromastus filiformis	5	216	247	184	57	704	4608	7.4	48.7
Balanus improvisus	6	56	12	293	173	534	5142	5.6	54.3
Odostomia impressa	7	226	160	123	10	519	5661	5.4	59.8
Molgula manhattensis	8				428	428	6089	4.5	64.3
Mya arenaria	9	39	242	133	1	415	6504	4.3	68.7
Boccardia hamata	10	3	1		361	365	6869	3.8	72.6
Nereis succinea	11	96	63	28	151	338	7207	3.5	76.2
Cassidinidea lunifrons	12	129	53	37	73	292	7499	3.0	79.3
Melita nitida	13	55	25	102	106	288	7787	3.0	82.3
Brachidontes recurvus	14	31	38	22	179	270	8057	2.8	85.2
Eteone heteropoda	15	15	63	165	3	246	8303	2.6	87.8
Polydora websteri	16	55	43	87	30	215	8518	2.2	90.0
Corophium lacustre	17	4			145	149	8667	1.5	91.6
Glycinde solitaria	18	79	29	32		120	8787	1.2	92.9
Crassostrea virginica	19	29	22	9	12	72	8859	0.7	93.6
Pseudeurythoe sp.	20	17	22	17	12	68	8927	0.7	94.4
Zygonemertes virescens	21	14	29	18		61	8988	0.6	95.0
Gyptis vittata	22	5	24	14	1	44	9032	0.4	95.5
Edotea triloba	23	27	5	3	2	37	9069	0.3	95.9
Stylochus ellipticus	24	7	1	24		32	9101	0.3	96.2
Nereiphylla fragilis	25	9	17	5		31	9132	0.3	96.5
Doridella obscura	26	3	5	19	1	28	9160	0.2	96.8
Nemertean sp. d	27	1	1	2	23	27	9187	0.2	97.1
Neomysis americana	28	21			1	22	9209	0.2	97.3

Table 7. - Part B - Site 2 (Cont'd.)

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Mitrella lunata	29	21				21	9230	0.2	97.6
Epitonium rupicolum	30	10	5	5		20	9250	0.2	97.8
Skeneopsis planorbis	31	2	16	1		19	9269	0.2	98.0
Nassarius vibex	32	11		7		18	9287	0.1	98.2
Pyramidella fusca	33	7		9	1	17	9304	0.1	98.4
Paracaprella tenuis	34	16				16	9320	0.1	98.5
Sabella microphthalma	35	16				16	9336	0.1	98.7
Mulinia lateralis	36			5	9	14	9350	0.1	98.8
Pinnotheres ostreum	37	8	1	1	4	14	9364	0.1	99.0
Scoloplos fragilis	38	7	1	6		14	9378	0.1	99.1
Acteocina canaliculata	39	3	4			7	9385	0.0	99.2
Gobioscoma bosci	40	1	1	2	2	6	9391	0.0	99.3
Glycera dibranchiata	41	2	2	2		6	9397	0.0	99.3
Balanus eburneus	42		4	1		5	9402	0.0	99.4
Mangelia plicosa	43	5				5	9407	0.0	99.4
Macoma baltica	44			3	1	4	9411	0.0	99.5
Crangon septemspinosa	45			2	1	3	9414	0.0	99.5
Panopeus herbstii	46	2		1		3	9417	0.0	99.5
Anadara transversa	47	3				3	9420	0.0	99.6
Sabellaria vulgaris	48	1	1	1		3	9423	0.0	99.6
Sympleustes glaber	49			2		2	9425	0.0	99.6
Cyathura polita	50			1	1	2	9427	0.0	99.7
Gammarus mucronatus	51		2			2	9429	0.0	99.7
Prionospio?	52		2			2	9431	0.0	99.7
Elasmopus levis	53		2			2	9433	0.0	99.7
Zygeupolia rubens	54		2			2	9435	0.0	99.7
Rhithropanopeus harrisii	55	1		1		2	9437	0.0	99.8
Upogebia affinia	56	1	1			2	9439	0.0	99.8
Urosalpinx cinerea	57	2				2	9441	0.0	99.8

Table 7. - Part B - Site 2 (Cont'd.)

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Lyonsia hyalina	58	2				2	9443	0.0	99.8
Hydroides dianthus	59	2				2	9445	0.0	99.8
Chrysaora quinquecirrha	60				1	1	9446	0.0	99.9
Leucon americanus	61			1		1	9447	0.0	99.9
Parahesione luteola	62		1			1	9448	0.0	99.9
Macoma phenax	63		1			1	9449	0.0	99.9
Cratena pilata	64	1				1	9450	0.0	99.9
Cymadusa compta	65	1				1	9451	0.0	99.9
Rictaxis punctostraitus	66	1				1	9452	0.0	99.9
Anomia simplex	67	1				1	9453	0.0	99.9
Tellina agilis	68	1				1	9454	0.0	99.9
Pectinaria gouldii	69	1				1	9455	0.0	99.9
Microciona prolifera					+				
Garvela franciscana					+				
Obelia bicuspita					+				
Gonothyraea loveni		+	+						
"Campanulina"					+				
Anguinella palmata		+	+						
Aeverrillia armata		+		+	+				
Electra crustulenta		+	+	+	+				
Pedicellina cernua					+				
# species		58	44	44	38	78			
# individuals		1986	2141	3348	1980	9455			

Table 7. - Part C - Site 3

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Balanus improvisus	1	43	16	5567	363	5989	5989	34.2	34.2
Peloscolex spp.	2	1005	853	605	181	2644	8633	15.1	49.3
Diadumene leucolena	3	882	240	317	23	1462	10,095	8.3	57.6
Melita nitida	4	281	100	733	178	1292	11,387	7.3	65.0
Polydora ligni	5	100	80	826	57	1063	12,450	6.0	71.1
Nereis succinea	6	254	226	107	329	916	13,366	5.2	76.3
Streblospio benedicti	7	123	101	462	27	713	14,079	4.0	80.4
Cassidinidea lunifrons	8	276	96	52	145	569	14,648	3.2	83.7
Boccardia hamata	9	128	27	44	277	476	15,124	2.7	86.4
Heteromastus filiformis	10	109	111	108	67	395	15,519	2.2	88.7
Polydora websteri	11	153	39	107	35	334	15,853	1.9	90.6
Brachidontes recurvus	12	61	29	24	151	265	16,118	1.5	92.1
Eteone heteropoda	13	12	18	172	2	204	16,322	1.1	93.2
Corophium lacustre	14	18	1	49	133	201	16,523	1.1	94.4
Odostomia impressa	15	87	38	70		195	16,718	1.1	95.5
Stylochus ellipticus	16	3		178	4	185	16,903	1.0	96.6
Mya arenaria	17	6	134	28	1	169	17,072	0.9	97.5
Crassostrea virginica	18	31	14	12	18	75	17,147	0.4	98.0
Doridella obscura	19	20	3	22	3	48	17,195	0.2	98.2
Zygonemertes virescens	20	17	8	23		48	17,243	0.2	98.5
Pseudeurythoe sp.	21	8	6	8	10	32	17,275	0.1	98.7
Mitrella lunata	22	20	6			26	17,301	0.1	98.8
Molgula manhattensis	23				21	21	17,322	0.1	99.0
Gammarus dalberi	24		20			20	17.342	0.1	99.1
Gobiosoma bosci	25	9	1	4	6	20	17,362	0.1	99.2
Pyramidella fusca	26	6	2	8		16	17,378	0.0	99.3
Balanus eburneus	27	7	3	3		13	17,391	0.0	99.3
Hydroides dianthus	28	8				8	17,399	0.0	99.4

Table 7. - Part C - Site 3 (Cont'd)

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Pinnotheres ostreum	29	4		3		7	17,406	0.0	99.4
Euplana gracilis	30	1		2	4	7	17,413	0.0	99.5
Sabellaria vulgaris	31	5	1			6	17,419	0.0	99.5
Gyptis vittata	32	5		1		6	17,425	0.0	99.5
Glycinde solitaria	33	3	2	1		6	17.431	0.0	99.6
Nereiphylla fragilis	34	4	1	1		6	17,437	0.0	99.6
Neopanope sayi	35	5				5	17,442	0.0	99.6
Epitonium rupicolum	36	3	1		1	5	17,447	0.0	99.7
Rhithropanopeus harrisii	37	3			1	4	17,451	0.0	99.7
Panopeus herbstii	38	3			1	4	17.455	0.0	99.7
Nassarius vibex	39	4				4	17.459	0.0	99.7
Tellina agilis	40	3			1	4	17,463	0.0	99.8
Parahesione luteola	41	3		1		4	17,467	0.0	99.8
Nemertean sp. d	42			1	2	3	17,470	0.0	99.8
Acteocina canaliculata	43		3			3	17,473	0.0	99.8
Amphiporus bioculatus	44	1		1	1	3	17,476	0.0	99.8
Edotea triloba	45		1		1	2	17,478	0.0	99.8
Nemertean sp. e	46		2			2	17,480	0.0	99.9
Cyathura polita	47	1	1			2	17,482	0.0	99.9
Cyclopoida	48	2				2	17,484	0.0	99.9
Scoloplos fragilis	49	1	1			2	17,486	0.0	99.9
Scolecolepides viridis	50				1	1	17,487	0.0	99.9
Cyathura burbancki	51			1		1	17,488	0.0	99.9
Syllid a	52			1		1	17,489	0.0	99.9
Larval shrimp	53		1			1	17,490	0.0	99.9
Mangelia plicosa	54		1			1	17,491	0.0	99.9
Neomysis americana	55	1				1	17,492	0.0	99.9
Urosalpinx cinerea	56	1				1	17,493	0.0	99.9
Opsanus tau	57	1				1	17,494	0.0	99.9

Table 7. - Part C - Site 3 (Cont'd.)

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Anadara transversa	58	1				1	17,495	0.0	99.9
Sabella microphthalma	59	1				1	17,496	0.0	99.9
Cordylophora caspia				+					
Garveia franciscana			+	+	+				
Obelia bicuspidata					+				
Gonothyraea loveni		+							
Sertularia argentea			+						
Victorella pavida		+							
Anguinella palmata		+	+						
Aeverrillia armata		+		+	+				
Membranipora tenuis		+							
Electra crustulenta		+	+	+	+				
# species		54	40	38	34	69			
# individuals		3723	2187	9542	2044	17,496			

Table 7. - Part D - Site 4

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Balanus improvisus	1	25	33	3964	695	4717	4717	38.2	38.2
Peloscolex spp.	2	397	564	266	64	1291	6008	10.4	48.6
Diadumene leucolena	3	483	220	195	4	902	6910	7.3	56.0
Polydora ligni	4	47	86	528	24	685	7595	5.5	61.5
Nereis succinea	5	186	163	91	214	654	8249	5.3	66.8
Melita nitida	6	85	89	297	117	588	8837	4.7	71.6
Heteromastus filiformis	7	149	169	84	67	469	9306	3.8	75.4
Brachidontes recurvus	8	57	65	59	274	455	9761	3.6	79.1
Streblospio benedicti	9	57	121	210	14	402	10,163	3.2	82.3
Odostomia impressa	10	97	134	128		359	10,522	2.9	85.2
Cassidinidea lunifrons	11	74	56	43	73	246	10,768	1.9	87.2
Mya arenaria	12	15	170	60		245	11,013	1.9	89.2
Boccardia hamata	13	21	20	25	166	232	11,245	1.8	91.1
Polydora websteri	14	59	53	63	12	187	11,432	1.5	92.6
Eteone heteropoda	15	6	27	130	1	164	11,596	1.3	93.9
Pseudeurythoe sp.	16	70	47		27	144	11,740	1.1	95.1
Crassostrea virginica	17	35	37	26	15	113	11,853	0.9	96.0
Gammarus daiberi	18	3	106			109	11,962	0.8	96.9
Stylochus ellipticus	19	6	2	67	1	76	12,038	0.6	97.5
Zygonemertes virescens	20	5	13	24		42	12,080	0.3	97.9
Corophium lacustre	21	5	1	4	24	34	12,114	0.2	98.1
Glycinde solitaria	22	19	8			27	12,141	0.2	98.4
Epitonium rupicolum	23	10	9			19	12,160	0.1	98.5
Doridella obscura	24	2		11	3	16	12,176	0.1	98.6
Gobiosoma bosci	25	7	2	2	4	15	12,191	0.1	98.8
Pyramidella fusca	26		8	6		14,	12,205	0.1	98.9
Pinnotheres ostreum	27	6	2	4	1	13	12,218	0.1	99.0
Mitrella lunata	28	9	4			13	12,231	0.1	99.1

Table 7. - Part D - Site 4 (Cont'd.)

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Gyptis vittata	29	10	1			11	12,242	0.0	99.2
Balanus eburneus	30	5	2	1	1	9	12,251	0.0	99.3
Scoloplos fragilis	31	3	4	2		9	12,260	0.0	99.3
Molgula manhattensis	32				7	7	12,267	0.0	99.4
Neopanope sayi	33	5	1	1		7	12,274	0.0	99.4
Nereiphylla fragilis	34	4		3		7	12,281	0.0	99.5
Nemertean sp. d	35	1	1	2	3	7	12,288	0.0	99.6
Congeria leucophaeta	36				6	6	12,294	0.0	99.6
Crangon septemspinosa	37			5		5	12,299	0.0	99.6
Edotea triloba	38	5				5	12,304	0.0	99.7
Neomysis americana	39	2	1	2		5	12,309	0.0	99.7
Rhithropanopeus harrisii	40	2		1	1	4	12,313	0.0	99.8
Macoma baltica	41		1	1	1	3	12,316	0.0	99.8
Panopeus herbstii	42	1	1	1		3	12,319	0.0	99.8
Hydrobia sp.	43				2	2	12,321	0.0	99.8
Nemertean sp. f	44		2			2	12,323	0.0	99.8
Acteocina canaliculata	45		2			2	12,325	0.0	99.9
Mangelia plicosa	46		2			2	12,327	0.0	99.9
Nassarius vibex	47	1		1		2	12,329	0.0	99.9
Baetidae	48				1	1	12,330	0.0	99.9
Sympleustes glaber	49			1		1	12,331	0.0	99.9
Cyathura polita	50		1			1	12,332	0.0	99.9
Monoculodes edwardsia	51		1			1	12,333	0.0	99.9
Palaemonetes pugio	52	1				1	12,334	0.0	99.9
Triphora nigrocincta	53	1				1	12,335	0.0	99.9
Bivalva a	54	1				1	12,336	0.0	99.9
Cyclopoida	55	1				1	12,337	0.0	99.9
Sponge a			+						

Table 7. - Part D - Site 4 (Cont'd.)

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Garveia franciscana					+				
Obelia bicuspidata					+				
Gonothyraea loveni		+	+						
Aeverrillia armata			+						
Membranipora tenuis		+							
Electra crustulenta		+	+	+	+				
# species		45	44	36	31	62			
# individuals		1978	2229	6308	1822	12,337			

Table 7. - Part E - Site 5

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Balanus improvisus	1	3445	76	2148	163	5832	5832	58.3	58.3
Peloscolex spp.	2	622	57	68	36	783	6615	7.8	66.1
Cassidinidea lunifrons	3	495	12	33	90	630	7245	6.3	72.5
Corophium lacustre	4	153	9	202	174	538	7783	5.3	77.8
Brachidontes recurvus	5	197	34	140	89	460	8243	4.6	82.4
Nereis succinea	6	259	13	57	88	417	8660	4.1	86.6
Melita nitida	7	298	3	23	40	364	9024	3.6	90.3
Boccardia hamata	8	121	17	15	97	250	9274	2.5	92.8
Congeria leucophaeta	9				149	149	9423	1.4	94.2
Polydora ligni	10	38	1	9	35	83	9506	0.8	95.1
Crassostrea virginica	11	46	3	18	6	73	9579	0.7	95.8
Gammarus daiberi	12	43	4	21		68	9647	0.6	96.5
Heteromastus filiformis	13	39	6	13	9	67	9714	0.6	97.2
Leptocheirus plumulosus	14		15	49		64	9778	0.6	97.8
Polydora websteri	15	10	2	5	39	56	9834	0.5	98.4
Neomysis americana	16	40			1	41	9875	0.4	98.8
Balanus eburneus	17	24		1		25	9900	0.2	99.0
Stylochus ellipticus	18	23			1	24	9924	0.2	99.3
Cyathura polita	19	12	1		1	14	9938	0.1	99.4
Gobiosoma bosci	20	7	1		1	9	9947	0.0	99.5
Euplana gracilis	21	1			8	9	9956	0.0	99.6
Rhithropanopeus harrisii	22	8				8	9964	0.0	99.7
Nemertean sp. d	23	2	1		3	6	9970	0.0	99.7
Hydrobia sp.	24			2	1	3	9973	0.0	99.7
Odostomia impressa	25	2	1			3	9976	0.0	99.7
Streblospio benedicti	26	3				3	9979	0.0	99.8
Scolecolepides viridis	27				2	2	9981	0.0	99.8
Palaemonetes pugio	28	2				2	9983	0.0	99.8

Table 7. - Part E - Site 5 (Cont'd.)

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Callinectes sapidus	29				1	1	9984	0.0	99.9
Rangia cuneata	30				1	1	9985	0.0	99.9
Pinnotheres ostreum	31			1		1	9986	0.0	99.9
Ampithoe longimana	32	1				1	9987	0.0	99.9
Pyramidella fusca	33	1				1	9988	0.0	99.9
Paraprionospio pinnata	34	1				1	9989	0.0	99.9
Micropogon undulatus	35	1				1	9990	0.0	99.9
Scoloplos fragilis	36	1				1	9991	0.0	99.9
Garvela franciscana					+				
Membranipora tenuis				+					
Electra crustulenta		+	+	+	+				
# species		29	19	20	25	40			
# individuals		5894	256	2806	1035	9991			

Table 7. - Part F - Site 6

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Balanus improvisus	1	341	69	58	102	570	570	32.7	32.7
Brachidontes recurvus	2	94	4	6	110	214	784	12.2	45.0
Peloscolex spp.	3	89	68	2	48	207	991	11.8	56.9
Corophium lacustre	4	43	19	59	37	158	1149	9.0	66.0
Boccardia hamata	5	86	16	2	45	149	1298	8.5	74.5
Leptocheirus plumulosus	6	1		71	4	76	1374	4.3	78.9
Nereis succinea	7	23	7	1	32	63	1437	3.6	82.5
Heteromastus filiformis	8	17	11	2	9	39	1476	2.2	84.8
Cassidinidea lunifrons	9	27	4	1	2	34	1510	1.9	86.7
Polydora ligni	10	5	1		26	32	1542	1.8	88.6
Melita nitida	11	13	3		13	29	1571	1.6	90.2
Gammarus daiberi	12	18		6		24	1595	1.3	91.6
Congeria leucophaeta	13				19	19	1614	1.0	92.7
Crassostrea virginica	14	13	1	1	2	17	1631	0.9	93.7
Cyathura polita	15	13	1	2		16	1647	0.9	94.6
Polydora websteri	16	6	3		6	15	1662	0.8	95.5
Macoma baltica	17	3	6	4		13	1675	0.7	96.2
Scolecolepides viridis	18	4	2	2	5	13	1688	0.7	97.0
Nemertean sp. d	19	6	2	1	4	13	1701	0.7	97.7
Mulinia lateralis	20			6	3	9	1710	0.5	98.2
Rangia cuneata	21				5	5	1715	0.2	98.5
Palaemonetes pugio	22	3				3	1718	0.1	98.7
Neomysis americana	23	2		1		3	1721	0.1	98.9
Stylochus ellipticus	24				2	2	1723	0.1	99.0
Hydrobia sp.	25			1	1	2	1725	0.1	99.1
Gobiosoma bosci	26	2				2	1727	0.1	99.2
Rhithropanopeus harrisii	27	1			1	2	1729	0.1	99.3
Edotea triloba	28	1		1		2	1731	0.1	99.4

Table 7. - Part F - Site 6 (Cont'd.)

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Balanus eburneus	29	2				2	1733	0.1	99.5
Callinectes sapidus	30				1	1	1734	0.0	99.6
Euplana gracilis	31				1	1	1735	0.0	99.7
Cryptochironomus sp.	32			1		1	1736	0.0	99.7
Pyramidella fusca	33			1		1	1737	0.0	99.8
Polydora sp.	34		1			1	1738	0.0	99.8
Streblospio benedicti	35	1				1	1739	0.0	99.9
Coelotanypus sp.	36	1				1	1740	0.0	99.9
Glycinde solitaria	37	1				1	1741		
Gonothyraea loveni		+							
Aeverrillia armata			+						
Electra crustulenta		+	+	+	+				
# species		29	19	22	24	40			
# individuals		816	218	229	478	1741			

Table 7. - Part G - Site 7

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Balanus improvisus	1	2016	4330	3254	187	9787	9787	58.8	58.8
Brachidontes recurvus	2	321	836	268	186	1611	11,398	9.6	68.5
Peloscolex spp.	3	381	702	77	63	1223	12,621	7.3	75.8
Corophium lacustre	4	197	177	700	108	1182	13,803	7.1	82.9
Cassidinidea lunifrons	5	214	310	55	39	618	14,421	3.7	86.6
Nereis succinea	6	76	203	63	88	430	14,851	2.5	89.2
Boccardia hamata	7	92	101	85	106	384	15,235	2.3	91.5
Gammarus daiberi	8	10	244	17		271	15,506	1.6	93.2
Congeria leucophaeta	9		1		237	238	15,744	1.4	94.6
Melita nitida	10	124	36	21	44	225	15,969	1.3	95.9
Heteromastus filiformis	11	61	43	38	13	155	16,124	0.9	96.9
Crassostrea virginica	12	47	57	24	18	146	16,270	0.8	97.7
Polydora ligni	13	27	64	17	26	134	16,404	0.8	98.5
Polydora websteri	14	6	50	9	22	87	16,491	0.5	99.1
Cyathura polita	15	28	11	2	3	44	16,535	0.2	99.3
Gobiosoma bosci	16	4	8	1	8	21	16,556	0.1	99.5
Balanus eburneus	17	6	14	1		21	16,557	0.1	99.6
Odostomia impressa	18	3	14	2		19	16,596	0.1	99.7
Hydrobia sp.	19	2		3	4	9	16,605	0.0	99.8
Rhithropanopeus harrisii	20	7				7	16,612	0.0	99.8
Stylochus ellipticus	21	4			2	6	16,618	0.0	99.8
Nemertean sp. d	22	1	1	1	2	5	16,623	0.0	99.9
Rangia cuneata	23				3	3	16,626	0.0	99.9
Macoma baltica	24		2	1		3	16,629	0.0	99.9
Neopanope sayi	25				2	2	16,631	0.0	99.9
Euplana gracilis	26				2	2	16,633	0.0	99.9
Callinectes sapidus	27				1	1	16,634	0.0	99.9
Edotea triloba	28			1		1	16,635	0.0	99.9

Table 7. - Part G - Site 7 (Cont'd)

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Palaemonetes pugio	29	1				1	16,636	0.0	99.9
Scolecolepides viridis	30	1				1	16,637	0.0	99.9
Cordylophora caspia				+					
Garveia franciscana					+				
Gonothyraea loveni		+							
"Campanulina"					+				
Sertularia argentea		+							
Electra crustulenta		+	+	+	+				
# species		26	21	23	25	36			
# individuals		3629	7204	4640	1164	16,637			

Table 7. - Part H - Site 8

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Balanus improvisus	1	779	93	452	109	1433	1433	29.0	29.0
Corophium lacustre	2	66	13	640	301	1020	2453	20.6	49.7
Congeria leucophaeta	3	4		3	793	800	3253	16.2	65.9
Cassidinidea lunifrons	4	209	3	72	54	338	3591	6.8	72.7
Peloscolex spp.	5	134	27	104	63	328	3919	6.6	79.4
Brachidontes recurvus	6	123	14	56	97	290	4209	5.8	85.3
Melita nitida	7	65	1	30	88	184	4393	3.7	89.0
Gammarus dalberi	8	40		71	1	112	4505	2.2	91.3
Nereis succinea	9	37	8	30	33	108	4613	2.1	93.4
Boccardia hamata	10	16	2	15	26	59	4672	1.1	94.6
Polydora ligni	11	11	3		51	54	4726	1.0	95.7
Crassostrea virginica	12	29	2	19	1	51	4777	1.0	96.8
Heteromastus filiformis	13	31	8	9	1	49	4826	0.9	97.8
Cyathura polita	14	13	1	5	6	25	4851	0.5	98.3
Rangia cuneata	15		4	3	12	19	4870	0.3	98.7
Euplana gracilis	16				10	10	4880	0.2	98.9
Hydrobia sp.	17			3	6	9	4889	0.1	99.0
Rhithropanopeus harrisii	18	8				8	4897	0.1	99.2
Scolecolepides viridis	19	2	4	1		7	4904	0.1	99.3
Polydora websteri	20	2		1	3	6	4910	0.1	99.5
Nemertean sp. d	21	2	1		2	5	4915	0.1	99.6
Stylochus ellipticus	22	1			4	5	4920	0.1	99.7
Gobiosoma bosci	23			2	2	4	4924	0.0	99.7
Balanus eburneus	24	4				4	4928	0.0	99.8
Cryptochironomus sp.	25			3		3	4931	0.0	99.9
Procladius sp.	26		1		1	2	4933	0.0	99.9

Table 7. - Part H - Site 8 (Cont'd.)

Species	Rank	F	W	Sp	Su	Total	Cumulative Number	Percentage	Cumulative Percentage
Callinectes sapidus	27				1	1	4934	0.0	99.9
Cordylophora caspia					+				
Electra crustulenta		+	+	+	+				
# species		21	15	21	24	29			
# individuals		1568	182	1519	1665	4934			

still open for fishing. Tonging was never observed here, most likely due to the low density of oysters. This is a relatively deep, hard-bottomed reef, washed by moderately strong tidal currents. Shells in this area were heavily fouled by a rich fauna.

One hundred and eight species and 8,038 individuals were found here over four sampling periods and there were no overwhelming dominants. The first 10 species contributed 76.9% of the individuals, but the 95% level was not reached until the 30 most abundant species had been included. The spionid, *Streblospio benedicti* was the numerical dominant on an annual basis, largely because of a large spring population. *Peloscolex* spp. was dominant in the fall and winter, while *M. manhattensis* ranked first in summer. *D. leucolena*, *P. ligni*, *H. filiformis* and *N. succinea* all contributed over 5% of the individuals. *O. impressa* and the amphinomid polychaete *Pseudeurythoe* sp. ranked second and third respectively in the fall.

Thomas' Rock

Thomas' Rock, site 2, is a large reef, slightly shallower than Brown Shoal, but subjected to similar currents. Limited tonging was observed. The bottom material was subjectively distinguishable from that of other reefs, being darker in color and softer in texture. The matrix between the larger shells seemed to be made up principally of weathered shell fragments rather than non-biogenic material.

The sampled fauna included 78 species and 9,455 individuals with the first 10 species contributing 72.6% of the individuals and the 95% level reached with the twenty-first species. *S. benedicti* was again numerically dominant, followed closely by *P. ligni*. *D. leucolena*, *Peloscolex* spp. and *H. filiformis* maintained their positions, while *N. succinea* declined in importance relative to the Brown Shoal situation. *M. manhattensis* and *B. hamata* were summer codominants and *O. impressa* was again especially important in the fall. The existence of a fall set of *M. arenaria* and a spring set of *B. improvisus* is apparent from Table 7b.

White Shoal

The third site is located on White Shoal which bisects the channel and rises to within a meter of the surface. The bottom is uniformly very hard, made up of large shells and oysters kept clean by relatively strong tidal currents. Very little nonbiogenic sediment was observed. Oystering was limited on this small reef.

Sixty-nine species and 17,496 individuals were collected. The first 10 species accounted for 88.7% of the individuals collected and the 95% mark was surpassed with species 15. *B. improvisus* was the overwhelming dominant supplying 34.2% of the individuals. This result was principally due to the very large spring populations which colonized the clean shell surfaces. *S. benedicti* and *M. manhattensis* dropped to positions 7 and 23 respectively, while *Peloscolex* spp., *D. leucolena*, *P. ligni* and *N. succinea* continued to make significant contributions. The amphipod *M. nitida* rose to fourth place in importance and the isopod *C. lunifrons* to eighth. *B. hamata* was ranked third in the summer collections and ninth on an annual basis.

Wrech Shoal

Wreck Shoal is a very extensive, heavily fished shoal. Its oyster production probably exceeds the combined total of all the other reefs. Site 4, on the outer portion of Wreck Shoal, is on the average, the second deepest site sampled. It is swept by strong currents. The bottom of the sampling area is hard, with a silty sediment matrix, although soft patches were occasionally encountered.

Sixty-two species and 12,337 individuals were found at Wreck Shoal, continuing the upestuary decline in the number of species collected. Patterns of numerical dominance were similar to those found at White Shoal. B. improvisus made up 38.2% of the fauna, largely due to its spring set which was somewhat less dramatic than at White Shoal. D. leucolena, P. ligni and N. succinea were again important subdominants. M. nitida and H. filiformis ranked sixth and seventh while B. recurvus rose to eight and S. benedicti dropped to ninth. O. impressa was abundant, ranking tenth, and B. hamata and M. arenaria were seasonally important.

Point of Shoals

Site 5 is located on Point of Shoals. This is a large area, in a wide embayment called Burwell Bay, with patches of hard bottom. The bottom between the hard patches consists of a silty substrate with a thin layer or scattering of shells. Currents are moderate in strength.

Only 40 species occurred at this site and dominance was much more pronounced than at the sites previously discussed. The ten highest ranking species accounted for 95.1% of the individuals collected and one species, B. improvisus, contained 58.3% of the individuals. Peloscolex spp., C. lunifrons, and the amphipod Corophium lacustre are only other species contributing over 5% of the total number of individuals, although B. recurvus, N. succinea, M. nitida and

B. hamata are still important components of the assemblage. C. leucophaeta was abundant in summer. D. leucolena did not occur and S. benedicti was represented by only three individuals.

The Swash

Site 6, the Swash, is another large, poorly defined area with a salinity regime similar to that at Point of Shoals. This area was the deepest sampled. It is on the east side of the channel and is washed by a fairly strong current, but its main distinguishing feature is its substrate. The sandy nature of the bottom, under and between the scattered hard spots, distinguish this site from all others investigated. The amount of oystering observed here was limited.

In general, the fauna was very similar to that at Point of Shoals although the density of organisms was considerably less. Forty species and 1,741 individuals were recovered, with 88.6% of the individuals amassed in the first 10 species and the 95% point including 16 species. B. improvisus is again numerically dominant and, aside from H. filiformis and the amphipod Leptocheirus plumulosus replacing M. nitida and C. leucophata, the top 10 species at the two sites are identical.

Horsehead Shoal

Horsehead Shoal, site 7, is a well-defined reef of moderate depth (1.8-3.7m) just to the west of the channel. Physically it is most nearly similar to White Shoal, having a hard bottom of clean shell washed by a strong tidal current. Possibly its distance from berthing is the only factor that limits more extensive oystering.

The 16, 637 individuals, second only to White Shoal, were distributed over 36 species with the ten most abundant species containing almost 96% of the individuals. B. improvisus continued to be dominant with 58.8% of the individuals. B. recurvus, Peloscolex spp. and C. lacustre supplied between 7 and 10% each. C. lunifrons, B. hamata and N. succinea were obvious components of the fauna in all seasons while M. nitida, Gammarus daiberi and C. leucophaeta were important in fall, winter, and summer respectively.

Deep Water Shoal

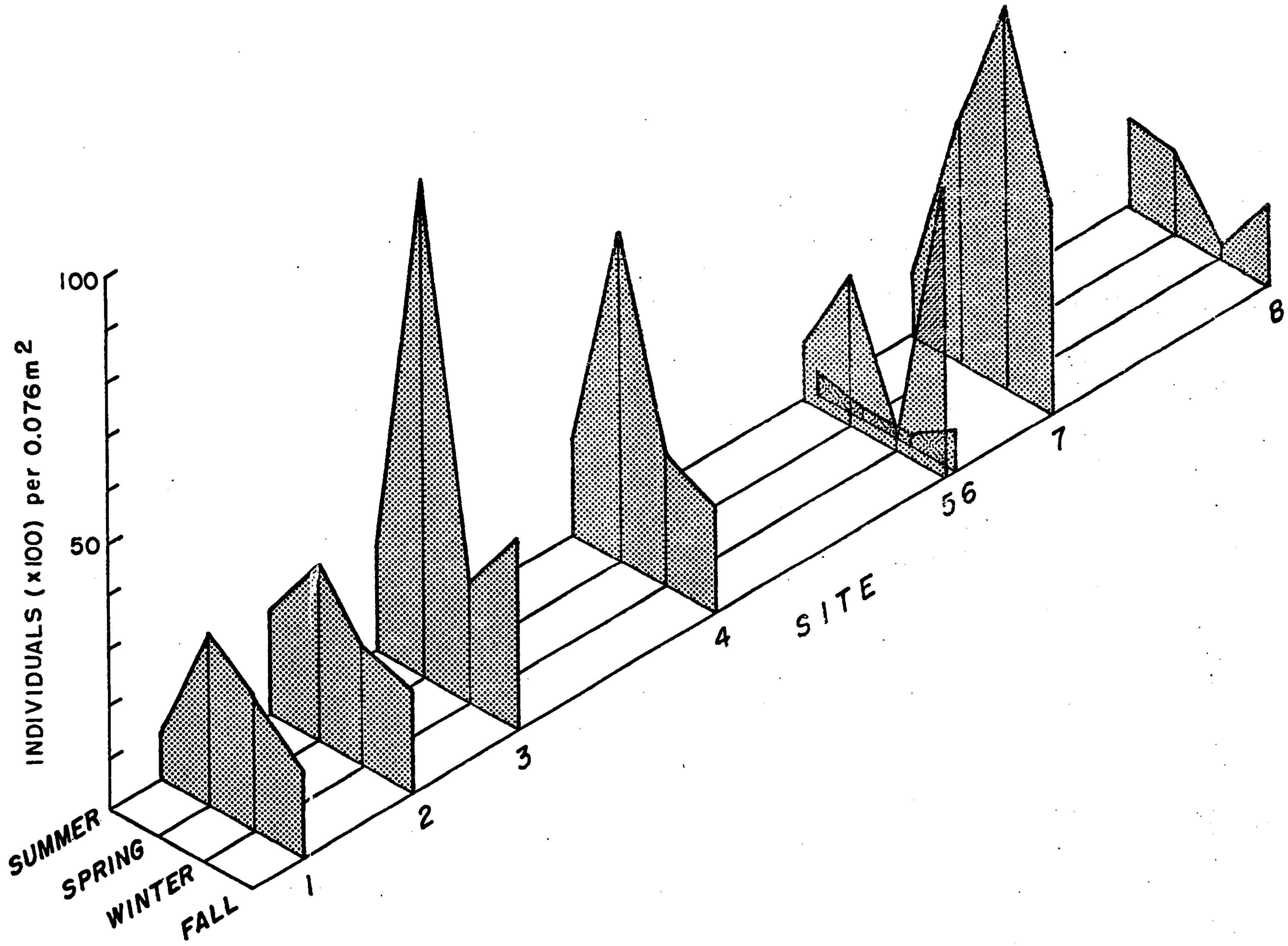
The most upestuary reef is Deep Water Shoal, the location of site 8. It is perched on the edge of a 90' deep channel which exposes it to extremely strong currents. The bottom ranges from hard shell to clay. The fauna is subjected to oligohaline conditions in certain seasons and on occasion the water is virtually fresh (Andrews et al., 1959).

The seasonal distribution of the 29 species and 4,934 individuals found here is unique in that the highest values for both categories occurred in the post-Agnes sampling period. B. improvisus contributed 20% of the individuals while C. lacustre and C. leucophaeta were dominant in spring and summer respectively. The 10 most abundant species, account for 94.6% of the fauna, were the same ten species most abundant at Horsehead Shoal.

SPATIAL AND TEMPORAL PATTERNS OF DENSITY

A density trend along the estuarine gradient and a consistent seasonal pattern between sites are both lacking (Fig. 6). The lowest

Figure 6. Total density of organisms per unit area, on the oyster reefs of the James River by site and season. Spacing is proportional to the actual distance between sites.



INDIVIDUALS (x100) per 0.076m²
100
50
SUMMER
SPRING
WINTER
FALL
1
2
3
4
SITE
56
7
8

density observed occurred at site 8 in winter and the highest in spring at site 3. In terms of absolute density, this result translates into a range of 2,395 to 125,573 individuals per square meter. On an annual basis, site 6 had the lowest, most uniform density, which was expected because of the sandy nature of the substrate. Sites 3 and 7, those with hard, clean shell bottoms, exhibited the highest densities. Moderate densities without drastic seasonal changes were observed at sites 1 and 2, the most speciose locations sampled.

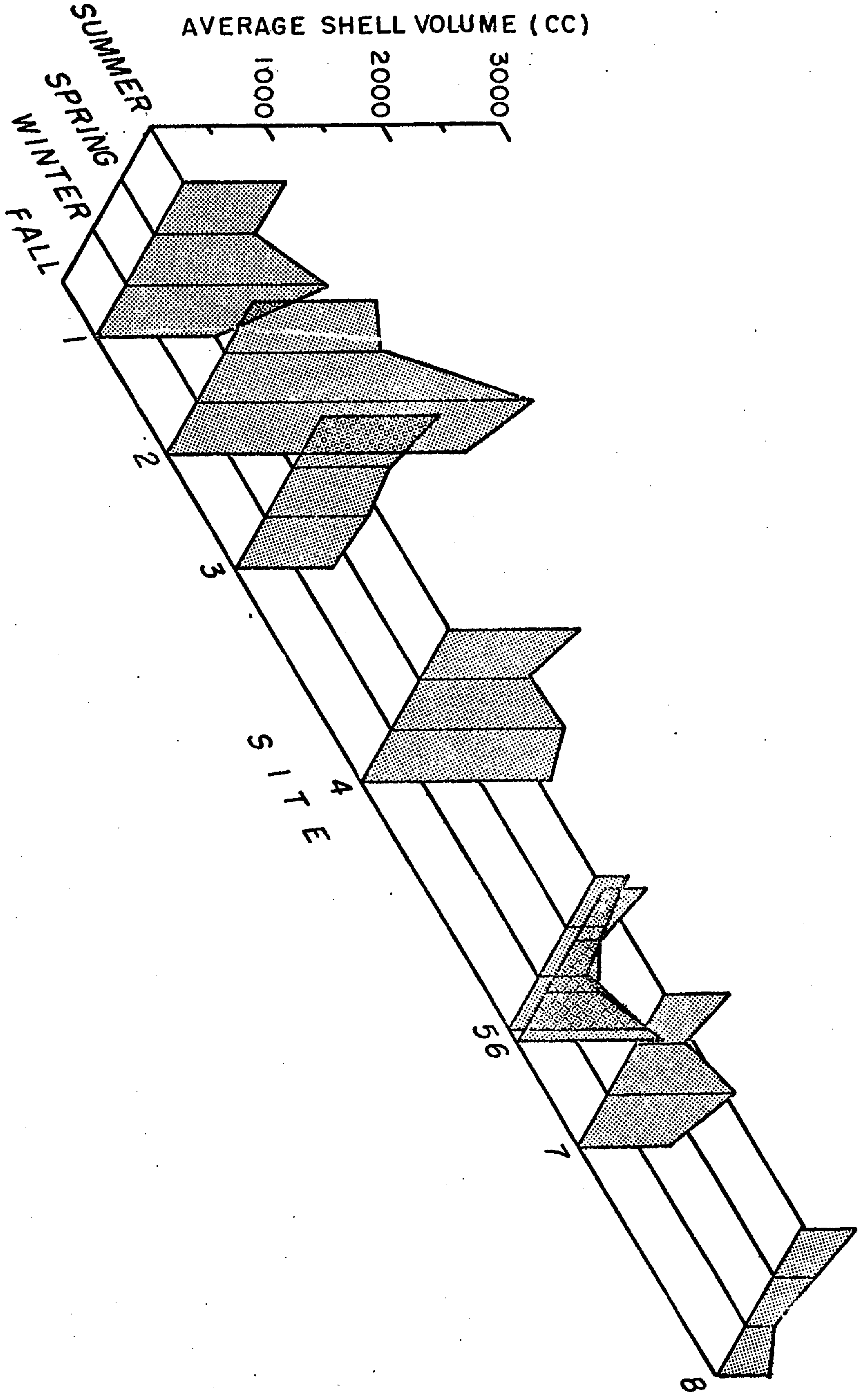
The five most downestuary sites all manifested peaks of density in the spring sampling period. This was not the result of a common phenomenon (Table 8). At sites 1 and 2 the peak was principally due to *S. benedicti*, although a few other species had corresponding pulses at site 2. *B. improvisus* was responsible for the spring peaks at sites 3, 4 and 5. However, the effect was enhanced at sites 3 and 4 by simultaneous population eruptions of *P. ligni* and *M. nitida*. *Peloscolex* spp., *D. leucolena* and *C. lunifrons* contributed to the fall peak at site 3, while *B. improvisus*, *Peloscolex* spp., *C. lunifrons*, *N. succinea* and *M. nitida* were all partly responsible for the high density observed at site 5 in the same season. At site 7, the winter peak was due to abundances of *B. improvisus*, *B. recurvus*, *Peloscolex* spp., *N. succinea* and *G. dalberi* and a fairly high density was maintained at this site through the spring by *B. improvisus* and *C. lacustre*.

Four sites experienced declines and four exhibited gains in density between the fall and winter sampling periods. In response to the spring reproductive periods of many species, seven sites showed increases in density in the third sampling period, however, six sites had subsequent declines with the passage of summer. The summer density

Table 8. Seasonally significant species at each site.

	SEASON			
Site	Fall	Winter	Spring	Summer
1			*S. benedicti*	*M. Manhattensus*
2			*S. benedicti*	*M. manhattensis*
3	*Peloscolex* spp.		*B. improvisus*	
	D. leucolena		*P. ligni*	
	C. lunifrons		*M. nitida*	
4			*B. improvisus*	
			P. ligni	
			M. nitida	
5	*B. improvisus*		*B. improvisus*	*C. leucophaeta*
	Peloscolex spp.			
	C. lunifrons			
	N. succinea			
	M. nitida			
6				
7		*B. improvisus*	*B. improvisus*	*C. leucophaeta*
		B. recurvus	*C lacustre*	
		Peloscolex spp.		
		N. succinea		
		G. daiberi		
8				*C. leucophaeta*

Figure 7. Average volume of shell collected at each site in each season. Average is per six replicate samples.


AVERAGE SHELL VOLUME (CC)
1000
2000
3000
SUMMER
SPRING
WINTER
FALL
1
2
3
4
5
6
7
8
SITE

decline was partially offset at sites 1 and 2 and sites 5, 7 and 8 by sets of *M. manhattensis* and *C. leucophaeta* respectively.

It is apparent from a comparison of Figs 6 and 7, which show the average volume of shell collected at each station, that the density of organisms is not a simple function of the volume of shell material in the samples.

DISTRIBUTION OF 18 PRINCIPAL SPECIES

A knowledge of the temporal and spatial distribution of the more important species is useful in understanding the complex interactions determining the faunal assemblage at a given time and place. The distributions of 18 principal species, which account for 93% of the individuals collected, are presented in Table 9.

The spionid *Streblospio benedicti* increased in abundance at sites 1 and 2 in winter and by spring it had become the dominant organism at both sites. In the fall and summer seasons, however, *S. benedicti* showed extremely low abundance. The winter-spring increase was not nearly as spectacular at sites 3 and 4 where the populations were higher in the fall and summer than at sites 1 and 2. Only four individuals of this species were found further upestuary than site 4.

A peculiar distributional pattern was demonstrated by the second important spionid to be considered, *Polydora ligni*. Populations increased at sites 1 and 2 in winter and spring but only during spring at sites 3 and 4. At sites 5, 6 and 8, the abundance of *P. ligni* declined from the fall levels not to rise again until the summer. At site 7 densities increased in winter, dropped in spring and rose slightly in summer.

Table 9. Spatial and temporal abundance of select species.

Values are per six samples.

a) Streblospio benedicti

Site	D	M	J	S
	Month			
1	16	242	1087	7
2	24	256	799	12
3	123	101	462	27
4	57	121	210	14
5	3	0	0	0
6	1	0	0	0
7	0	0	0	0
8	0	0	0	0

b) Polydora ligni

Site	D	M	J	S
	Month			
1	45	417	330	6
2	80	238	588	117
3	100	80	826	57
4	47	86	528	24
5	38	1	9	35
6	5	1	0	26
7	27	64	17	26
8	3	0	0	51

c) Polydora websteri

Site	D	M	J	S
	Month			
1	7	28	47	0
2	55	43	87	30
3	153	39	107	35
4	59	53	63	12
5	10	2	5	39
6	6	3	0	6
7	6	50	9	22
8	2	0	1	3

d) Boccardia hamata

Site	D	M	J	S
	Month			
1	0	19	11	7
2	3	1	0	361
3	128	27	44	277
4	21	20	25	166
5	121	17	15	97
6	86	16	2	45
7	92	101	85	106
8	16	2	15	26

e) *Nereis succinea*

	Month			
Site	D	M	J	S
1	36	252	122	28
2	96	63	28	151
3	254	226	107	329
4	186	163	91	214
5	259	13	57	88
6	23	7	1	32
7	76	203	63	88
8	37	8	30	33

f) *Heteromastus filiformis*

	Month			
Site	D	M	J	S
1	86	151	146	100
2	216	247	184	57
3	109	111	108	67
4	149	169	84	67
5	39	6	13	9
6	17	11	2	9
7	61	43	38	13
8	31	8	9	1

g) *Peloscolex* spp.

	Month			
Site	D	M	J	S
1	203	584	385	25
2	100	280	408	62
3	1005	853	605	181
4	397	564	266	64
5	622	57	68	36
6	89	68	2	48
7	381	702	77	63
8	134	27	104	63

h) *Mya arenaria*

	Month			
Site	D	M	J	S
1	32	45	62	4
2	39	242	133	1
3	6	134	28	1
4	15	170	60	0
5	0	0	0	0
6	0	0	0	0
7	0	0	0	0
8	0	0	0	0

i) *Brachidontes recurvus*

	Month			
Site	D	M	J	S
1	0	0	0	1
2	31	38	22	179
3	61	29	24	151
4	57	65	59	274
5	197	34	140	89
6	94	4	6	110
7	321	836	268	186
8	123	14	56	97

j) *Congeria leucophaeta*

	Month			
Site	D	M	J	S
1	0	0	0	0
2	0	0	0	0
3	0	0	0	0
4	0	0	0	6
5	0	0	0	149
6	0	0	0	19
7	0	1	0	237
8	4	0	3	794

k) *Odostomia impressa*

	Month			
Site	D	M	J	S
1	179	23	51	10
2	226	160	123	10
3	87	38	70	0
4	97	134	128	0
5	2	1	0	0
6	0	0	0	0
7	3	14	2	0
8	0	0	0	0

l) *Cassidinidea lunifrons*

	Month			
Site	D	M	J	S
1	6	19	5	7
2	129	53	37	73
3	276	96	52	145
4	74	56	43	73
5	495	12	33	90
6	27	4	1	2
7	214	310	55	39
8	209	3	72	54

m) *Melita nitida*

	Month			
Site	D	M	J	S
1	12	33	33	11
2	55	25	102	106
3	281	100	733	178
4	85	89	297	117
5	298	3	23	40
6	13	3	0	13
7	124	36	21	44
8	65	1	30	88

n) *Corophium lacustre*

	Month			
Site	D	M	J	S
1	1	2	2	17
2	4	0	0	145
3	18	1	49	133
4	5	1	4	24
5	153	9	202	174
6	43	19	59	37
7	197	177	700	108
8	66	13	640	301

o) *Balanus improvisus*

	Month			
Site	D	M	J	S
1	0	0	0	39
2	56	12	293	173
3	43	16	5567	363
4	25	33	3964	695
5	3445	76	2148	163
6	341	69	58	102
7	2016	4330	3254	187
8	779	93	452	109

p) *Stylochus ellipticus*

	Month			
Site	D	M	J	S
1	2	0	2	2
2	7	1	24	0
3	3	0	178	4
4	6	2	67	1
5	23	0	0	1
6	0	0	0	2
7	4	0	0	2
8	1	0	0	2

q) Diadumene leucolena

Site	D	M	J	S
	Month			
1	90	431	255	54
2	516	219	205	0
3	882	240	317	23
4	483	220	195	4
5	0	0	0	0
6	0	0	0	0
7	0	0	0	0
8	0	0	0	0

r) Molgula manhattensis

Site	D	M	J	S
	Month			
1	0	1	1	422
2	0	0	0	428
3	0	0	0	21
4	0	0	0	7
5	0	0	0	0
6	0	0	0	0
7	0	0	0	0
8	0	0	0	0

Polydora websteri was moderately abundant at sites 2, 3 and 4 but only present in populations of from 6 to 82 per six replicate samples at the other five sites. The highest density in the down-estuary sites occurred at site 3, while site 7 had the highest populations of the upestuary sites.

Boccardia hamata was poorly represented at site 1 but was considerably more abundant at sites 2, 3 and 4 where it was much more abundant in summer than during the rest of the year. At sites 5 and 6 the species was more abundant in fall and summer than in the intervening seasons, with fall showing the highest densities. However, at sites 7 and 8 it had more uniform abundances throughout the year.

Like B. hamata, the isopod Cassidinidea lunifrons had a limited occurrence at site 1, but further upestuary was never less than 12th in abundance at a site. Except at site 7 it was always most abundant in the fall with a secondary population peak in summer.

The tube-dwelling amphipod Corophium lacustre occurred at all sites, but reached its maximum development upestuary, especially at sites 1, 2, 3 and 4, reduced seasonal peaks occurred in the summer.

The amphipod Melita nitida reached its highest population levels at sites 3 and 4 in the spring. However, it showed no consistent seasonal abundance pattern.

Balanus improvisus was represented at site 1 only in spring and summer. At site 2 it was present all year, with a moderate population increase in spring insuring a reasonable population throughout the summer. A similar pattern was exhibited at sites 3 and 4, but with the spring set being very heavy and the summer decline more substantial.

Peaks of abundance at site 5 occurred in fall and spring, while site 6 had low abundances the year around. The largest populations of _B. improvisus_ were recorded at site 7 which showed low densities of this species only in summer. A modest population was supported at site 8 with the highest abundances occurring in fall and spring.

The distribution of _Stylochus ellipticus_, the flatworm often indicated as an oyster predator, was correlated with that of _B. improvisus_. It was rare at site I, more common, with a spring increase, at site 2, and very abundant at the time of the spring set of _B. improvisus_ at sites 3 and 4. It had a sporadic and sparse occurrence at the upestuary sites, except at site 5 where 23 individuals were found in the fall.

The capitellid _Heteromastus filiformis_ was present at all sites without a significant seasonal trend. It was, however, far less abundant at the four upestuary sites than at the downestuary four.

Nereis succinea was present at all sites in all seasons with no significant patterns of seasonal or temporal abundance.

Winter and spring were the seasons of highest abundance of _Peloscolex_ spp. at sites I and 2. Fall or winter were the seasons of highest abundance at the other sites.

The anemone _Diadumene leucolena_ was limited to the four downestuary sites. It had a peak of abundance at site I in winter, while at sites 2, 3 and 4 more individuals were recorded in the fall than in the other three seasons combined.

The presence of the tunicate _Molgula manhattensis_ was also limited to the lower four sites. Except for one specimen each in winter and spring at site I, it occurred only in the summer samples when it was a major component at sites 1 and 2.

Mya arenaria was also limited to the four downestuary sites. Sites 2, 3 and 4 showed a large population increase in the winter samples as a result of the large fall set. A large mortality occurred before the spring samples and only six individuals were retrieved in the summer collections.

The hooked mussel Brachidontes recurvus was moderately abundant at sites 2, 3 and 4 with a population increase seen in summer. Further upestuary this species was always important, with no consistent pattern of seasonal abundance.

The occurrence of the bivalve Congeria leucophaeta was limited to sites 4, 5, 6, 7 and 8, and except for its sporadic appearances at sites 7 and 8, it was limited to the summer collections in which it was very abundant.

The pyramidellid Odostomia impressa occurred at all sites but 6 and 8. Large numbers were found at the lower four sites with seasonal peaks in fall at the first three sites and in winter at site 4. It suffered a large population reduction in the summer and was not found above site 2 in that season.

COMMUNITY STRUCTURE STATISTICS

Average community structure parameters are presented in Table 10. The mean number of species per sample decreased monotonically with increasing distance up the estuary. There was also a downward trend for informational diversity and its components along the same gradient. The largest drop in these three statistics occurred between sites 4 and 5. Variations in the trend of decreasing informational diversity

Table 10. Community structure parameters. Values are means for each site and are based on calculations using only noncolonial species. (Code: H' = informational species diversity; J' = evenness; SR = species richness).

Site	H'	J'	SR	Species	Individuals
1	3.7616	0.6501	7.2517	55.25	2009.5
2	3.7525	0.6997	5.2997	42.0	2339.0
3	3.1585	0.6096	4.4182	37.0	4374.0
4	3.2203	0.6220	4.4858	36.25	308425
5	2.5879	0.5821	2.9362	22.25	1803.9
6	2.9583	0.6686	3.4869	21.75	435.0
7	2.3949	0.5404	2.5417	21.5	4159.25
8	2.5442	0.5998	2.6739	19.25	1233.5

occurred at: site 3, where low evenness forced the H' diversity below that of site 4; site 6, where there was exceptionally high evenness; and site 8, where high evenness raised the diversity level above that of site 7.

Figure 8 illustrates the seasonal and spatial patterns of informational diversity, evenness and species richness. At site I diversity appears to be primarily related to species richness, but at every other site diversity and evenness are very well correlated. All sites, except site I, experienced a decrease in diversity between the winter and spring samples due principally to a corresponding decrease in evenness. Evenness increased at these same seven sites in summer and even though three of them experienced a decline in species richness, diversity increased, often dramatically, at all sites except site 2. Only at sites I and 2, where species richness played a larger role, was there a decrease in informational diversity in the summer (post-Agnes) samples.

The absolute ranges exhibited by diversity and its components at each site over the four sampling periods are presented in Table II. Site 8 was the most stable with respect to informational diversity and species richness, and the second most stable in evenness.

CLASSIFICATORY RESULTS

Test of Beta Levels

Using the same similarity matrix, based on Sorensen's index of similarity, three tests were made with different levels of beta, the cluster intensity coefficient used in flexible grouping, to determine the most appropriate level for the present data. A beta value of 0.0

Figure 8. Seasonal and spatial patterns of informational diversity and its components; a) diversity, b) evenness, c) species richness.

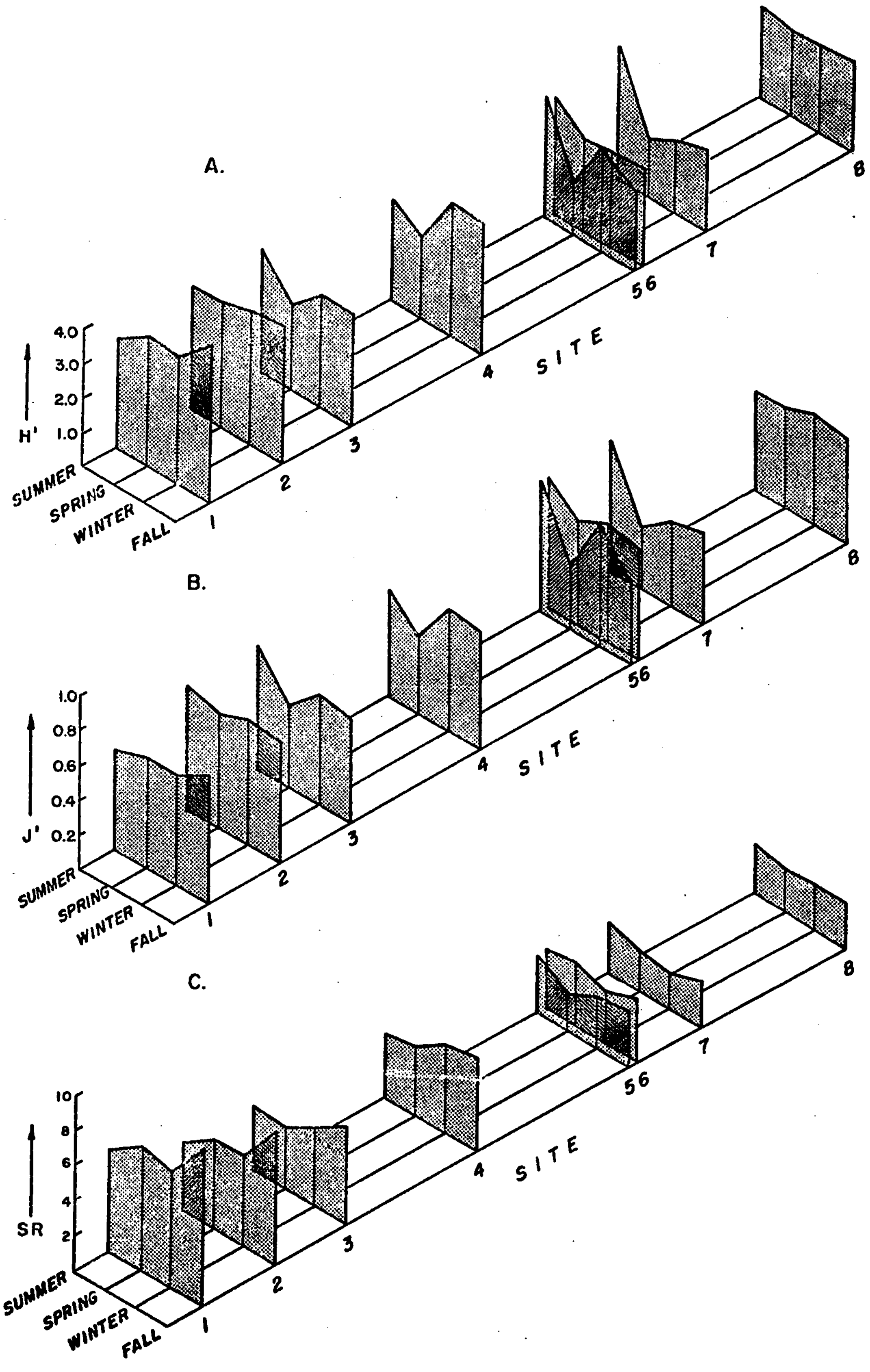

A.
4.0
3.0
2.0
1.0
H'
SUMMER
SPRING
WINTER
FALL
1
2
3
4
SITE
56
7
8
B.
1.0
0.8
0.6
0.4
0.2
J'
SUMMER
SPRING
WINTER
FALL
1
2
3
4
SITE
56
7
8
C.
10
8
6
4
2
SR
SUMMER
SPRING
WINTER
FALL
1
2
3
4
SITE
56
7
8

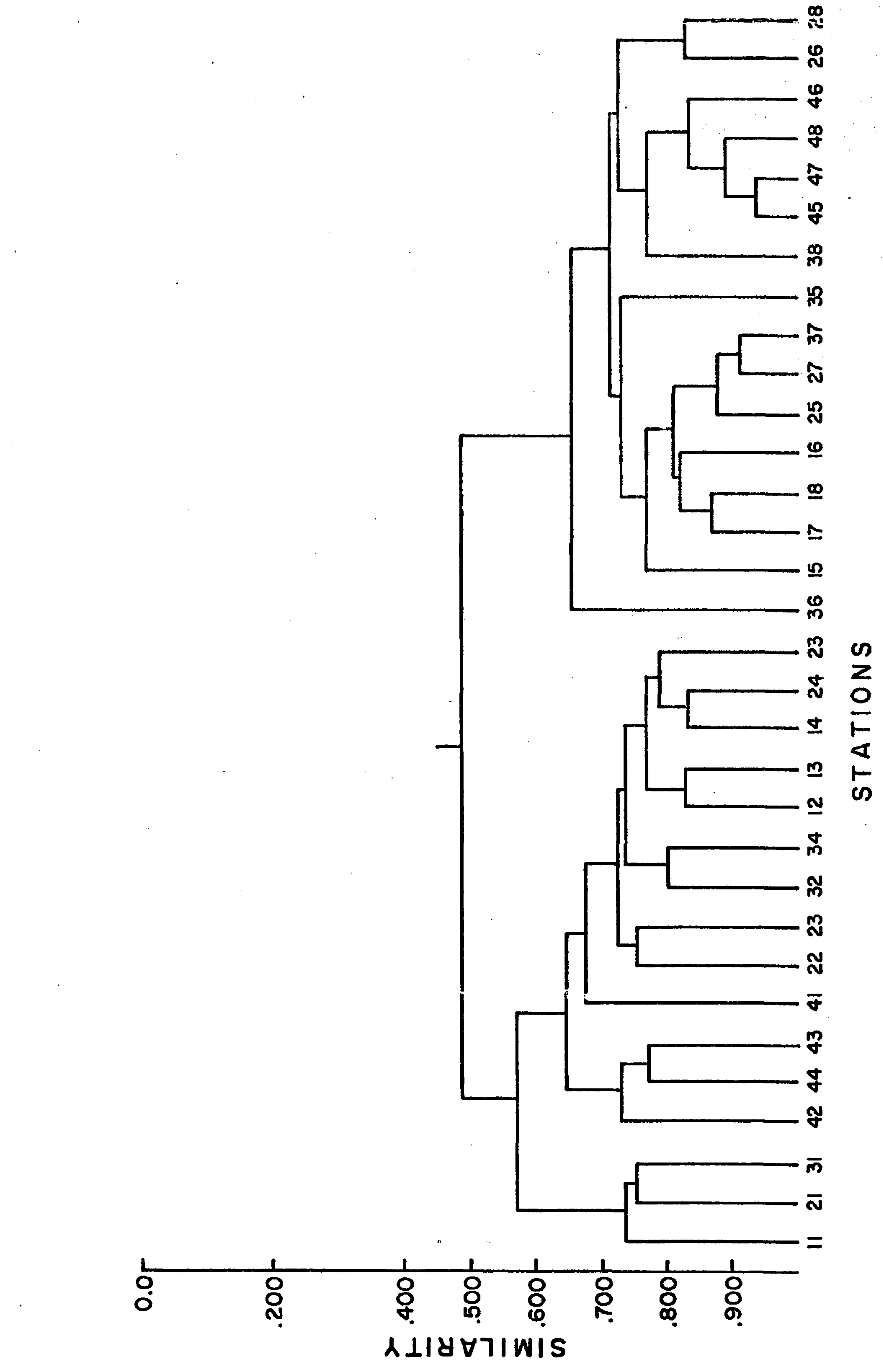
Table II. Ranges of informational diversity, evenness, and species richness by site.

Site	H'	J'	SR
1	1.4059	0.1634	3.2854
2	0.5109	0.0624	3.0272
3	1.1174	0.2481	2.1149
4	1.5213	0.2695	1.8056
5	1.9547	0.3938	1.1715
6	0.7274	0.1433	0.7581
7	1.7792	0.3935	0.8356
8	0.1841	0.0670	0.5089

Figure 9. Dendrogram resulting from the use of Sorensen's index and the flexible sorting clustering strategy with $\beta = 0.0$. The first numeral of the station code indicates the season of the sample (fall 1, winter 2, spring 3 and summer 4) and the second digit represents the site of the sample.


SIMILARITY
0.0
.200
.400
.500
.600
.700
.800
.900
STATIONS
11
31
21
42
43
44
41
22
33
32
34
12
13
14
24
23
36
15
17
18
16
25
27
37
35
38
45
47
48
46
26
28

Figure 10. Dendrogram resulting from the use of Sorensen's index and the group averaging clustering strategy. See Fig. 9 for station code.


0.0
.200
.400
.500
.600
.700
.800
.900
SIMILARITY
11
21
31
42
44
43
41
22
23
32
34
12
13
14
24
23
36
15
17
18
16
25
27
37
35
38
45
47
48
46
26
28
STATIONS

gave branching (Fig. 9) identical to that of group averaging (Fig. 10), with the exception that the higher fusions were at a lower level of similarity in the flexible scheme. Some chaining in the secondary fusions can be observed in each.

A beta value of -0.25 gave clusters with no evidence of chaining and which, on even cursory examination, appeared to be ecologically meaningful since the stations were clustered into temporally or spatially similar groups (Fig. 11).

With one exception, involving the positioning of station 35, a beta of -0.50 gave the same branching pattern as the -0.25 test (Fig. 12). Reference to the original data matrix indicated that the exception is most likely a misclassification in the -0.50 clusters. The increased effect of space-dilation can be seen in the lower similarity of the higher fusions of the -0.50 dendrogram with respect to one constructed with beta at -0.25.

It was concluded that the -0.25 was the most appropriate to use with the data under consideration. Higher levels compromise the clustering power to the point of masking ecological similarities, and lower levels cause unnecessary misclassifications without increasing the meaningfulness of the clusters formed.

Station-group Analysis

The 32 stations were subjected to analysis by the Canberra metric and Sorensen's similarity indices and flexible grouping with beta set at -0.25. The similarity matrices were also clustered using group averaging to point out misclassifications in the intense flexible

Figure 11. Dendrogram resulting from the use of Sorensen's index and the flexible sorting clustering strategy with $\beta = -0.25$. See Fig. 9 for station code.

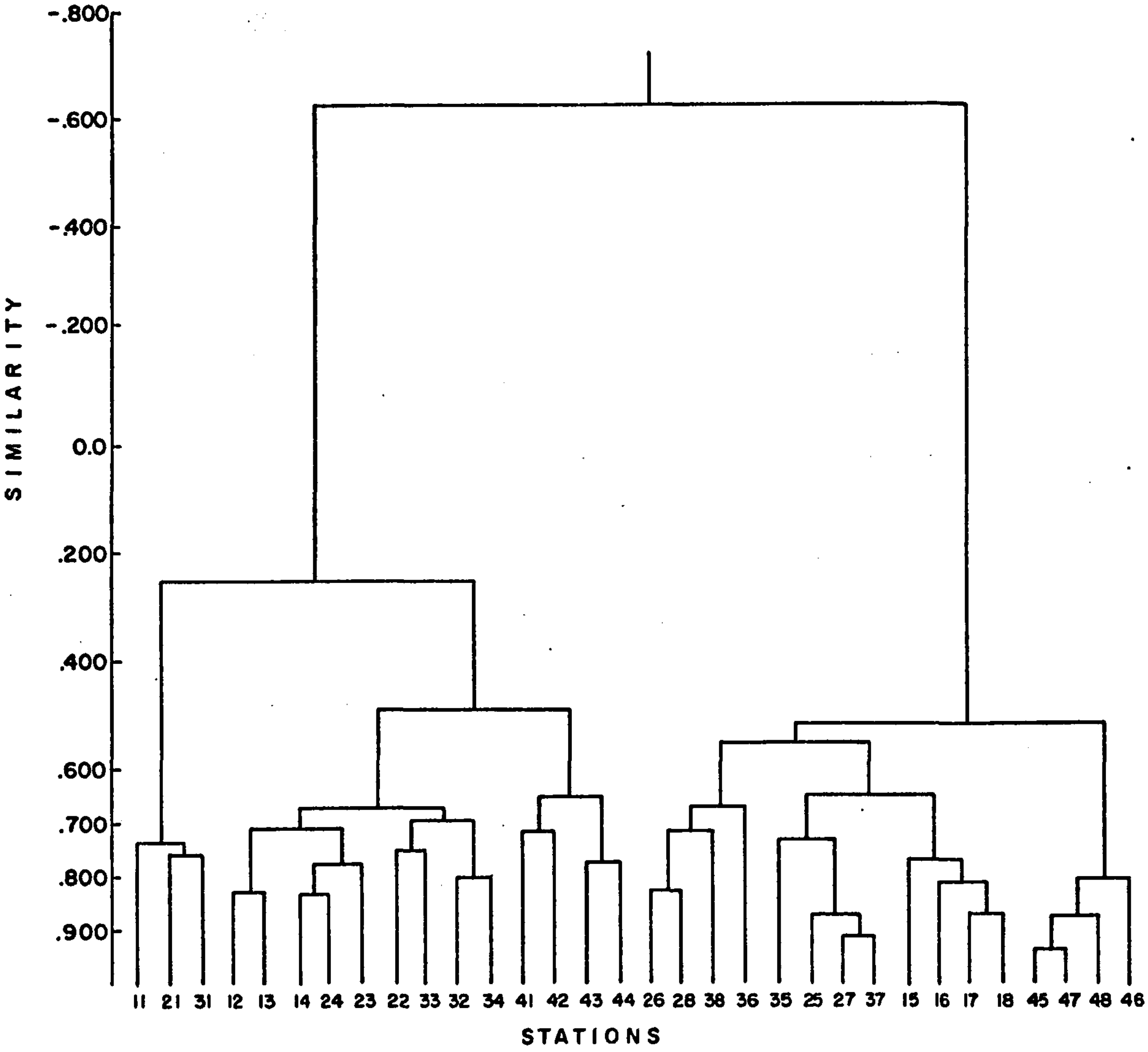

SIMILARITY
-.800
-.600
-.400
-.200
0.0
.200
.400
.600
.700
.800
.900
11 21 31 12 13 14 24 23 22 33 32 34 41 42 43 44 26 28 38 36 35 25 27 37 15 16 17 18 45 47 48 46
STATIONS

Figure 12. Dendrogram resulting from the use of Sorensen's index and the flexible sorting clustering strategy with $\beta = -0.50$. See Fig. 9 for station code.

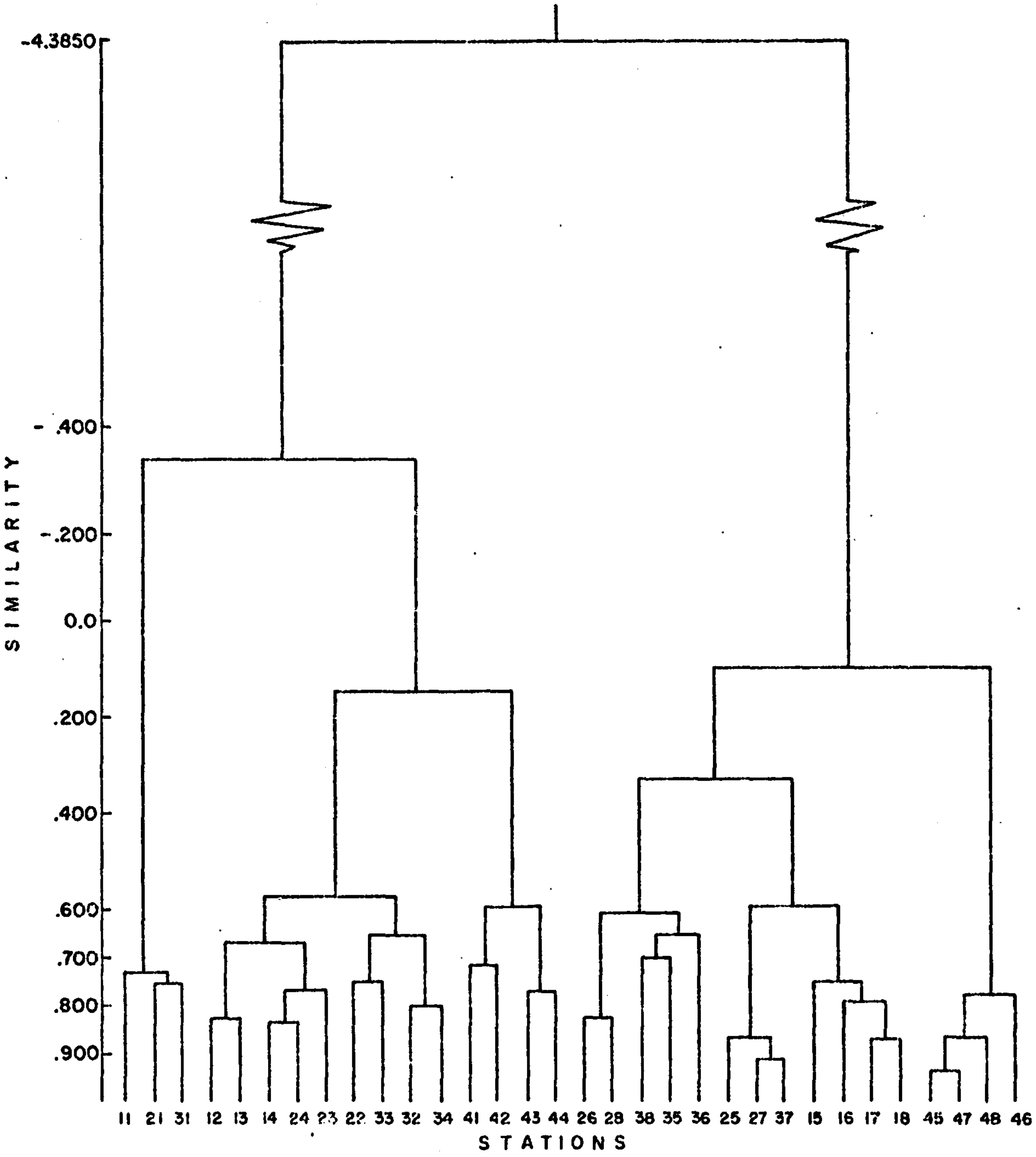
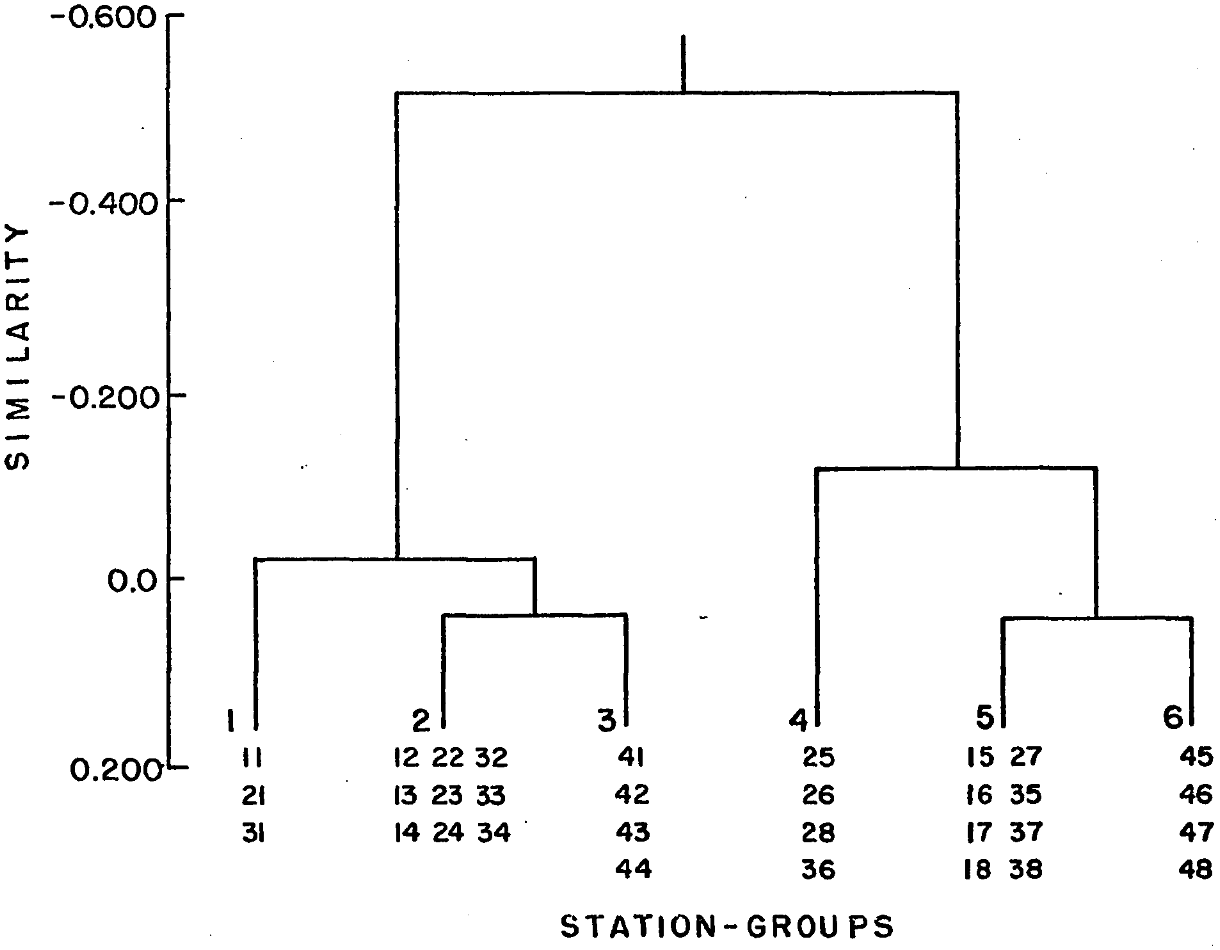

-4.3850
-.400
-.200
0.0
.200
.400
.600
.700
.800
.900
SIMILARITY
11 21 31 12 13 14 24 23 22 33 32 34 41 42 43 44 26 28 38 35 36 25 27 37 15 16 17 18 45 47 48 46
STATIONS

Figure 13. Dendrogram of station classification, taken to the 6 station-group level, by the Canberra metric index and the flexible sorting clustering strategy ($\beta = -0.25$). See Fig. 9 for station code.


SIMILARITY
-0.600
-0.400
-0.200
0.0
0.200
1
11
21
31
2
12 22 32
13 23 33
14 24 34
3
41
42
43
44
4
25
26
28
36
5
15 27
16 35
17 37
18 38
6
45
46
47
48
STATION-GROUPS

strategy. The samples are described by a two digit code. The first numeral indicates the season of the sample (fall 1, winter 2, spring 3 and summer 4) and the second digit represents the site of the sample.

When truncated at the six group level (Fig. 13) the Canberra metric index gave an intuitively satisfying picture of the interstation relationships on the oyster reefs. The first dichotomy (a) divides the samples into those occurring at four downestuary sites and those occurring at the four upestuary sites, suggesting salinity as the overriding factor controlling the composition of the faunal assemblages.

A second dichotomy (b) also appears to be salinity related, as it separates all the stations at site 1 before the Agnes freshet from the remainder of the downestuary stations. These site 1 samples were the most speciose encountered, each containing between 61 and 73 species.

The second arm of dichotomy b was broken into two station-groups. Station-group 2 contains all pre-Agnes samples from sites 2, 3 and 4. This group was composed of two subgroups. Subgroup a contained the fall and winter samples which had from 40 to 58 species per station, subgroup b contained the spring samples which were slightly less speciose (36 to 44 species), but, more importantly, differed from the previous seasons' samples in levels of density and dominance (cf. Fig. 6 and Table 7).

Station-group 3 included the four downriver post-Agnes (summer) stations. These stations contained fewer species and fewer individuals than the other stations made at the same sites.

Station-group 4 contained four stations characterized by between 15 and 22 species and 182 and 256 individuals, the four lowest numbers of individuals recorded. Three of the four were winter stations and two were from the sandy-bottomed site 6.

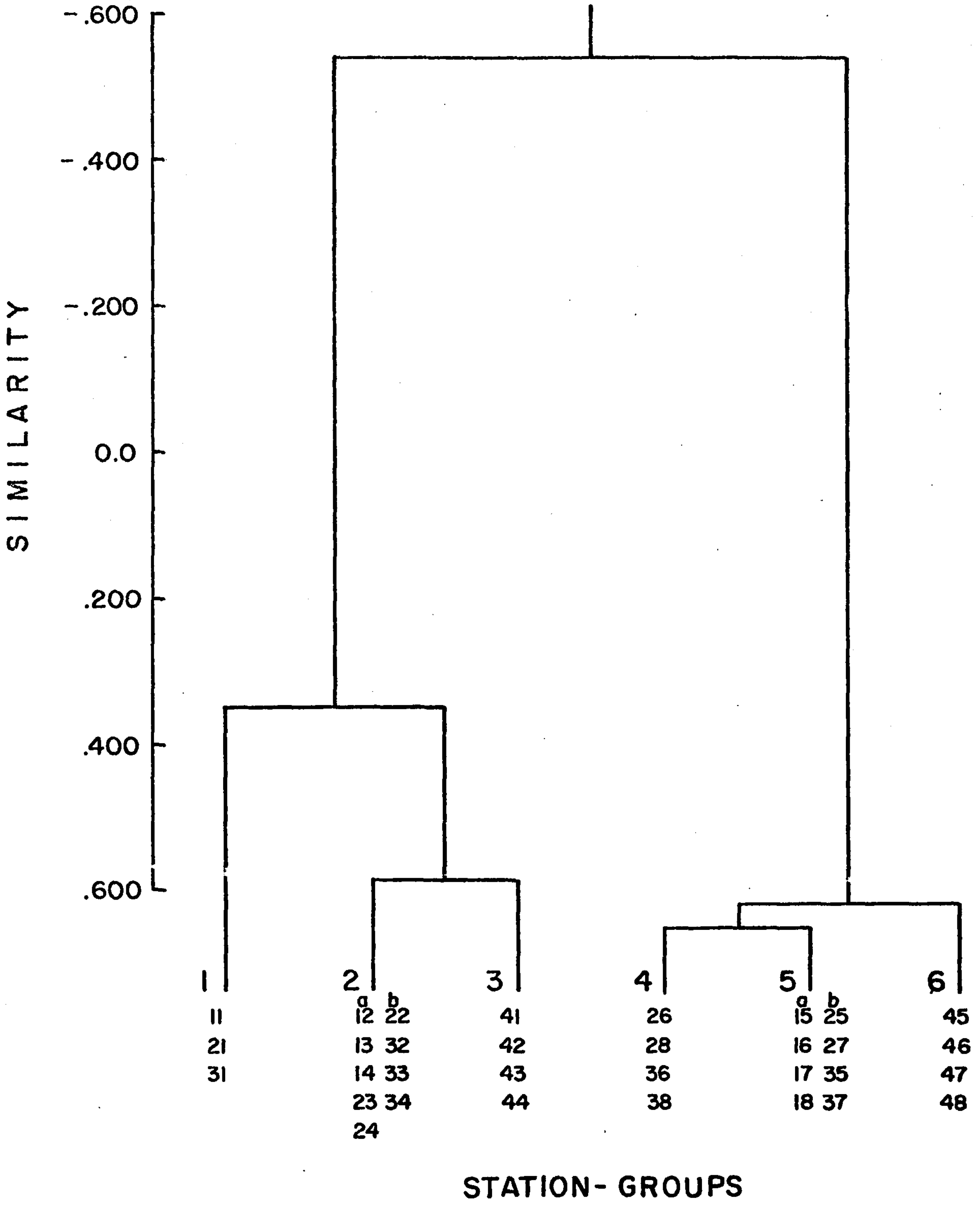
Station-group 5 contained the remaining upestuary pre-Agnes samples, which included 21-29 species in moderate to high densities. This station-group was divisible into two subgroups and quantitative differences in the sample data suggest that the dichotomy is based on substrate considerations. Subgroup a contains stations with an average shell substrate volume of 750 cc and above, while the average volume in subgroup b was always less than 460 cc.

Station-group 6 contained the four upestuary post-Agnes stations. The most characteristic feature of this group was the dominating presence of _Congeria leucophaeta_. Other causes for the 5-6 dichotomy apparently lay with more subtle quantitative changes, and qualitative changes in the rarer species.

The binary index of Sorensen at the 6-group level (Fig. 14) yielded groups that, but for the transposition of two stations, were identical to those of the Canberra metric 6-group level (Fig. 13). The differences are the placement of station 25 in station-group 5 and the placement of station 38 in station-group 4. Inclusion of 38 in station-group 4 increased the heterogeneity of that group. Inclusion of station 25 into group 5 was not surprising as qualitatively it resembles stations 15 and 35.

Subgroups are again well defined in station-groups 2 and 5. Subgroups a and b in station-group 2 are the same except that station 22 is in subgroup b rather than a as in the Canberra metric analysis. Station 22 is qualitatively more similar to 32 than to 12, which con-

Figure 14. Dendrogram of station classification, taken to the 6 station-group level, by the use of Sorensen's index and the flexible sorting clustering strategy ($\beta = -0.25$). See Fig. 9 for station code.


SIMILARITY
-.600
-.400
-.200
0.0
.200
.400
.600
1
2
3
4
5
6
a
b
a
b
11
21
31
12
13
14
23
24
22
32
33
34
41
42
43
44
26
28
36
38
15
16
17
18
25
27
35
37
45
46
47
48
STATION- GROUPS

tains several species not present in either 22 or 32.

There was little relationship between the subgroups of station-group 5 of the Sorensen and Canberra metric analyses. The Sorensen division put all upriver fall stations into subgroup a and the winter and spring stations into subgroup b. For the most part, the fall collections contained more species than did the winter and spring samples and the two subgroups are a reflection of this.

RANK ANALYSIS

The use of absolute numbers in a community analysis is often misleading. A species with low constancy could be so abundant in one sample that its importance would seem greater than that of a constant species, even when averaged over several sampling periods. For example, at site I *Streblospio benedicti* ranked first due to an overwhelming abundance in one season (Table 7a). One way to analytically dampen the effect of this phenomenon is to use rank scores which assign values reflecting relative abundance regardless of the absolute number of individuals involved. The five most abundant species at each station, which included between 50.5 and 94.4% of the individuals, were given scores as rank dominants.

Twenty-one species were accorded rank dominant status in this manner. In Table 12 a-h are listed the rank dominants at each site in order of their summated scores and the score attained in each season. Comparison of this table with Table 7 presents some interesting contrasts, e.g., *Peloscolex* spp. is the most important taxon at the downestuary sites in the rank analysis while this distinction is shared by *S. benedicti* and *Balanus improvisus* in the abundance analysis. The summated

Table 12a.

Rank analysis dominant species at Site 1. Highest possible score = 20.

Species	Fall	Winter	Spring	Summer	Total
Peloscolex spp.	5	5	4		14
Diadumene leucolena	1	4	2	2.5	9.5
Polydora ligni		3	3		6
Streblospio benedicti		1	5		6
Heteromastus filiformis			1	4	5
Molgula manhattensis				5	5
Odostomia impressa	4				4
Pseudeurythoe sp.	3				3
Nereis succinea		2		1	3
Balanus improvisus				2.5	2.5
Neomysis americana	2				2

Table 12b.

Rank analysis dominant species at Site 2.

Species	Fall	Winter	Spring	Summer	Total
Peloscolex spp.	1	5	3		9
Streblospio benedicti		4	5		9
Diadumene leucolena	5		1		6
Heteromastus filiformis	3	3			6
Polydora ligni		1	4		5
Molgula manhattensis				5	5
Odostomia impressa	4				4
Balanus improvisus			2	2	4
Boccardia hamata				4	4
Brachidontes recurvus				3	3
Cassidinidea lunifrons	2				2
Mya arenaria		2			2
Nereis succinea				1	1

Table 12c.

Rank analysis dominant species at Site 3.

Species	Fall	Winter	Spring	Summer	Total
Peloscolex spp.	5	5	2	2	14
Balanus improvisus			5	5	10
Diadumene leucolena	4	4			8
Nereis succinea	1	3		4	8
Melita nitida	3		3	1	7
Polydora ligni			4		4
Boccardia hamata				3	3
Cassidinidea lunifrons	2				2
Mya arenaria		2			2
Heteromastus filiformis		1			1
Streblospio benediciti			1		1

Table 12d.

Rank analysis dominant species at Site 4.

Species	Fall	Winter	Spring	Summer	Total
Peloscolex spp.	4	5	2		11
Balanus improvisus			5	5	10
Diadumene leucolena	5	4			9
Nereis succinea	3	1		3	7
Heteromastus filiformis	2	2			4
Polydora ligni			4		4
Melita nitida			3	1	4
Brachidontes recurvus				4	4
Mya arenaria		3			3
Boccardia hamata				2	2
Odostomia impressa	1				1
Streblospio benedicti			1		1

Table 12e.

Rank analysis dominant species at Site 5.

Species	Fall	Winter	Spring	Summer	Total
Balanus improvisus	5	5	5	4	19
Peloscolex spp.	4	4	2		10
Corophium lacustre			4	5	9
Brachidontes recurvus		3	3		6
Cassidinidea lunifrons	3			1	4
Boccardia hamata		2		2	4
Congeria leucophaeta				3	3
Melita nitida	2				2
Nereis succinea	1		1		2
Leptocheirus plumulosus		1			1

Table 12f.

Rank analysis dominant species at Site 6.

Species	Fall	Winter	Spring	Summer	Total
Balanus improvisus	5	5	3	4	17
Brachidontes recurvus	4		1	5	10
Peloscolex spp.	3	4		3	10
Corophium lacustre	1	3	4	1	9
Boccardia hamata	2	2		2	6
Leptocheirus plumulosus			5		5
Heteromastus filiformis		1			1
Gammarus daiberi			1		1
Mulinia lateralis			1		1

Table 12g.

Rank analysis dominant species at Site 7.

Species	Fall	Winter	Spring	Summer	Total
Balanus improvisus	5	5	5	4	19
Brachidontes recurvus	3	4	3	3	13
Peloscolex spp.	4	3	1		8
Corophium lacustre	1		4	2	7
Congeria leucophaeta				5	5
Cassidinidea lunifrons	2	2			4
Boccardia hamata			2	1	3
Gammarus dalberi		1			1

Table 12h.

Rank analysis dominant species at Site 8.

Species	Fall	Winter	Spring	Summer	Total
Balanus improvisus	5	5	4	3	17
Corophium lacustre	1	2	5	4	12
Peloscolex spp.	3	4	3		10
Brachidontes recurvus	2	3		2	7
Cassidinidea lunifrons	4		2		6
Congeria leucophaeta				5	5
Nereis succinea		1			1
Gammarus daiberi			1		1
Melita nitida				1	1

Table 13.

Rank analysis dominant species at all stations for all sampling periods.
Highest possible score = 160.

Species	1	2	3	4	5	6	7	8	Total
Balanus improvisus	2.5	4	10	10	19	17	19	17	98.5
Peloscolex spp.	14	9	14	11	10	10	8	10	86
Brachidontes recurvus		3		4	6	10	13	7	43
Corophium lacustre					9	9	7	12	37
Diadumene leucolena	9.5	6	8	9					32.5
Nereis succinea	3	1	8	7	2			1	22
Boccardia hamata		4	3	2	4	6	3		22
Polydora ligni	6	5	4	4					19
Cassidinidea lunifrons		2	2		4		4	6	18
Heteromastus filiformis	5	6	1	4		1			17
Streblospio benedicti	6	9	1	1					17
Melita nitida			7	4	2				14
Congeria leucophaeta					3		5	5	13
Molgula manhattensis	5	5							10
Odostomia impressa	4	4		1					9
Mya arenaria		2	2	3					77
Leptocheirus plumulosus					1	5			6
Gammarus daiberi						1	1	1	3
Pseudeurythoe sp.	3								3
Neomysis americana	2								2
Mulinia lateralis						1			1

total scores attained by each species at each site (maximum 20) and overall (maximum 160) are presented in Table 13. By virtue of their dominance at every site, B. improvisus and Peloscolex spp. each accumulated twice as many points as the third ranked species. Other widely distributed species, e.g. Corophium lacustre and Polydora ligni, scored lower because their maximum population development was limited to only part of their range.

The number of species attaining rank dominance at a given number of sites is presented in Table 14. Two taxa, B. improvisus and Peloscolex spp. were ranked at all eight sites. Only five other species, Brachidontes recurvus, Nereis succinea, Boccardia hamata, Cassidinidea lunifrons and Heteromastus filiformis were dominants at more than 50% of the sites.

Rank scores are summarized by season in Table 15. Of the ten species receiving the highest total rank scores, nine were dominants in all four seasons. These were the only species to exhibit a year around dominance (Table 16).

DISTRIBUTION OF HIGHER TAXONOMIC CATEGORIES

The number and percentage of noncolonial species and the percentage of individuals in each of four categories: annelids, molluscs, crustaceans and others, are presented in Fig. 15. There is a parallel decline in the number of species in each category moving upriver, such that the proportions of species in each category change little. However, annelids which provided almost 65% of the individuals at site 1 decreased upestuary, accounting for less than 13% at site 8. Crustaceans, although less than 10% of the individuals at site 1, increased in importance upestuary

Table 14. Number of species attaining rank dominance at from one to eight sites.

Number of Sites of Dominance	Number of Species Attaining Dominance
1	3
2	3
3	4
4	4
5	3
6	2
7	0
8	2

Table 15. Seasonal pattern of rank dominance by species. First number is the total rank score attained by a species in that season and the number in parenthesis is the number of sites where it was dominant.

Species	Fall	Winter	Spring	Summer	Total
Balanus improvisus	20(4)	20(4)	29(7)	29.5(8)	98.5
Peloscolex spp.	29(8)	35(8)	17(7)	5 (2)	86
Brachidontes recurvus	9(3)	10(3)	7(3)	17 (5)	43
Corophium lacustre	3(3)	5(2)	17(4)	12 (4)	37
Diadumene leucolena	14(4)	12(3)	3(2)	2.5(1)	32.5
Nereis succinea	5(3)	7(4)	1(1)	9 (4)	22
Boccardia hamata	2(1)	4(2)	2(1)	14 (6)	22
Polydora ligni		4(2)	15(4)		19
Cassidinidea lunifrons	13(5)	2(1)	2(1)	1 (1)	18
Heteromastus filiformis	5(2)	7(4)	1(1)	4 (1)	17
Streblospio benedicti		5(2)	12(4)		17
Melita nitida	5(2)		6(2)	3 (3)	14
Congeria leucophaeta				13 (3)	13
Molgula manhattensis				10 (2)	10
Odostomia impressa	9(3)				9
Leptocheirus plumulosus		1(1)	5(1)		6
Mya arenaria		7(3)			7
Gammarus daiberi		1(1)	2(2)		3
Pseudeurythoe sp.	3(1)				3
Neomysis americana	2(1)				2
Mulinia lateralis			1(1)		1

Table 16. Seasonality of rank dominance.

Number of Seasons of Rank Dominance	Number of Species
1	7
2	4
3	1
4	9

Figure 15. Distribution of higher taxonomic categories along the estuarine gradient. a) The number and percentage of species in each higher taxon. b) The percentage of individuals in each higher taxon.

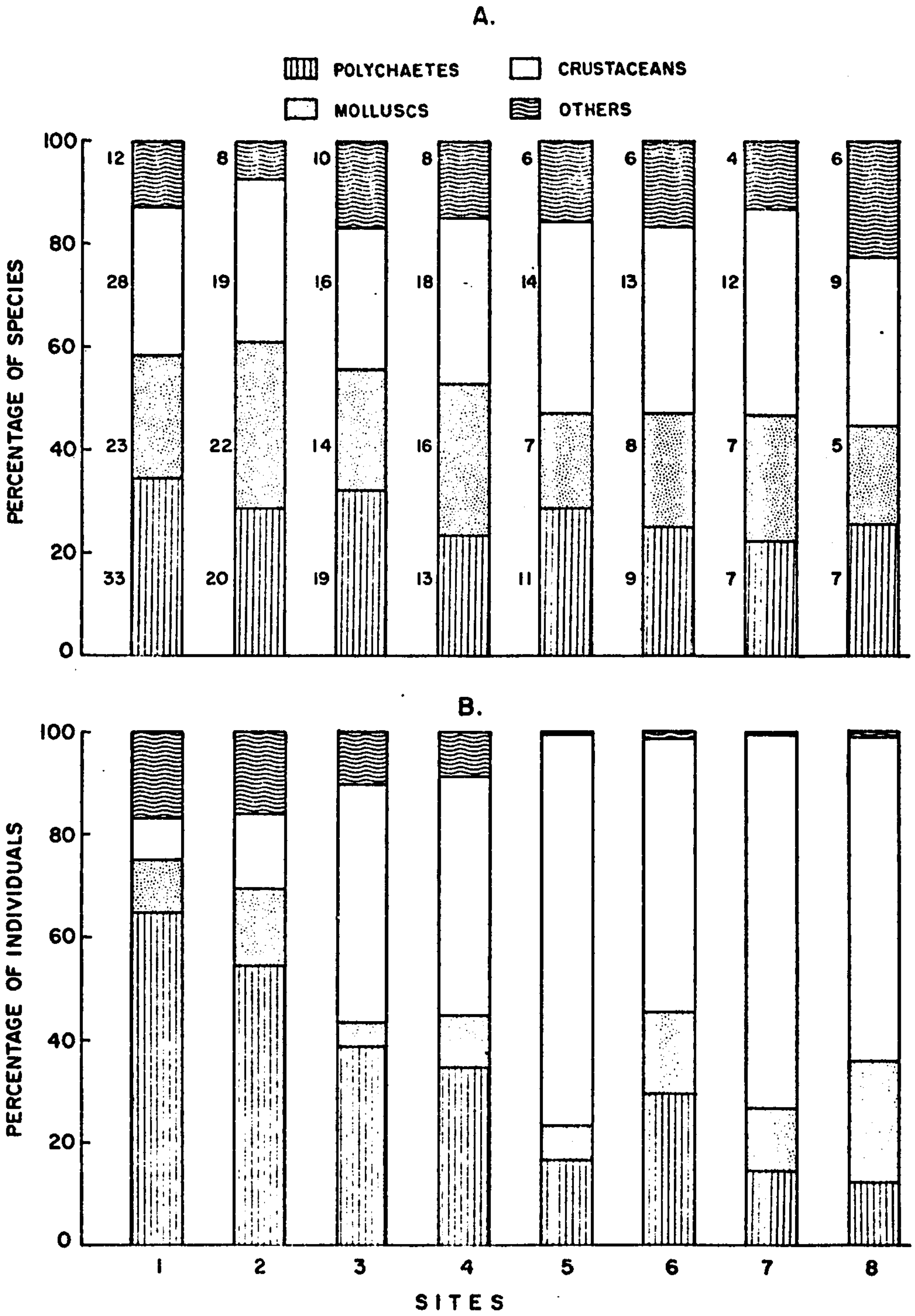
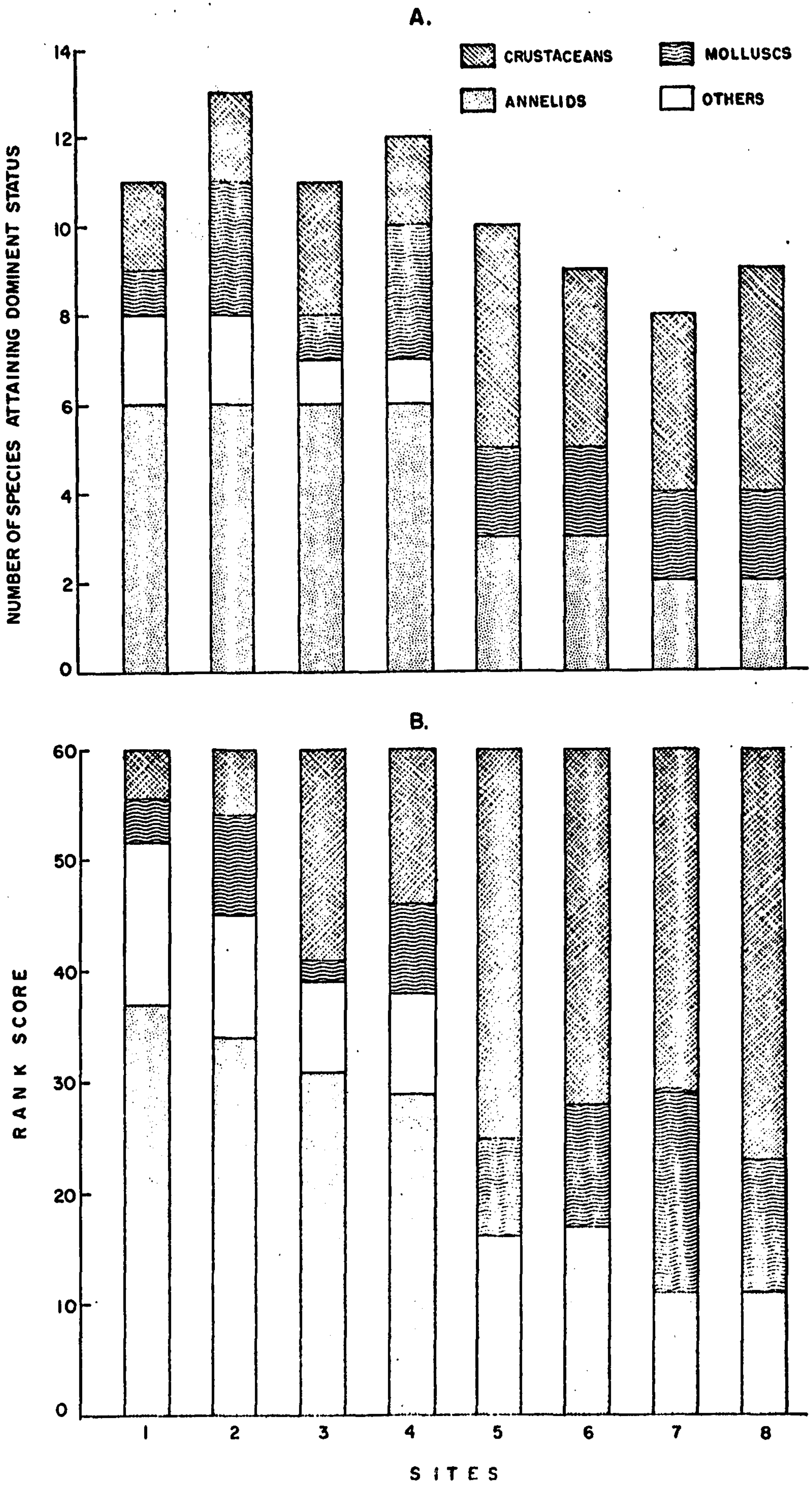

A.
POLYCHAETES
CRUSTACEANS
MOLLUSCS
OTHERS
PERCENTAGE OF SPECIES
100
80
60
40
20
0
12
28
23
33
8
19
22
20
10
16
14
19
8
18
16
13
6
14
7
11
6
13
8
9
4
12
7
7
6
9
5
7
B.
PERCENTAGE OF INDIVIDUALS
100
80
60
40
20
0
1
2
3
4
5
6
7
8
SITES

Figure 16. Rank score analysis of the higher taxonomic categories a) Number of species in each higher taxa attaining dominance, b) the summated rank scores achieved by each higher taxon.

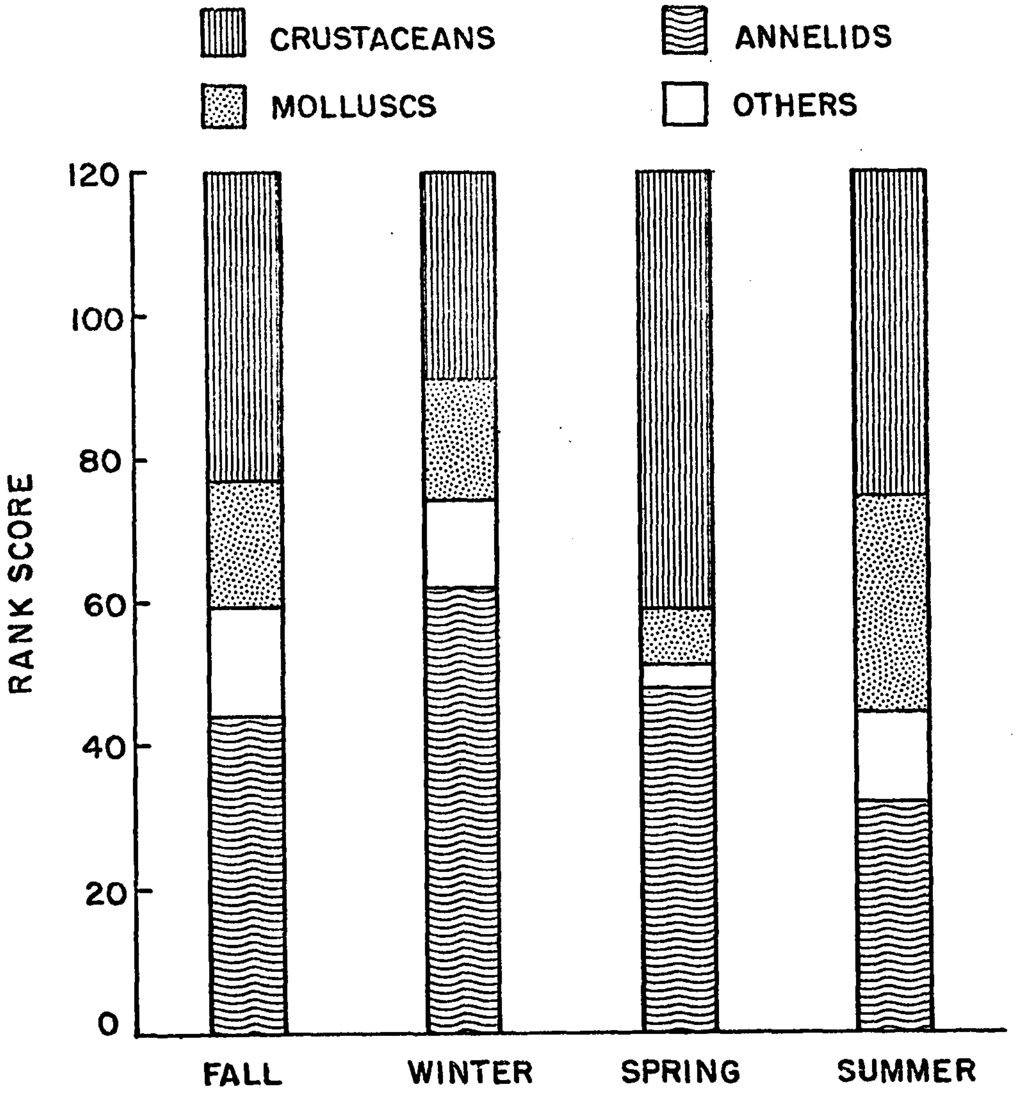

A.
CRUSTACEANS
MOLLUSCS
ANNELIDS
OTHERS
NUMBER OF SPECIES ATTAINING DOMINENT STATUS
0
2
4
6
8
10
12
14
B.
RANK SCORE
0
10
20
30
40
50
60
1
2
3
4
5
6
7
8
SITES

to become the overwhelming dominant group at the four upestuary sites. Molluscs did not show a discernible pattern. Other taxa were important at the lower four sites because of the abundance of *Diadumene leucolena* and *Molgula manhattensis*.

Partitioning (Fig. 16a) of species attaining rank score dominance (Table 12) into the four categories shows a clear break between stations 4 and 5 where there is a distinct drop in the number of annelids and and increase in the number of crustaceans attaining dominance. Again molluscs exhibited no consistent pattern and the importance of "others" terminated at site 4. The summated rank scores achieved by each group (Fig. 16b) confirm and enhance the results shown by Fig. 15b. The rank score dominance of annelids was best developed at the downestuary sites and declined upestuary, while crustaceans were unimportant downestuary but increased upestuary. Molluscs were relatively dominant at the upestuary sites, but dominance of the other taxa was again limited to the four downestuary sites.

Overall seasonal patterns of the partition of rank dominance among the four categories are shown in Fig. 17. Dominance was most equitably distributed in fall, whereas in winter annelids accounted for over half of the rank score points with crustaceans suffering a corresponding decline. By spring the crustaceans had attained over half of the rank score points at the expense of the three other groups. Both annelids and crustaceans declined from their spring levels in summer when the molluscs had their most dominant season and "others" gained importance by influx of *M. manhattensis*.

Figure 17. Seasonal pattern of rank score dominance of higher taxonomic categories.

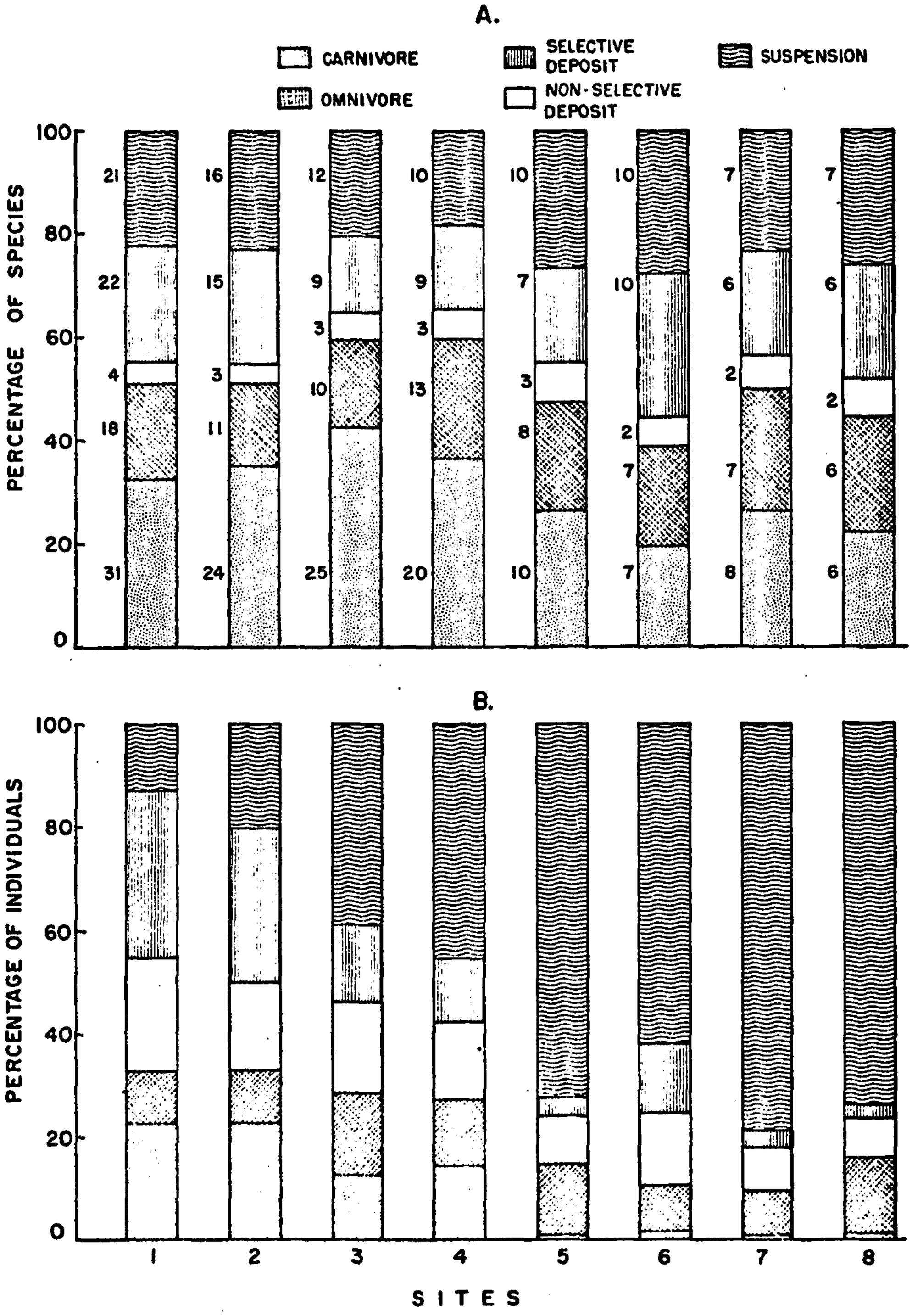


CRUSTACEANS
ANNELIDS
MOLLUSCS
OTHERS
RANK SCORE
120
100
80
60
40
20
0
FALL
WINTER
SPRING
SUMMER

DISTRIBUTION OF FEEDING, PURCHASE AND DISPERSAL TYPES

The five assigned feeding types with their code numbers are: 1) carnivores, including carrion feeders; 2) omnivores, including general scavengers; 3) non-selective deposit feeders; 4) selective deposit feeders, including detritus feeders and herbivores; and 5) suspension feeders. The five purchase types are: 1) motile epifauna; 2) attached epifauna; 3) free infauna; 4) tube-dwelling infauna, including those with semi-permanent burrows; and 5) shell-borers. Larval dispersal types and their code numbers are: 1) nonpelagic; 2) short pelagic, i.e. two or three days and 3) pelagic. Due to the lack of information on, or conflicting account of, the biology of many species, these designations cannot be considered rigid. Indeed, some species exhibit a remarkable degree of plasticity, expecially in their feeding and larval dispersal methods. Whereas each species was assigned only to the type in each category which was believed to be most characteristic of its behavior, it is realized that in some cases this represents a superficial description of a species' biology. When no information was available on a species, it was assigned to the most appropriate category based on generic or familiar characteristics. A wide range of references was used to insure as much accuracy as possible including Abbott (1968), Allen (1958), Barnes (1963), Daro and Polk (1973), Enequist (1949), Feeley and Wass (1971), Franz (1967), Fretter and Graham (1962), Hunt (1925), Hurst (1965), Jorgenson (1966), Kume and Dan (1957), MacGinitie and MacGinitie (1968), Miner (1950), Muus (1967), Nicol (1960), Pettibone (1963), Phelps (1964), Sanders (1956, 1958, and 1960), Schultz (1969), Thorson (1950), Wells (1959), Wells and

Figure 18. Distribution of feeding types along the estuarine gradient; a) the number and percentage of species in each category, b) the percentage of individuals in each feeding type.


A.
CARNIVORE
OMNIVORE
SELECTIVE DEPOSIT
NON-SELECTIVE DEPOSIT
SUSPENSION
PERCENTAGE OF SPECIES
100
80
60
40
20
0
21
22
4
18
31
16
15
3
11
24
12
9
3
10
25
10
9
3
13
20
10
7
3
8
10
10
10
2
7
7
7
6
2
7
8
7
6
2
6
6
B.
PERCENTAGE OF INDIVIDUALS
100
80
60
40
20
0
1
2
3
4
5
6
7
8
SITES

Wells (1961) and Yonge (1950).

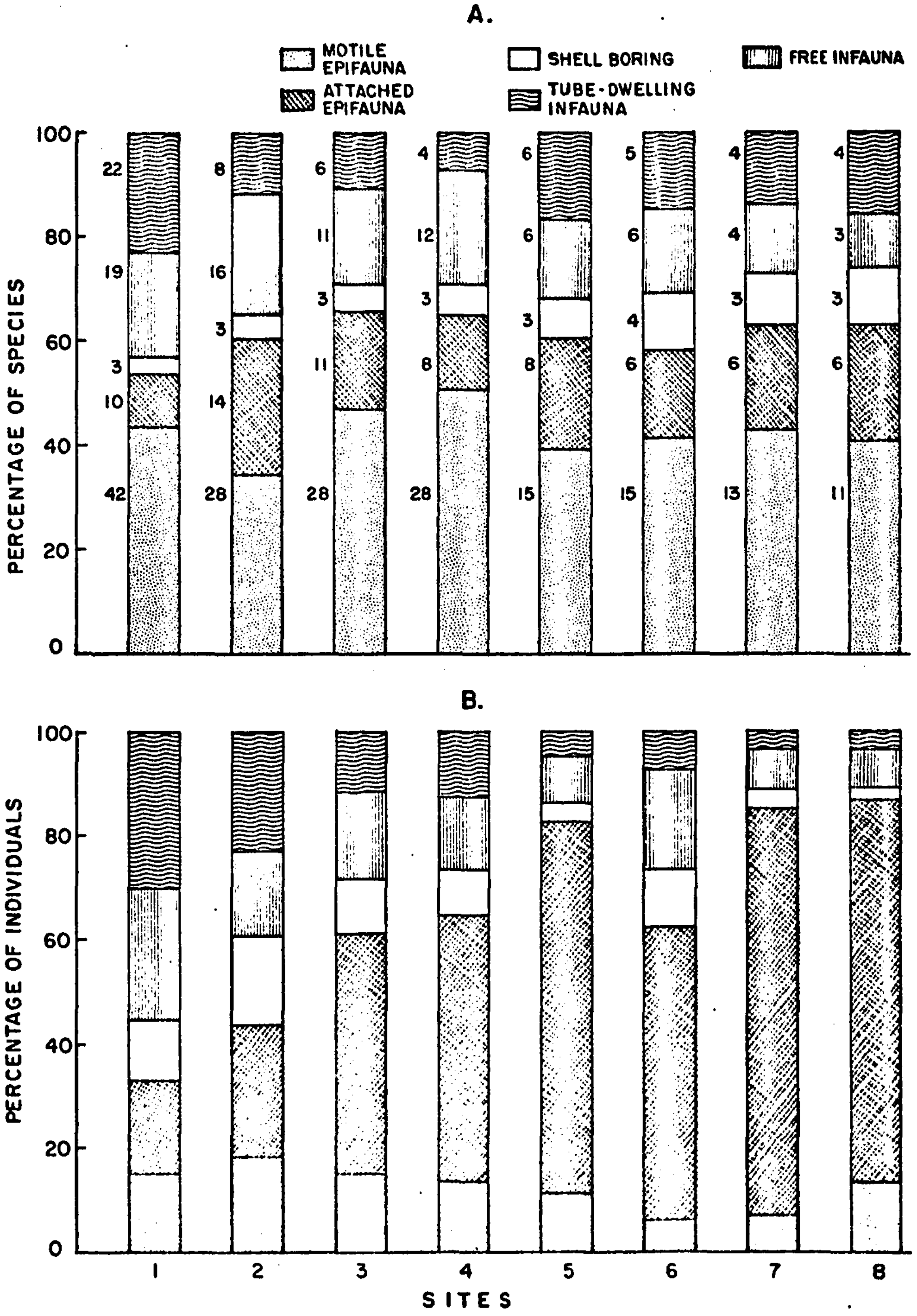
The number and percentage of species in each feeding type for each site (Fig. 18a) shows a parallel decline in the number of species in each category while the proportions remained relatively constant along the estuarine gradient. One noteworthy characteristic of this representation was the large reduction in carnivorous species between sites 4 and 5. The percentage of the total individuals in each category at a site showed very definite changes along the estuarine gradient (Fig. 18b).

The carnivores, which accounted for 13-23% of the individuals at the lower four sites, never reached the 2% level at the upestuary sites. The most abundant carnivore at the downestuary sites was Diadumene leucolena. Some other abundant predators at the downestuary sites were the polychaetes Pseudeurythoe sp., Eteone heteropoda and Glycinde solirarla, the nemertean Zygonemertes virescens and the ectoparasite Odostomia impressa. Upestuary predators included Stylochus ellipticus, nemertean species d, Rhithropanopeus harrisi and Gobiosoma bosci. Omnivores, of which Nereis succinea was the most abundant, maintained a relatively constant level of relative importance across the sites, while the non-selective deposit feeders were less important at the upestuary sites reflecting the decreased abundance of Peloscolex spp. and Heteromastus filiformis relative to their population levels at the downestuary sites. Selective deposit feeders, exemplified by Streblospio benedicti and Polydora ligni, were the most abundant feeding type at site 1 but decreased steadily to site 4 and, except at site 6, never supplied more than 4% of the individuals at sites 5-8. At site 1, only 13% of the individuals, largely Molgula manhattensis, were classified as suspension feeders. This percentage increased in an upestuary direction concordant with the increasing importance of Balanus improvisus, and at the upestuary sites suspension feeders accounted for over 60% of the individuals. Trophic unevenness increased in an upestuary direction, with the largest change occurring between sites 4 and 5.

The number and percentage of species in the five purchase types repeated the pattern of previous analyses (Fig. 19a). There was a parallel decline in the number of species in each category, with the exception of the shell-borers, which remained constant. Tube-dwelling infauna was the most abundant purchase type at site 1 reflecting the high population levels of S. benedicti found there (Fig. 19b). This category decreased in importance upestuary, however, and was never more than 8% of the individuals at the upestuary sites where N. succinea and H. filiformis were the most abundant members. Free infauna reached its maximum importance at site 1 but there was no distinct pattern in its abundance at other sites. Shell-boring fauna was slightly more important at the four downestuary sites than it was upestuary and the same was true for the motile epifauna. The purchase type with the greatest change along the estuarine gradient was the attached epifauna which, lead by B. improvisus, increased in dominance moving upstream and was the overwhelming dominant at the four upestuary sites.

The oyster reef assemblage has often been characterized as an epifaunal community. To evaluate the validity of this observation the five purchase types can be further generalized into just two groups, infauna and epifauna. Free and tube-dwelling infauna were

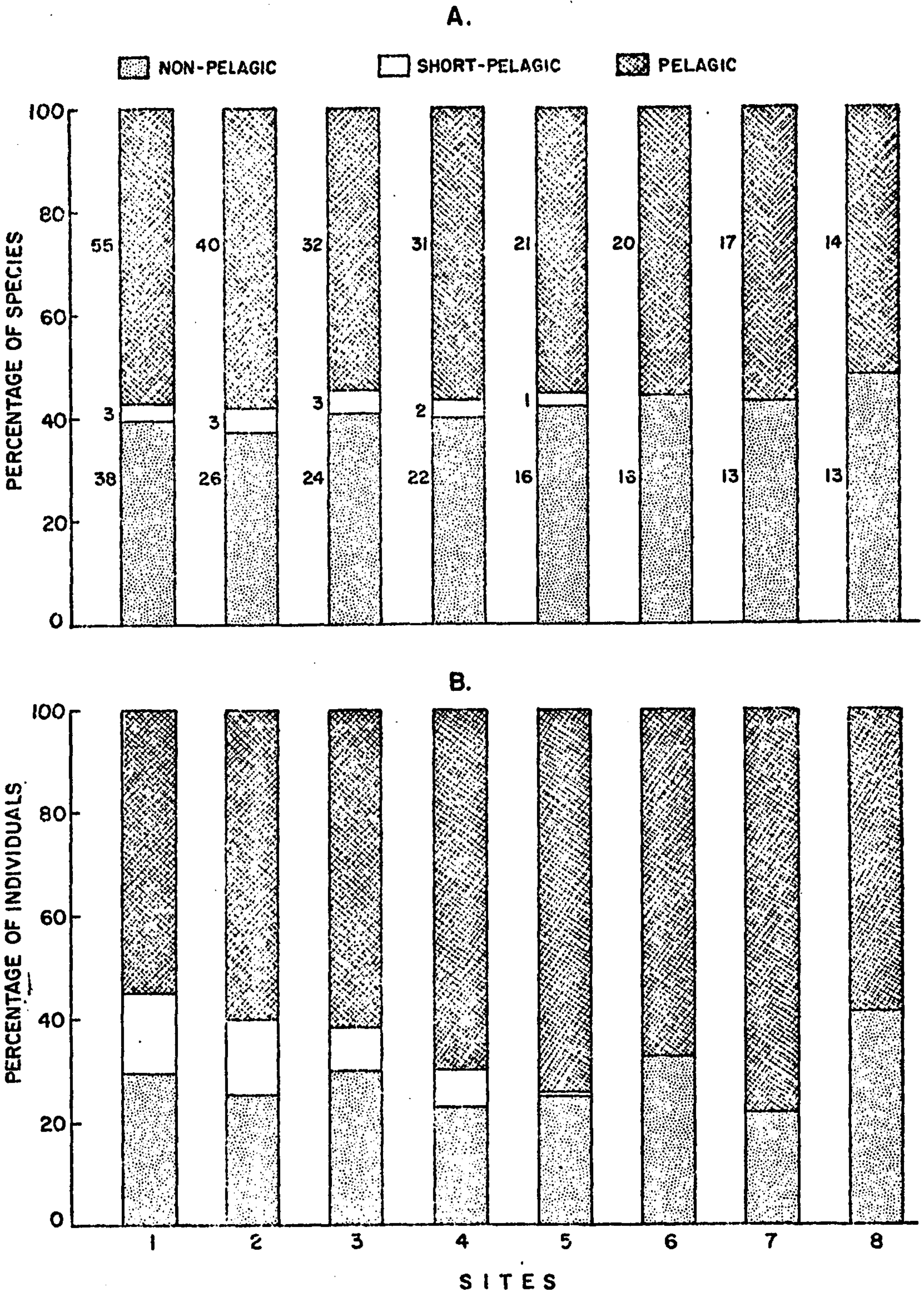
Figure 19. Distribution of purchase types along the estuarine gradient; a) the number and percentage of species in each category, b) the percentage of individuals in each purchase type.


A.
MOTILE EPIFAUNA
SHELL BORING
FREE INFAUNA
ATTACHED EPIFAUNA
TUBE-DWELLING INFAUNA
PERCENTAGE OF SPECIES
100
80
60
40
20
0
22
19
3
10
42
8
16
3
14
28
6
11
3
11
28
4
12
3
8
28
6
6
3
8
15
5
6
4
6
15
4
4
3
6
13
4
3
3
6
11
B.
PERCENTAGE OF INDIVIDUALS
100
80
60
40
20
0
1
2
3
4
5
6
7
8
SITES

lumped to represent infauna, while the epifauna includes the three remaining purchase types. This analysis does not include the 17 colonial species collected, all of which are epifaunal in habit. At site 1 the 43% of the species in the infaunal category was the largest percentage achieved by this group. There was a slight trend of declining number of infaunal species in an upestuary direction. Considering the percentages of individuals, site 1 is the only site where infauna was dominant and there was a marked decrease in an upestuary direction with the infauna accounting for only about 11% of the individuals at sites 7 and 8.

The number and percentage of species in each of the three designated dispersal types is shown in Fig. 20a. The short pelagic dispersal type did not occur above site 5 and there was a slight upward trend in the percentage of nonpelagically dispersing species in an upestuary direction. Although site 8 had the highest proportion of nonpelagically dispersing individuals, the trend of increasing nonpelagic dispersal was not consistent (Fig. 20b). In fact, the percentage of pelagically dispersing individuals increased up to site 5 and the average proportion of nonpelagically dispersing individuals was almost identical between the four downestuary and four upestuary sites.

Figure 20. Distribution of larval dispersal types along the estuarine gradient; a) the number and percentage of species in each category, b) the percentage of individuals in each purchase type.


A.
NON-PELAGIC
SHORT-PELAGIC
PELAGIC
PERCENTAGE OF SPECIES
100
80
60
40
20
0
55
3
38
40
3
26
32
3
24
31
2
22
21
1
16
20
16
17
13
14
13
B.
PERCENTAGE OF INDIVIDUALS
100
80
60
40
20
0
1
2
3
4
5
6
7
8
SITES

DISCUSSION

DENSITY AND DIVERSITY

The presence of accumulated shells of Crassostrea virginica and associated molluscs increases both the complexity and amount of space available for utilization in an environment. Other investigators (Barnes, Coughlan and Holmes, 1973) have shown that the response of the biota to this increased spatial heterogeneity is an increase in both density and diversity over that exhibited in a similar unshelled environment. Sanders (1968) explained the higher diversity of sand bottom fauna, relative to mud fauna from the same given area, on the basis of the increased microhabitat diversity found in the sandy substrate. The phenomenon of density increasing with diversity does not hold with the mud-sand contrast, however, as the lower diversity mud is often more densely populated.

A well established hypothesis in ecology (Segerstrale, 1957) notes that a decline in diversity along an environmental gradient in the direction of increasing stress is accompanied by an increasing number of individuals. In other words, density and diversity are often inversely related along a stress gradient as in the mud-sand example cited above. Other examples of this phenomenon include the latitudinal and littoral gradients of density and diversity. An estuarine gradient also represents such a stress gradient and the decrease in number of species in a landward direction in an estuary has been documented (Wells, 1961).

Diversity does decrease in an upestuary direction on the James River oyster reefs, but a corresponding pattern of increasing density was absent. Obviously, the multiplicity of factors in an estuarine situation are compounded in this case by the involvement of substrate complexity. Because of these factor interactions, it is not possible to draw inferences on the effect of the estuarine gradient on the density of oyster reef macrofauna.

The principal factor responsible for the density levels observed is probably the quality of the shell surface exposed at each site. Sites 3 and 7, which exhibited the highest faunal densities, were characterized by hard shell bottoms, shallowness and strong currents. The action of the current probably prevented siltation, thereby maintaining a larger proportion of the shell surface clean and utilizable by the fauna. It is also possible that the currents maintained a deeper oxygenated layer in the sediments at these sites, which would serve to increase the space available to infaunal species and even to make shell layers below the top available to epifauna. Although the volume of shell material recovered at other sites was greater than at sites 3 and 7, the majority of this material was buried shell, as evidenced by its blackened color, and was not available for colonization.

The explanation for the very low density and relatively high diversity at site 6 lies in the fact that between and under this site's scattering of shells is a fine sand substrate. As noted above, stable sands are characterized by low density and high diversity.

The five downestuary sites showed density peaks in the spring because species with northern affinities, which normally spawn in the summer in the central portion of their ranges, spawn in the Chesapeake Bay region in the spring, and sometimes again in the fall, when water temperatures are optimal. Common species which exhibit this pattern include the acorn barnacle, Balanus improvisus, the soft-shell clam Mya arenaria, and the polychaete Streblospio benedicti. Four sites experienced secondary density peaks in the fall.

Density declined at all sites, except site 8, between the spring and summer sampling periods. A decline after an intensive period of larval setting is probably a general phenomenon as physical and biological factors come into play which ameliorate population eruptions. The physical, density independent, factors may have been more important than usual during the summer of 1972 because of the freshet caused by Tropical Storm Agnes.

The absolute density of the fauna of the James River oyster reefs was decidedly higher than that found on estuarine soft-bottoms. The densities of from 2,395 to 125,573 individuals/m^2 exceed those reported from any other Chesapeake Bay habitat. The previous high of 32,913/m^2 was reported by Orth (1973) from an eelgrass bed near the mouth of the James River. For comparative purposes, maximum values reported from other estuarine benthic studies include 8,865/m^2 in Hampton Roads (Boesch, 1973), 1,365/m^2 in Moriches Bay, New York (O'Connor, 1972) and 629/m^2 in the Pamlico River Estuary, North Carolina (Tenore, 1972). The latter study was conducted in a salinity regime similar to that of this study.

Above site I, the patterns of the components of informational diversity, species richness and evenness, indicate that the evenness distribution parallels that of diversity very closely, while the distribution of species richness does not. Thus within the mesohaline and oligohaline habitats studied, evenness variations are responsible for the within-habitat differences in species diversity. Site I, near the upper salinity boundary of the mesohaline zone, had a seasonal pattern of species diversity which seemed to be more closely related to changes in species richness than to evenness. This conclusion is consistent with the conclusions of Boesch (1972) for the polyhaline and euhaline zones.

An appreciation of the nature of the species occurring in the upper reaches of estuaries is necessary to understand why diversity patterns in these regions should be controlled by evenness distributions. Estuaries become more physiologically stressful and unpredictable in a landwards direction from the sea to freshwater, causing a progressive diminution of species with increasing distance up the estuary. As salinity lowers and it and temperature, among other factors, become more unstable, fewer species can establish viable populations. The upper reaches of the world's estuaries are populated by eurytopic species, opportunists, whose physiological plasticity allows them to take advantage of this instability to escape competitive and predative pressures from more specialized, but stenotopic species. The species with this capability are limited in number. Their wide range of environmental tolerances has permitted them to have wide distributions, e.g. *Macoma balthica*, *Mya arenaria*, *Nereis succinea*, *N. diversicolor*, Corophium lacustre and C. volutator, to name just a few. Indeed, many of these nonspecialized opportunists are often labelled as "pollution indicators" although, in estuaries, they are the normal residents.

Species with the potential of colonizing the mesohaline, and especially the oligohaline, region of the James River are few. Other species with the potential to colonize this region are located in similar regions of other estuaries. The upper reaches of estuaries are separated from one another by distances and complex hydrological conditions which make seasonal range extensions of mesohaline and oligohaline fauna between estuaries difficult. Other circumstantial evidence to support this hypothesis included the fact that pelagic dispersal stages of estuarine organisms are usually reduced in time relative to that of marine species (Carriker, 1967) and, in order to travel from one mesohaline zone to another, the larvae have to pass through areas of high predation. Hence, the upper reaches of estuaries are populated by a limited suite of species which is seldom subsidized by seasonal range extensions. This means that the number of species seasonally remains fairly constant and the pattern of dominance, i.e. evenness, of these few species will have the controlling effect on informational species diversity. The results of this study support this hypothesis.

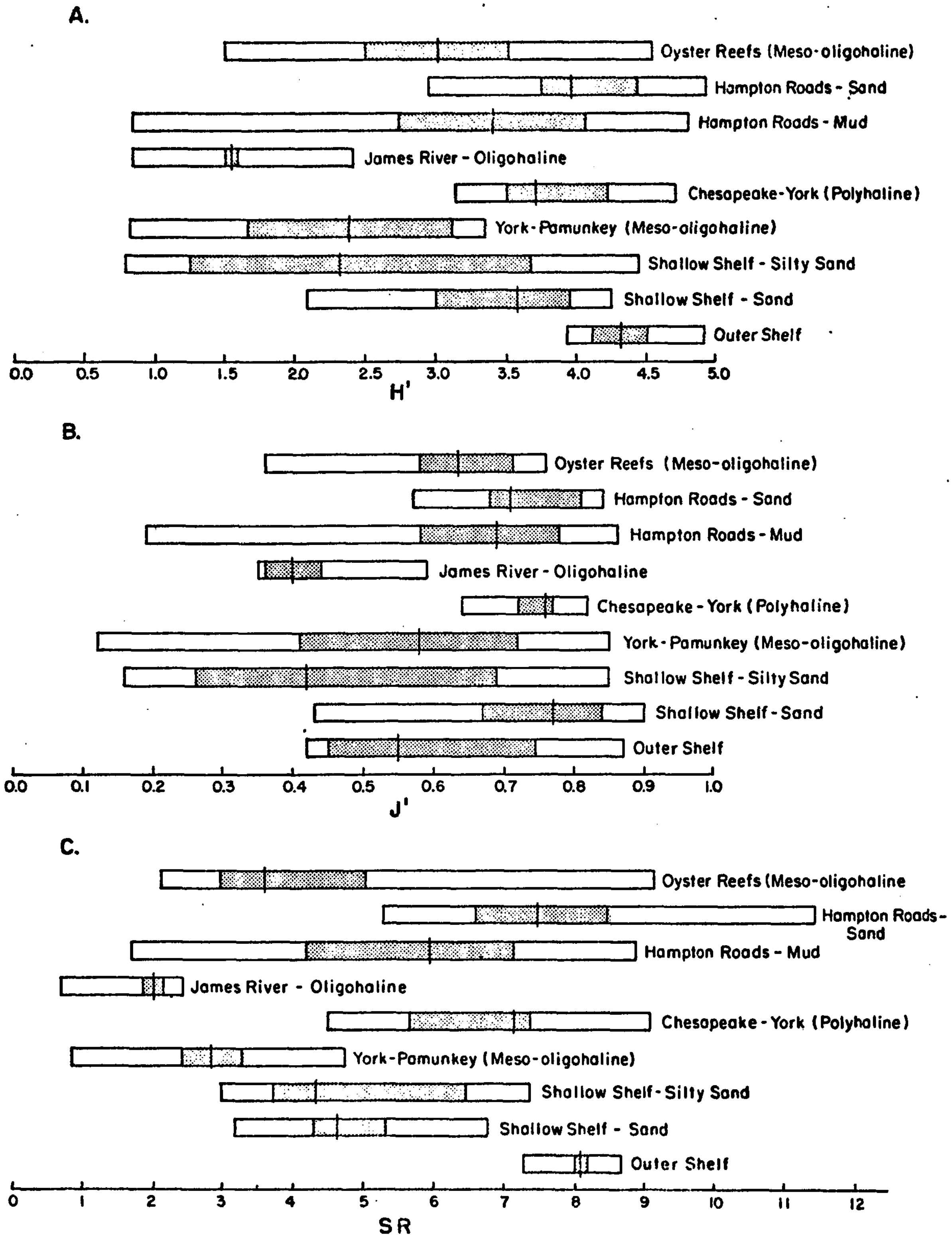
Seasonal patterns of informational species diversity were not as pronounced as those found for density. Sites 2 through 8 experienced a decrease in diversity between the winter and spring sampling periods, undoubtedly precipitated by a decline in evenness, which was caused by the prolific spring larval set. The six most upestuary sites showed an increase in diversity by summer as the population eruptions of spring were attenuated by physical and biotic factors causing an increase in evenness. The loss of informational diversity observed only at sites 1 and 2 after Tropical Storm Agnes was caused by a decline in the species richness component as a result of the loss of species excluded by salinity reduction.

Boesch (1973) presented a hypothetical model of seasonal behavior of species diversity, evenness and species richness of faunal assemblages on sand and mud bottoms in Hampton Roads, i.e. the polyhaline zone of the James River Estuary. An attempt was made to construct an analogous model for the mesohaline zone of this estuary based on the data collected from the oyster reefs. The great variation between the sites precluded the construction of a satisfactory predictive model. The most concordant behavior of the sites was the decline in diversity in the spring followed by a rise in summer.

The greatest structural stability during the course of this study was exhibited by site 8, the site with the least environmental stability. This is consistent with Copeland's (1970) hypothesis that communities adapted "to energy-requiring stresses are more likely to resist changes than those adapted to relatively constant environments." Structural stability did not increase monotonically along the estuarine gradient, however, and site 7 had the second highest range of species diversity and evenness.

A comparison of the levels of informational diversity and its components has been made between several Virginian soft-bottom environments and the James River oyster reefs (Fig. 21). The effect of the

Figure 21. Comparison of observed community structure statistics with those of other studies in the Virginia region; a) species diversity, b) evenness, c) species richness. Crossbar is median, hatched area the central quartiles and unhatched area the outer quartiles. Values are derived from Boesch (1972, 1973).


A.
Oyster Reefs (Meso-oligohaline)
Hampton Roads - Sand
Hampton Roads - Mud
James River - Oligohaline
Chesapeake-York (Polyhaline)
York-Pamunkey (Meso-oligohaline)
Shallow Shelf - Silty Sand
Shallow Shelf - Sand
Outer Shelf
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0 4.5 5.0
H'
B.
Oyster Reefs (Meso-oligohaline)
Hampton Roads - Sand
Hampton Roads - Mud
James River - Oligohaline
Chesapeake - York (Polyhaline)
York - Pamunkey (Meso-oligohaline)
Shallow Shelf - Silty Sand
Shallow Shelf - Sand
Outer Shelf
0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
J'
C.
Oyster Reefs (Meso-oligohaline
Hampton Roads - Sand
Hampton Roads - Mud
James River - Oligohaline
Chesapeake - York (Polyhaline)
York-Pamunkey (Meso-oligohaline)
Shallow Shelf - Silty Sand
Shallow Shelf - Sand
Outer Shelf
0 1 2 3 4 5 6 7 8 9 10 11 12
SR

great spatial heterogeneity found on the oyster reefs on the faunal diversity can be seen by comparing the diversity values from the reefs to others from similar salinity regimes. Not only is the median reef diversity higher than would be expected based on their location in the estuary, but the maximum values exceed all others except the polyhaline and outer continental shelf areas. Factors controlling diversity in these other areas are discussed by Boesch (1972). The evenness values exhibited by the oyster reef samples compared favorably with all the other regions. The 75th percentile of evenness values overlapped the central quartiles of all the higher salinity areas save the Chesapeake-York polyhaline zone. The high level of habitat diversity also had an influence on the species richness component as the maximum oyster reef species richness value exceeded that of all other areas except the Hampton Roads sand biotope. These high levels were only experienced at site I, however, and, in general, the oyster reefs exhibited species richness values not much greater than those shown by soft-bottom assemblages from similar salinity regimes. This is a further indication of the overriding influence of reduced salinities in limiting the number of species which can colonize the upper reaches of estuaries.

CONTROL OF SPECIES DISTRIBUTIONS

It is apparent that the density and diversity patterns exhibited are of a complex nature. The actual abundance pattern realized by a species at a given estuarine location is principally the result of an interaction of an upstream increase in salinity stress, a downstream increase in competition and predatory stresses and substrate conditions.

There are, of course, countless more subtle factors at work. In terms of Sander's stability-time hypothesis an estuary is more biologically accommodated in a downestuary direction and more physically controlled upestuary. Since both density and diversity are influenced by the factors controlling the distributions of individual species, it would be informative to speculate on these factors in the context of the more abundant species.

Streblospio benedicti experienced population gains in winter and spring at sites 1 and 2, and by spring it was the numerical dominant at both sites. The number of individuals present at these two sites in the fall and spring was very low. At sites 3 and 4 a much less intense winter-spring population enhancement occurred but the fall and summer population levels were actually higher than those at sites 1 and 2. This peculiar distribution can be explained by an interaction between the salinity and biotic factors. S. benedicti is limited by salinity since only four individuals were found above site 4. However, biotic factors are less intense at sites 3 and 4 than at sites 1 and 2 allowing greater survival of spring populations into the summer and fall. In 1972 this effect would probably have been even more pronounced had it not been for the Agnes freshet.

Dean (1965) reported S. benedicti spawning in the Mystic River Estuary, Connecticut from June to October. My results suggest that, in the Chesapeake Bay, it spawns from February to June, although spawning may have been interrupted in June 1972, and the normal situation could be for it to spawn continuously from February into the fall.

Polydora ligni, perhaps the most abundant polychaete in the

Chesapeake Bay (Orth, 1971b), showed a definite winter-spring population increase at sites 1 and 2, but at sites 3 and 4 no significant increase was noted until spring. Low salinity at the latter sites probably prohibited recruitment until after the March sampling. P. ligni was much less abundant at the four upestuary sites, where there was an increase in abundance in the summer. Salinity was highest then, allowing colonization from late spawners from downestuary. Populations observed there in the fall (December) represent the survivors of the late 1971 set protected from biotic pressure.

The shell-boring congener of P. ligni, Polydora websteri, reached its maximum abundance at sites 2, 3 and 4. Scarcity of one of its preferred substrates, live oysters, and perhaps increased biotic pressure, may have caused its lack of abundance at site 1. Above site 4, P. websteri showed a pattern of abundance almost identical to that of P. ligni. P. websteri did not show the extreme seasonality of P. ligni and it is possible that this species spawns on a year around basis as in Louisiana (Hopkins, 1958).

Boccardia hamata, the fourth spionid considered was most abundant at the upestuary sites suggesting that it is competitively inferior to the closely related, and ecologically similar, P. ligni and P. websteri. B. hamata was able to establish itself in great numbers at the downestuary sites in summer when P. ligni and P. websteri declined indicating competitive exclusion confined it to the upestuary sites in the pre-Agnes period. B. hamata is a summer spawner on both the east and west coasts (Dean and Blake, 1966) which explains the seasonal abundance pattern exhibited during the present study.

The nereid *Nereis succinea* was ubiquitous, being found at all sites in all seasons. It seemed to be equally successful at all sites except 6; its sandy substrate apparently was not suitable. A similar ubiquity was noted by Tenore (1972) for *N. succinea* in the Pamlico River, North Carolina. Hanks (1968) and Tenore (1972) both found that *N. succinea* spawns in the spring. In the James River, *N. succinea* showed no pronounced seasonal distribution which would indicate the presence of a definite spawning period. Sexual epitokes are seen swimming throughout the warm period of the year, especially during August, September and October (C. P. Mangum, pers. comm.).

The capitellid *Heteromastus filiformis* was also present at all sites in all seasons. Above site 4, however, it was present only in reduced numbers indicating that salinity was not optimal in that region of the estuary. *H. filiformis* did not exhibit an obvious seasonality. It could have been affected by the Agnes freshet in late June as there was a slight decline in its population between spring and summer. This result takes on added significance in light of Tenore's (1972) finding that *H. filiformis* was most abundant in summer.

As noted previously, *Peloscolex* spp. contains at least two species, *P. gabriellae* and *P. heterochaetus*. At sites 1 and 2 *Peloscolex* spp. were most abundant in the winter and spring samples, while elsewhere fall and winter were usually the seasons of greatest abundance. Site 6 was the site with the lowest density of *Peloscolex*, reflecting preference for finer substrates. Population levels of *Peloscolex* were low in summer, especially at sites 1 through 5, indicating that salinity, at least in some cases, could be a limiting factor.

The barnacle Balanus improvisus reproduces very prolifically in the spring and usually maintains high population levels throughout the year at the upestuary sites. The actual density exhibited at a site, of course, is related to the amount of hard substrate available. At site 1, not one individual was found until the spring set added a few. Sites 2, 3 and 4 were sparsely populated until spring when there was a heavy covering of all available space, especially at sites 3 and 4. The salinity reduction caused by runoff from Tropical Storm Agnes undoubtedly gave the young barnacles at sites 1-4 some relief from biotic pressures allowing a larger than normal crop to survive the summer. The very low salinities experienced at sites 5-8 during the summer of 1972 probably had an adverse effect on the barnacle population, allowing relatively few individuals to survive until September at these sites.

The flatworm Stylochus ellipticus had a distribution well correlated to that of B. improvisus reflecting their predator-prey relationship (Landers and Rhodes, 1970). This is especially true at the four downestuary sites, whereas upestuary salinities apparently limited S. ellipticus. The higher salinities of September, however, allowed a few individuals of S. ellipticus to be present at all the upestuary sites.

The amphipod Melita nitida occurred at all sites but its center of distribution was at sites 3 and 4. The downestuary population decline was apparently due to biotic factors, while salinity stress may have limited population size above site 4. Bousfield (1973) reported this species to be often associated with the bases of hydroids and ectoprocts. Neither of these groups, however, were abundant enough to relate the distribution of M. nitida to them. Dependence on a fine substrate is suggested by its low abundance at the sandy site 6.

The tube-dwelling amphipod Corophium lacustre is a dominant species in Chesapeake Bay estuaries having a salinity distribution ranging from 25 0/00 to almost fresh water (Bousfield, 1973). On the James River oyster reefs, the distribution of C. lacustre can be explained by downestuary biotic pressures. Its greatest abundance was at the up-estuary sites, especially sites 7 and 8, with few individuals occurring at sites 1-4 in the pre-Agnes period. The summer breeding period of C. lacustre (Bousfield, 1973) coincided with the reduced summer salinities in 1972 and hence it was able to establish itself on the lower sites, especially 2 and 3, in the absence of severe biotic pressure. At the same time, lower than usual salinity conditions at sites 5-8 throughout much of the summer may have inhibited the development of maximal populations at these sites.

The isopod Cassidinidea lunifrons was apparently excluded by biotic pressures from site 1, but high densities were found, at least at certain times, at all other sites except site 6. The low population levels at site 6 and the pattern of distribution at other sites suggest that C. lunifrons is dependent on the hard substrate provided by shells.

The soft-shell clam Mya arenaria reproduces in the Chesapeake Bay region in both spring and fall but both sets are usually decimated in the summer by predation or physiological stresses (J. Lucy, pers. comm.). A fall set was evidenced in this study by the abundance of young clams found in the winter samples. These populations were significantly reduced by spring and no spring recruitment was observed. By the end of summer only six individuals were found. At least part of this decline can probably be assigned to the stresses associated with Tropical Storm Agnes. Only a few large individuals were ever found. The upestuary distribution was very definitely limited by salinity as not one individual was found above site 4.

The hooked mussel Brachidontes recurvus, although it appeared at all sites, was most abundant on the hard-bottomed upestuary sites. Low abundance at the higher salinity sites, expecially site 1, indicates that its downestuary distributional limit was controlled by biotic pressure. After the downestuary dimunition of biological stresses by Tropical Storm Agnes, B. recurvus was able to colonize sites 2, 3 and 4 in significant numbers.

Congeria leucophaeta, an estuarine endemic bivalve, was very severely limited in its downestuary distribution by predation and/or competition. It showed a very marked seasonal pattern of distribution which was probably accentuated by the relaxation of biological stresses caused by Tropical Storm Agnes. Only eight individuals were found in the pre-Agnes period at sites 7 and 8. After Agnes, C. leucophaeta was found at the five most upestuary sites, with large populations observed at sites 5, 7 and 8.

The distribution of the pyramidellid, Odostomia impressa was controlled by salinity, only occurring infrequently above site 4. The O. impressa population was decimated by the Agnes freshet with only 20 individuals being found at sites 1 and 2 in the post-Agnes period. As O. impressa has nonpelagic larvae it will undoubtedly be some time before it regains its upestuary density.

The tunicate Molgula manhattensis exhibited a distribution almost completely opposite that of *C. leucophaeta*. Only two individuals were found at site 1 before the Agnes freshet. By September, *M. manhattensis* was present at sites 1-4 with dense populations at sites 1 and 2. The combination of a summer reproductive period with restored salinities over relatively clean shell surfaces contributed to successful recruitment, accentuating the normally great seasonality (Andrews, 1973).

The anemone, *Diadumene leucolena*, occurred at sites 1 through 4, being limited upestuary by salinity stress. The high population levels observed in the fall of 1971 indicate a summer or early fall reproductive period. The stress of the Agnes freshet however, greatly reduced the population in the summer of 1972 and abundance of this species will probably be below normal for at least a year. This result is in contrast with the conclusion of Andrews (1973) who states: "The whitish sea anemone (*D. leucolena*) is tolerant of wide ranges of salinities, and specimens were exceptionally large and abundant on all substrates in the post-Agnes period."

Of the 18 species reviewed, eight had distributional patterns indicating their penetration upestuary was limited by salinity. These species are: *S. benedicti*, *P. ligni*, *H. filiformis*, *S. ellipticus*, *M. arenaria*, *O. impressa*, *M. manhattensis* and *D. leucolena*. Only the upestuary tails of their distributions were seen in this study and they are probably successful on a much broader salinity range.

Six species, *B. hamata*, *B. improvisus*, *C. lacustre*, *C. lunifrons*, *B. recurvus* and *C. leucophaeta* had centers of distribution in the upper reaches of the estuary and decreased in abundance in a downestuary direction. Their eurytolerance allowed them to withstand the physiological stress of this zone and to maintain viable populations, often in high densities, in the absence of the interspecific stresses, predation and competition, characteristic of sites lower in the estuary.

Two other species, P. websteri and M. nitida, showed a diminution of population levels at the lower sites, apparently in response to biological factors, as well as a reduction at the upper sites corresponding to reduced upestuary salinity, thus the peaks of abundance occurred in the center of the mesohaline zone.

A fourth type of distribution pattern was exhibited by N. succinea and Peloscolex spp. which simply were ubiquitous with regard to the salinity gradient. Perhaps N. succinea alone should be considered ubiquitous as the category Peloscolex spp. contains at least two species and I have no data on the distributions of the component species.

The response of these species to the Agnes freshet in June was mixed. In interpreting these results it must be remembered that sampling covered only one yearly cycle, therefore, there is no information on the natural, year to year fluctuations in population levels. Fully realizing the limitations of the data I will try to catagorize the types of responses observed.

Only six of the 18 species experienced a definite population decline between the spring and summer. In the cases of D. leucolena, O. impressa, M. arenaria and Peloscolex spp. the losses were extreme, while those of S. benedicti and H. filiformis were less dramatic. M. arenaria and D. leucolena also suffered range contractions. A summer decline in abundance of M. arenaria is a normal occurrence in the Chesapeake Bay region as noted above. The population reductions experienced by the other species showing this type of response, however, were probably more directly related to the very low salinities of the immediate post-Agnes period, as four of them had previously exhibited limited upestuary penetration.

The second category of response was that shown by *B. hamata*, *C. leucophaeta* and *M. manhattensis*. These species registered remarkable population gains in the summer samples and the latter two also experienced range extensions. This was made possible by the coincidence of their reproductive periods, the recovery of salinity levels, and the space opened by the decline of many shell-fouling species.

B. improvisus, *C. lacustre* and *B. recurvus* exhibited a third category of response characterized by an atypical, relatively high abundance at the four downestuary sites, coupled with a relatively low abundance at the four upestuary sites. A relatively high proportion of the spring set of *B. improvisus* evidently survived at the downestuary sites because the decrease in salinity reduced biotic stress, while at the upestuary sites salinity was limiting for much of the summer, resulting in abnormally low population levels. On the other hadd, *C. lacustre* and *B. recurvus* probably set after the freshet peaked. They opportunistically flourished in the open space on the downestuary sites whereas upestuary suboptimal salinities limited recruitment.

The two species of *Polydora* exhibited a fourth response pattern to the freshet characterized by a relatively high abundance at the upestuary sites with a below normal population at the downestuary sites. Larvae of *P. websteri* are found in the water column throughout the year in Louisiana (Hopkins, 1958) and from April to August in Maine (Blake, 1969a) so it appears safe to assume that *P. websteri* reproduces throughout much of the year in the Chesapeake Bay region. Orth (1971b) demonstrated that the peak of *P. ligni* reproduction occurs in the spring, but significant numbers of larvae were still found at the end of May. Larvae of this species occur in Maine waters through the end of September (Blake, 1969a). *P. ligni* may reproduce throughout the warm period of the year as was found for the European species *P. ciliata* (Daro and Polk, 1973). Indeed, Daro and Polk (1973) found that three to four generations of *P. ciliata* are normally produced each year with generations after the first not showing heavy settlement because of larval mortality and interspecific competition. Hence, both common species of *Polydora* found in this study undoubtedly have a potential for recruitment that lasts at least through the summer months.

The occurrence of the freshet effectively interrupted recruitment of *Polydora* in the study area. This may have been caused by the cessation of adult spawning, increased larval mortality, or a combination of both. Before successful recruitment was re-established much of the space on the lower four reefs was utilized by more tolerant species, e.g. *B. recurvus* and *C. lacustre*, or by species with well-timed reproductive cycles, e.g. *M. manhattensis* and *B. hamata*. Salinities at all sites were at yearly highs by late summer which put the upestuary sites within the optimal salinity range of the *Polydora* species. As *Polydora* recruitment resumed, the larvae were relatively more successful in settling at the upestuary sites than at the more heavily fouled downestuary sites.

The flatworm *S. ellipticus* suffered a population loss, while experiencing a range extension, between June and September which can be considered a modified category 4 response.

A fifth category of response was no significant change. If the species which exhibited this response N. succinea, M. nitida and C. lunifrons, were affected by the freshet, the sampling design was not adequate to demonstrate it.

DISTRIBUTION OF MAJOR TAXA

The percentage distribution of individuals among the major taxa changed along the estuarine gradient while the proportion of species in each group remained relatively constant, without a clearcut change in total density. The change in numerical dominance was from annelids, at the lower end of the estuarine segment surveyed, to arthropods at the upper end. The arthropods were also the most diverse group on the oyster reefs.

Comparisons of the proportions of species in major groups from seven recent estuarine studies (Table 17) indicates that no generalizations can be made about the relative diversity of taxa. In two studies (Boesch 1973, Sanders et al. 1965) annelids were represented by more species than any other group, in two studies (Tenore 1972, Wells 1961) molluscs were the most diverse, in one (Maurer and Watling, 1973) molluscs and arthropods were equally represented, and in two others (Marsh 1973, present study) the arthropods were the most speciose. The most consistent difference between these studies is the relative importance of "others" in habitats which provided a firm substrate for fouling organisms, e.g. oyster shells (Wells 1961, Maurer and Watling 1973, present study) or eelgrass (Marsh, 1973).

Table 17. Percentage of species in each of four taxonomic categories from recent estuarine studies.

Author	Annelids	Molluscs	Arthropods	Others
Boesch (1973)	33.9	25.0	27.4	13.7
Larsen (this study)	25.4	22.5	28.9	23.2
Marsh (1973)	18.0	23.0	40.0	19.0
Maurer and Watling (1973)	15.0	30.1	30.1	24.8
Sanders et al. (1965)	44.7	14.9	27.7	12.8
Tenore (1972)	28.6	45.7	11.4	14.3
Wells (1961)	13.9	32.7	25.1	28.4

The major taxa found in benthic estuarine investigations is influenced by several factors, probably not the least of which is the method of sampling and care of processing employed. While the present study has shown that the various higher taxonomic categories decrease in species richness roughly in parallel fashion within the salinity regime sampled, it cannot be said that this pattern holds for the entire estuarine gradient.

The above comparisons only demonstrate how the species are distributed among the major taxa and give no indication of the numerical success of the species and higher taxa involved. This information may be gleaned from an examination of how the individuals are distributed among the major taxa. Recently, two other investigators have employed the distribution of individuals among major taxa in their analyses of benthic systems. Massé (1972) was able to attribute changes in the relative abundances of higher taxa to differences in wave exposure and trophic conditions in several shallow water areas on the French Mediterranean coast. In the other study, the distribution of individuals among the higher taxa was related to the fineness of the sediment (O'Connor, 1972). Neither of these studies involved a salinity gradient.

Data presented by Tenore (1970) can be modified for the purposes of comparison. This study in the Pamlico River Estuary, North Carolina is not ideal for comparison because, unlike the James River Estuary, this estuary is stressed over its entire length by high temperatures, low oxygen and unstable sediments (Tenore, 1970) which probably override some of the effects of the salinity gradient. The benthic community is characterized by low diversity and significant seasonal cycles.

Nevertheless, if the spring samples are excluded, because of the obvious dominance of postsettlement juvenile molluscs, there was an upestuary increase in the relative abundance of arthropods (Table 18) principally due to insect larvae and the isopod Cyathura polita. Annelids maintained a relatively constant percentage above the most downestuary transect, molluscs declined slowly in importance in an upestuary direction, although they were the dominant group, and the group of other taxa declined upestuary. The increasing importance of arthropods and declining importance of "other" taxa, in an upestuary direction, are the two points of similarity between Tenore (1970) and the present study.

The increasing importance of arthropods in an upestuary direction is due to completely different species in the Pamlico and James Rivers; a larval insect and an isopod in the Pamlico River and the barnacle Balanus improvisus and amphipod Corophium lacustre in the James River. Combining this fact with the lack of agreement on the distribution of annelids and molluscs along the gradients makes it appear that there is very little evidence to support a hypothesis of a general pattern of higher taxa distribution in estuarine regions. Rather the parallel decline of species in the higher taxonomic categories considered in the present study, and the few abundant species responsible for the trends observed, suggest that the higher taxonomic category dominant in the upper reaches of an estuary is determined by that species, or few species, most favored by the environmental conditions in that particular estuary.

Table 18. Percentage of number of individuals in each major taxon with distance upestuary. Modified from Tenore (1970).

	Transect			
Taxon	1	2	3	4
Annelids	19.4	39.9	35.5	36.8
Molluscs	61.8	55.2	50.7	36.2
Arthropods	0.9	1.4	10.4	27.0
Others	17.9	3.5	3.1	0.0

DISTRIBUTION OF FEEDING TYPES

Feeding behavior is extremely basic to a species survival, and also affects the nature and stability of faunal communities (Heatwole and Levins 1972, Levinton 1972, and Jones 1973). The distribution of species among various feeding types has been considered in two previous estuarine investigations. In three British estuaries, Alexander, Southgate and Bassindale (1935) found that the number of suspension and deposit feeding species declined in parallel along the salinity gradient to a point where neither existed. In the present study there also was a parallel decline in the number of species in each feeding type but the numbers never dropped to zero.

Wolff (1973), in his monograph on the ecology of the estuaries in the Delta region of the Netherlands, examined the distribution of species in seven feeding types along the estuaries. He found a distribution of species analagous to the trends shown by number of individuals in the present study. That is, deposit-feeders dwindle toward freshwater, while suspension feeders increase in importance from the sea all the way to nontidal freshwater, and predators experience a minimum in the brackish water area.

The fundamental differences in the results of these three studies indicate that conclusions based on feeding type distributions in estuarine areas (Jones, 1973) should be made very cautiously.

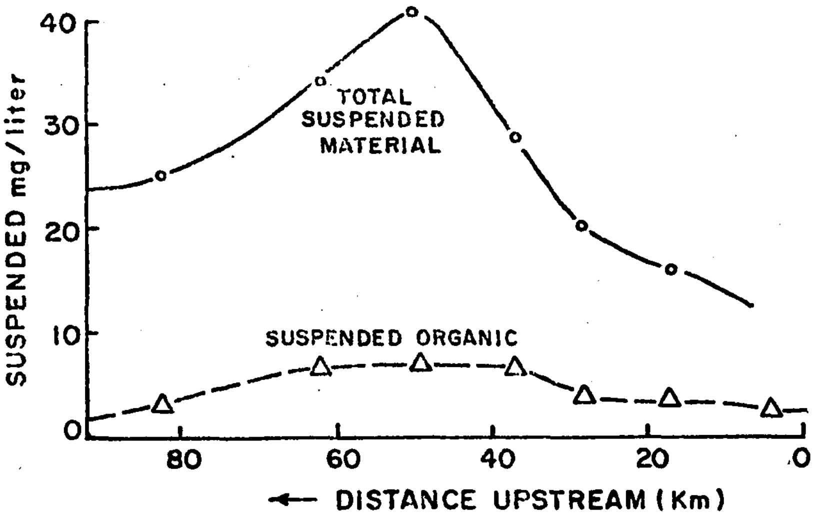
What underlying environmental factors control these distributions is not clear. The uniform sedimentary nature of the biotope studied in the James River allows us to dismiss trophic group amensalism (Rhoads and Young, 1970) and substrate characteristics (Sanders, 1958) as mechanisms of control.

Pearson (1971) found no statistical correlation between sediment type and the distribution of suspension and nonselective deposit feeders, although such a relationship did exist for predators, scrapers and selective deposit feeders. Suspension and nonselective deposit feeders were not found where currents were very weak or very strong, but did occur where they were moderate and decreasing in intensity. These areas could be characterized as areas high in suspended sediment and deposition. His results support those of Nikitin (1971).

The same logic can be used to explain the distribution of suspension feeders in the James River. Nichols (1972) has shown that the levels of total suspended material, and suspended organic materials, is greatest in the upper reaches of the estuary, i.e. above site 4 (Fig. 22). Also the plant debris component decreases in a downriver direction. Nichols attributes these decreases in suspended load principally to dilution of the sediment laden river water with sea water, and not to deposition. Hence, those suspension feeders which can withstand the physiological stresses of the upper estuary are able to be numerically successful because of a rich food resource, while selective deposit feeders, especially those which feed at the surface, may be inhibited by fouling of their feeding mechanism by the suspended load.

Nichols (1972) noted a decline in the organic content of the sediment in a downestuary direction. This decline, however, was slight and irregular, and provides no plausible explanation for the paucity of nonselective deposit feeders at the upestuary sites. Perhaps the organic material in the sediment is in some way not utilizable by deposit feeders.

Figure 22. The distribution of total suspended material and suspended organic material in the James River Estuary. Modified from Nichols (1972).


40
30
20
10
0
SUSPENDED mg/liter
TOTAL SUSPENDED MATERIAL
SUSPENDED ORGANIC
80
60
40
20
0
← DISTANCE UPSTREAM (Km)

Levinton (1972) theorized that infaunal suspension feeders live in a trophically unpredictable environment, relative to infaunal deposit feeders. While the amount of suspended material in the James River Estuary is surely unpredictable due to variations in levels of land runoff, at its lowest levels it is undoubtedly sufficient to maintain a dense suspension feeding population as the river is always noticeably turbid. Furthermore, Nichols' (1972) results indicate that at least the absolute levels of total organic material in the sediments is higher at the upestuary sites than they are downestuary. Hence, this theory is insufficient to account for the trophic distributions observed.

Levinton contends that suspension feeders have populations which fluctuate strongly over time and that they have evolved mechanisms for rapid increase in number, partially in response to the opportunistic appearance of food. These characteristics are not unique to suspension feeders, and indeed during the present study there were deposit feeders whose numbers fluctuated as greatly as suspension feeders. Also, the opportunistic increase in food Levinton refers to is a cyclic increase. A species whose life cycle is geared to a predictable event, be it trophic or other, can hardly be considered to be opportunistic. Although there is much merit in Levinton's hypothesis, it will need extensive field testing before it can be predictively applied.

DISTRIBUTION OF PURCHASE TYPES

The distribution of purchase types along estuarine gradients has also been investigated twice previously. Alexander et al. (1935) found that the importance of infaunal organisms increased in an upestuary direction. Sanders et al. (1965) showed that the interstitial environment is relatively stable in a fluctuating type estuary while epifaunal animals are exposed to limiting salinity stresses. They note that in gradient type estuaries, like the James River, the water salinity changes are unpredictable and of long duration and therefore the sediment salinities follow those of the overlying water. This means that in a gradient estuary, infauna and epifauna are exposed to similar salinity stresses. Therefore, the distributions of these groups cannot be attributed to differences in salinity stresses in their respective microhabitats.

The increasing upestuary dominance of attached epifauna may not be due to an increasing advantage of this type of purchase, but to some secondary relationship. It may be that those species which can withstand the physiological stresses of this area, and which are suspension feeders and can therefore maintain large populations, just happen to be epifaunal in this particular situation, e.g. _Balanus improvisus_. The increased importance of infaunal species downestuary is due partly to the decreasing success of suspension feeders and the increased success of deposit feeders which tend to be infaunal.

DISTRIBUTION OF LARVAL DISPERSAL TYPES

There has recently been renewed interest in mechanisms of larval dispersal. A thorough review of the field by Mileikovsky (1971) and theoretical discussions by Vance (1973 a,b) indicate the increasing sophistication developed in this branch of marine ecology. Practical discussions of larval ecology in environmental situations are contained in Ockelmann (1965), Sanders and Grassle (1971), Stancyk (1973) and Wolff (1973).

The trend of a decreasing number of species with planktotrophic larvae toward the poles is well established (Mileikovsky, 1971) and it now seems apparent that there is a similar trend with increasing depth (Mileikovsky 1971, Sanders and Grassle 1971). Modifications of larval dispersal, away from pelagicism, in the unpredictable polar regions gives the larvae increased independence from erratic planktonic food resources, reduces pressure from planktonic predators and allows the larvae to excape more quickly from variable currents, temperatures and salinities. Mileikovsky (1971) cites other environmental pecularities of the deep sea as reasons for the decreased importance of a pelagic dispersal stage in these regions. Although the environment of the abyssal depths is harsh (Mileikovsky, 1971) it is also constant. In such a biologically accommodated situation the most economical method of dispersal would be the most advantageous, and according to Mileikovsky the most economical method is nonpelagic. One of the major advantages endowed to a species with a pelagic dispersal stage is the ability to take advantage of an opportunity and to recover quickly from a catastrophic population loss. Neither of these would be advantageous to an abyssal species as there are no environmental barriers or catastrophic occurrences.

In estuaries there can be several advantages to nonpelagic development. There are the obvious advantages of nonpelagic development noted above which take on added significance in the estuarine environment. There is also the advantage of not having to depend upon a complex larval behavioral mechanism to cope with the multidimensional current systems. Finally, for a species capable of surviving the physiological stresses of the upper estuary, who has had to sacrifice specialization for genetic variability, there would be little advantage to broadcast great numbers of larvae to areas where they cannot survive the biological stresses. In other words, in this situation, wide dispersal is not an asset and some sort of direct development or at least reduced pelagic development would be beneficial. There is evidence that pelagic stages of estuarine species are shorter than those of euhaline species (Carriker 1967).

Stancyk, (1973) discusses developmental modification along these lines in echinoderms and Wolff (1973) demonstrates the increasing importance of nonpelagic dispersal stages with increasing distance from the sea. In the present study, however, there was only a slight increase in the percentage of nonpelagically dispersing species in an upestuary direction, and no trend at all in the percentage of individuals in each class.

This lack of pattern may only be an artifact as developmental types were assigned from the literature. Mileikovsky (1971) points out that in many groups, especially in polychaetes, there is reporductive type instability at the species level and, in fact, intraspecific changes in larval development can occur seasonally. It is entirely possible that intraspecific changes occur along the estuarine gradient. Generalities to the effect that estuarine animals "are generally characterized by having planktonic larvae" (Grassle, 1967) cannot be taken as truisms.

The results of this study were inconclusive on this matter. However, there seems to be evidence that developmental modifications may take place along the estuarine gradient just as they do along latitudinal and depth gradients. Further research in this area will hopefully be fruitful.

COMPARISON OF CLASSIFICATORY TECHNIQUES

The allocation of sites into groups by the Canberra metric measure was intuitively more satisfying than the groups produced with the Sorensen index and for this reason it was used for all analyses. The Sorensen index, however, did produce groupings of stations that would have been useful had the Canberra metric measure not been available. Thus the worker with discrete data can get the most insight into his data with the Canberra metric index, while the Sorensen index is valuable in analyzing qualitative data.

THE FAUNAL DISCONTINUITY

The results of the classificatory analysis separated the sites into two groups, the downestuary sites 1-4 and those upestuary, 5-8.

It is possible that this discontinuity is an artifact caused by the relatively large distance between sites 4 and 5. If there is a constant change in fauna along the estuary, the distance between sites 4 and 5 would make site 4 seem more similar to the downestuary sites and site 5 more similar to the upestuary sites than site 4 and 5 are to each other. However, in all probability the explanation is more basic than this. The salinity gradient is apparently steepest between sites 4 and 5 and the largest drop in informational diversity and number of species occurs here. The rank score dominance shifted from <u>Peloscolex</u> to <u>Balanus</u> at this point and significant changes occurred in higher taxa dominance and importance of functional types. In short, it would seem that a faunal discontinuity of some type occurs between sites 4 and 5 or at about 10o/oo salinity.

Wass (1972) commented that in the Chesapeake Bay "the faunistic breakpoints seem more likely to occur near 10 and 25 ppt than at the 'Venice System' levels of 5 and 18 ppt". This view was seconded by Andrews (1973). Boesch (1972), however, based on samples from the York River Estuary cites the only precipitous drop in species diversity at the polyhaline-mesohaline border between 17 and 22o/oo.

Historically there has been much discussion as to where faunal breakpoints occur (Segerstrale, 1959), or even if they do occur (Wolff, 1973). Others have placed the oligohaline-mesohaline border at 2o/oo (Valikangas, 1926), 9o/oo (Brunelli, 1933) and 3o/oo (Ekman, 1953 and Remane and Schlieper, 1958). Its location in a given situation depends mostly on the stability of the salinity, i.e. organisms can withstand lower salinity if it is not fluctuating (Bassindale, 1943). Many authors (cf. Segerstrale, 1959) also divide the mesohaline into two subzones at about 8-10o/oo. It is possible that the break observed in the James River represents subzonation of the mesohaline zone and, due to the limited range of sampling, the oligo-mesohaline border was not crossed, i.e. was above site 8.

Another possibility is that the discontinuity has no relation to salinity at all. If this is the case it is not proper to discuss it in terms of standardized salinity regimes. The alternative controlling factor may be physical, rather than physiological in nature, which is suggested by the results of Nichols (1972). Hence the distribution of certain species above site 4 might be limited by high loads of suspended sediments which may occur unpredictably in that region of the river. The lack of a corresponding faunal break in the York River supports this view, as the York River has a very small drainage basin relative to the James River, and therefore is less likely to exhibit the extremely high values of suspended sediment.

With the information on hand we cannot conclude which factor is responsible for the faunal discontinuity.

THE NATURE OF THE OYSTER ASSEMBLAGE

The meaning of the word "community" has changed with the evolution of synecology (Mills, 1969). Today, as in the past, this word does not have a concise definition accepted by all disciplines, or even by all workers within a single discipline. However, there has been a trend away from defining a community as a functional superorganism, with most of its members interdependent, towards the less rigorous definition that a community is a group of organisms found together at a given time and place.

The term "oyster community" has often connotated functional interdependence. The preoccupation of most investigators with the oyster itself, only considering associated fauna as it potentially affects the oyster, naturally disposes an emphasis on functional interaction. For many species thought to have a detrimental effect on oysters, either through predation or competition for space, there is often little or no hard evidence of such interaction. Likewise, beneficial aspects of the associates have been ignored. It would seem that the action of predators would reduce the competition levels between the oyster and associated species. The oyster drill's appetite for the "oyster pest" Crepidula fornicata would be an example, as would the graxing of fish on the shell-boring spionid worms and the predation of Stylochus ellipticus on Balanus improvisus.

Due to sampling problems oyster reefs have been avoided by quantitative ecologists. This lack of information, in combination with the emphasis on a few well known interactions between the oyster and associated species, has lead many people to believe that the reef fauna represents a distinct component of the estuarine ecosystem (Chestnut, 1970). While the presence of accumulated shell visually demarcates reef areas from the more typical estuarine soft-bottoms, there is little evidence to show whether or not the fauna of the two bottom types differ other than in the presence of the oyster.

If the oyster reef assemblage were indeed a distinct functional community, with the living oyster as its central feature, one would expect it to show certain characteristics to an uncommonly high degree. A significant portion of the species would be spatially and temporally faithful members of the assemblage. The long-lived nature of the oyster, Crassostrea virginica in this case, would allow for long-lived associates and the development of complex associations between the oyster and cohabiting species. Finally it would be expected that oyster assemblages would be quite similar, at least over a limited geographic range, and less similar to other estuarine assemblages from the same region.

Temporal limitation of species' distributions in the present study was demonstrated by the fact that only 34% of all species recorded occurred in all sampling periods. Another 15 species were present in all sampling periods before Tropical Storem Agnes and may have exhibited a year around presence had it not been for the freshet. Even allowing that the sampling program was not adequate to determine the seasonality of rare species, less than half of the species probably had the potential to be temporally faithful oyster associates.

Spatially the results give even less support for a faithful oyster community. Only 19 species occurred at more than 50% of the stations and no more than seven species attained dominance at more than 50% of the sites. Ranking of species by station and sample constancy included three species, <u>Boccardia hamata</u>, <u>Polydora websteri</u> and <u>Odostomia impressa</u>, as the only highly ranked species with documented functional relationships to the oyster.

The abundance and rank analyses showed that the fauna associated with the oyster was not uniform over the estuarine gradient. Indeed, all analyses, i.e. diversity, classification, functional types, etc., emphasized the changing nature of the associated fauna along the gradient.

Perusal of the appended list of species found in this study discloses only 10 commonly considered to be faithful or obligate oyster associates. They are the boring spong <u>Cliona truitti</u>, the predacious flatworm <u>Stylochus ellipticus</u>, the phyllodocid worm <u>Nereiphylla fragilis</u>, the shell-boring spionids <u>Boccardia hamata</u> and <u>Polydora websteri</u>, the prosobranch gastropods <u>Crepidula convexa</u>, <u>Eupleura caudata</u> and <u>Urosolpinx cinerea</u>, the pyramidellid <u>Odostomia impressa</u> and the decapod <u>Pinnotheres ostreum</u>. Not included in this list are species whose association with the oyster is coincidental, such as those species who use the shell as they would any hard substrate.

<u>C</u>. <u>truitti</u>, one of several species of this genus which have been

cited as oyster pests, was found in only two shells at one site in a single sampling period. These reefs are within the salinity tolerance range of this species so its absence might be explained by the occasional freshets experienced by the James River which can inhibit the development of *C. truitti* for several years afterwards (Hopkins, 1962).

The predacious flatworm *Stylochus ellipticus* was fairly abundant. Landers and Rhodes (1970) verified that this worm exhibits ingestive conditioning with different prey populations, either oysters or barnacles. *S. ellipticus* populations at Cape Charles, Virginia contained barnacle predators exclusively. These authors cite failure by others to induce oyster predation by *S. ellipticus* from several local areas. During the present investigation, the highest abundance of this flatworm occurred in the spring, during the peak setting of the barnacle *Balanus improvisus*, indicating that in the James River too, *S. ellipticus* is primarily a barnacle predator.

The large phyllodocid *N. fragilis* occurred uncommonly at the down-river stations in the pre-Agnes sampling periods. This polychaete was found in crevices in the oyster valves and is probably predacious on other members of the assemblage. In this sense, a weak case can be made for it being beneficial to the oyster, but since it was found in an eelgrass community (Marsh, 1973) it cannot be considered to be dependent on the oyster or shells, for a habitat or for prey.

The shell-boring polychaetes *B. hamata* and *P. websteri* were found in abundance. *B. hamata* has not been previously reported from Chesapeake Bay, nor from Virginia since Webster's (1879) record. Neither of these species is an obligate borer and Blake (1969b) noted that both can be abundant in several estuarine habitats. Most of the spionids were collected from mud tubes on shells, in shell crevices, between barnacles shells, and in empty barnacle shells.

C. convexa was included in this list because of the impact its congener *C. fornicata* has had on European oyster grounds, since its accidental introduction into northern Europe (Korringa 1951a). *C. convexa* however, is a smaller, thinner-shelled species and probably never occurs in densities sufficient to become a pest. Many empty *Crepidula* shells were observed with drill holes suggesting that it is a favored prey of the oyster drills.

The oyster drills *E. caudata* and *U. cinerea*, well documented as oyster predators (Galtsoff, 1964), were represented in this study by only six individuals. Site I, the most downestuary site, was the only site within these drills salinity range (Galtsoff, 1964).

The pyramidellid *O. impressa*, abundant at the downestuary sites, is well known as an ectoparasite (Fretter and Graham, 1962). It cannot be assumed that it preyed primarily on *C. virginica*, however, as several potential prey species existed on the reefs and it ranked as the 14th most abundant species in a nearby eelgrass community (Marsh, 1973) lacking *C. virginica*.

The pea crab, *P. ostreum*, seems to be the single associate whose complex life cycle is geared to the biology of the oyster (Christensen and McDermott, 1958). The percentage of oysters infested with *P. ostreum* was within the range reported for the James River by Haven (1959).

It would appear that the fauna associated with oyster reefs does not represent a cohesive community with a great deal of interdependence

Table 19. Number and percentage of fauna common between recent middle Atlantic benthos studies and oyster reefs of the James River.

Author	Type	Area	Taxa identified to species	Number and percentage common to present study No.	%
Bender et al. (1973)	soft-bottom	James River- Hampton Roads, Va	103	69	67.0
Boesch (1971)	soft-bottom	York River, Va.	176	64	36.4
Boesch (1973)	soft-bottom	Hampton Road, Va.	161	71	44.1
Marsh (1973)	*Zostera* (epifauna)	York River, Va.	95	40	42.1
Maurer and Watling (1973)	oyster reef	Delaware Bay and tributaries, Del.	132	59	44.7
May (1972)	oyster reef	MacKay River, Ga.	21	11	52.4
Tenore (1972)	soft-bottom	Pamlico River, N. C.	31	16	51.6
Wells (1961)	oyster reef	Newport River, N. C.	297	52	17.5

between its members. Furthermore, many of the relationships that do exist between the oyster and cohabiting species are not exclusive, but involve C. virginica, or another species opportunistically.

The total James River oyster reef fauna, including colonial species, was compared to other recent oyster and estuarine soft-bottom community studies by tabulating the number and percentage of species found in the other investigations which also occurred on the James River reefs (Table 19). The three oyster fauna studies available for comparison were accomplished by qualitative sampling (dredge or hand collection), but since I am making qualitative, and not quantitative comparisons, this feature should not invalidate the contrast. Only taxa identified fully to the species level were used in the calculation. Previous oyster reef investigations exhibited between 17.5 and 52.4% common fauna, while the soft-bottom studies showed between 36.4 and 67.0% of their fauna to be common to the present study. The study of Bender, Diaz and Larsen (1973) was expected to show a very similar fauna because its sampling area included the upper mesohaline zone of the James River where four of the oyster reefs studies were located. A part of this high similarity, however, may be due to the few samples which contained some oyster shell and fragments. The low similarity between the results of Wells (1961) and the present study was caused by the exceptionally high number of species he collected in the rich Carolinian faunal province at higher salinities. Actually, his species list contains over one third of the species found on the James River beds. These comparisons show that, within the region considered, the oyster reef assemblages are qualitatively as similar to soft-bottom faunal assemblages as they are to each other.

The reefs contain certain abundant species such as *B. hamata* and *Cassidinidea lunifrons* which are seldom, if ever, collected in other Chesapeake Bay habitats. Furthermore, they contain an abundance of individuals of species like the acorn barnacle *B. improvisus*, the sea squirt *Molgula manhattensis*, the bivalve *Congeria leucophaeta*, several hydroids and bryozoans, which take advantage of the hard substrate provided by the oyster and its shell. While qualitatively the oyster reef fauna might be almost indistinguishable from soft-bottom communities, there are important quantitative differences. The species involved have a wide distribution, but only reach their maximum population development potential when hard substrate is available.

In the sedimentary environment characteristic of the middle Atlantic coastal plain the oyster reefs provide the only natural hard substrate. The manmade substrates, pilings, cast-off ballast, etc., do not have enough area to allow maximum development of a hard substrate community. If such a substrate did occur, however, it would be colonized by a community, which, at equilibrium would probably bear great similarity, in structure and function, to the oyster reef assemblage. This supposition is consistent with the implication of Korringa (1951b) who found no difference in the fauna of live and dead shells of the European oyster *Ostrea edulis*.

The oyster reef assemblage appears to be one manifestation of a larger estuarine assemblage. It differs from soft-bottom assemblages principally in quantitative aspects. The controlling feature of the assemblage's character is the increased spatial heterogeneity provided by the shell surfaces, which allows the development of dense populations and relatively high diversities. The assemblage is not spatially or temporally homogeneous but undergoes significant changes in community structure both seasonality and along the estuarine gradient.

Appendix 1. Phylogenetic listing of taxa taken during benthic sampling of the James River oyster reefs, 1971-1972, and stations of occurrence.

Porifera	SITES
Microcinona prolifera (Ellis and Solander)	1,2
Cliona truitti Old	1
Sponge a	4
Cnidaria	
Hydrozoa	
Cordylophora caspia (Pallas)	1,3,7,8
Garveia franciscana (Torrey)	1,2,3,4,5,7
Clytia hemisphaerica (Linnaeus)	1
Obelia bicuspidata Clark	1,2,3,4,
Gonothyraea loveni (Allman)	1,2,3,4,6,7
"Campanulina"	2,7
Sertularia argentea Linnaeus	3,7
Scyphozoa	
Chrysaora quinquecirrha (Desor)	2
Anthozoa	
Edwardsia elegans Verrill	1
Diadumene leucolena (Verrill)	1,2,3,4
Platyhelminthes	
Turbellaria	
Stylochus ellipticus (Girard)	1,2,3,4,5,6,7,8
Euplana gracilis (Girard)	3,5,6,7,8

Appendix I. (Cont'd.

Rhynchocoela	
Heteronemertini	
Zygeupolia rubens (Coe)	1
Enopla	
Amphiporus bioculatus (MCIntosh)	3
Tetrastemma jeani McCaul	1
Zygonemertes virescens (Verrill	1,2,3,4
Species d	1,2,3,4,5,6,7,8
Species e	3
Species f	4
Ectoprota	
Victorella pavida Kent	1,3
Anguinella palmata Van Beneden	1,2,3
Aeverrillia armata (Verrill)	1,2,3,4,6
Membranipora tenuis Desor	1,3,4,5
Electra crustulenta (Pallas)	1,2,3,4,5,6,7,8
Entoprocta	
Pedicellina cernua (Pallas)	2
Phoronidea	
Phoronis architecta Andrews	1

Appendix 1. (Cont'd.)

Annelida

Amphinomidae	
Pseudeurythoe sp.	1,2,3,4
Arabellidae	
Drilonereis filum (Claparede)	1
Capitellidae	
Heteromastus filiformis (Claparede)	1,2,3,4,5,6,7,8
Chaetopteridae	
Spiochaetopterus oculatus (Gitay)	1
Chrysopetalidae	
Paleanotus heteroseta Hartman	1
Cirratulidae	
Tharyx setigera Hartman	1
Glyceridae	
Glycera americana Leidy	1
Glycera dibranchiata Ehlers	1,2
Goniadidae	
Glycinde solitaria (Webster)	1,2,3,4,5
Hesionidae	
Gyptis vittata (Webster and Benedict)	1,2,3,4,5
Parahesione luteola (Webster)	1,2,3
Maldanidae	
Clymenella torquata (Leidy)	1
Nereidae	
Nereis succinea (Frey and Leuckart)	1,2,3,4,5,6,7,8

Appendix I. (Cont'd.

Orbiniidae	
Scoloplos fragilis (Verrill)	1,2,3,4,5
Pectinariidae	
Pectinaria gouldii (Verrill)	1,2
Phyllodocidae	
Eteone heteropoda Hartman	1,2,3,4
Nereiphylla fragilis (Webster)	2,3,4
Pilargidae	
Ancistrosyllis jonesi Pettibone	1
Sabellariidae	
Sabellaria vulgaris Verrill	1,2,3
Sabellidae	
Fabricia sabella (Ehrenberg)	1
Sabella microphthalma Verrill	1,2,3
Serpulidae	
Hydroides dianthus (Verrill)	1,2,3
Spionidae	
Boccardia hamata (Webster)	1,2,3,4,5,6,7,8
Polydora ligni Webster	1,2,3,4,5,6,7,8
Polydora websteri Hartman	1,2,3,4,5,6,7,8
Polydora sp.	6
Prinonospio?	1,2
Paraprionospio pinnata (Ehlers)	1,5
Scolecolepides viridis (Verrill)	1,3,5,6,7,8
Spio?	1
Streblospio benedicti Webster	1,2,3,4,5,6
Spionid a	1

Appendix I. (Cont'd)

Syllidae	
Syllid a	1,3
Terebellidae	
Terebellid?	1
Oligochaeta	
Peloscolex heterochaetus (Michaelson)	spp. 1,2,3,4,5,6,7,8
Peloscolex gabriellae Marcus	
Mollusca	
Pelecypoda	
Anadara transversa (Say)	1,2,3
Brachidontes recurvus (Rafinesque)	1,2,3,4,5,6,7,8
Anomia simplex Orbigny	2
Crassostrea virginica (Gmelin)	1,2,3,4,5,6,7,8
Congeria leucophaeta (Conrad)	4,5,6,7,8
Mercenaria mercenaria (Linnaeus)	1
Mulinia lateralis (Say)	1,2,6
Rangia cuneata (Gray)	5,6,7,8
Tellina agilis Stimpson	1,2,3
Macoma balthica (Linnaeus)	2,4,6,7
Macoma mitchelli Dall	2
Mya arenaria (Linnaeus)	1,2,3,4
Lyonsia hyalina Conrad	1,2
Bivalve a	4

Appendix I. (Cont'd.)

Gastropoda

Skeneopsis planorbis (Fabricius)	1,2
Epitonium rupicolum (kurtz	1,2,3,4
Hydrobia sp.	4,5,6,7,8
Cerithiopsis greeni (Adams)	1
Triphora nigrocincta Adams	4
Crepidula convexa Say	1
Eupleura caudata (Say)	1
Urosalpinx cinerea (Say)	1,2,3
Mitrella lunata (Say)	1,2,3,4
Nassarius vibex (Say)	1,2,3,4
Mangelia plicosa Adams	1,2,3,4
Odostomia impressa Say	1,2,3,4,5,7
Odostomia dux Dall and Bartsch	1
Pyramidella fusca Adams	1,2,3,4,5,6
Rictaxis punctostriatus (Adams)	2
Acteocina canaliculata (Say)	1,2,3,4
Doridella obscura Verrill	1,2,3,4
Cratena pilata (Gould)	1,2

Appendix I. (Cont'd.)

Arthropoda	
Copepoda	
Centropages hamatus (Lilljeborg)	1
Acartia sp.	1
Cyclopoid sp.	1,3,4
Cirripedia	
Balanus eburneus Gould	2,3,4,5,6,7,8
Balanus improvisus Darwin	1,2,3,4,5,6,7,8
Mysidacea	
Neomysis americana (Smith)	1,2,3,4,5,6
Cumacea	
Cyclaspis varians Calman	1
Leucon americanus Zimmer	1,2
Oxyurostylis smithi Calman	1
Isopoda	
Cyathura polita (Stimpson)	1,2,3,4,5,6,7,8
Cyathura burbancki Frankenburg	1,3
Cassidinidea lunifrons (Richardson)	1,2,3,4,5,6,7,8
Edotea triloba (Say)	1,2,3,4,6,7

Appendix I. (Cont'd)

Amphipoda	
Ampelisca abdita Mills	1
Ampithoe longimana Smith	5
Cymadusa compta (Smith)	2
Leptocheirus plumulosus Shoemaker	5,6
Corophium lacustre Vanhoffen	1,2,3,4,5,6,7,8
Unciola irrorata Say	1
Elasmopus levis Smith	2
Gammarus daiberi Bousfield	1,3,4,5,6,7,8
Gammarus mucronatus Say	1,2
Melita nitida Smith	1,2,3,4,5,6,7,8
Monoculodes edwardsi Holmes	4
Pleusymtes glaber (Boeck)	1,2,4
Stenothoe minuta Holmes	1
Paracaprella tenuis Mayer	1,2
Decapoda	
Palaemonetes pugio Holthuis	4,5,6,7
larval shrimp	1,3
Crangon septemspinosus (Say)	1,2,4
Upogebia affinis (Say)	1,2
Callinectes sapidus Rathburn	1,5,6,7,8
Neopanope sayi (Smith)	1,3,4,7
Panopeus herbstii Milne-Edwards	1,2,3,4
Rhithropanopeus harrisii (Gould)	2,3,4,5,6,7,8
Pinnotheres ostreum Say	1,2,3,4,5

Appendix I. (Cont'd.)

Insecta	
Trichoptera	1
Baetidae	1,4
Cryptochironomus sp.	6,8
Procladius sp.	8
Coelotanypus sp.	6
Chordata	
Urochordata	
Molgula manhattensis (DeKay)	1,2,3,4
Vertebrata	
Opsanus tau (Linnaeus)	3
Micropogon undulatus (Linnaeus)	5
Gobiosoma bosci (Lacepede)	1,2,3,4,5,6,7,8

Appendix II. Seasonality of individual species. + indicates the presence of a colonial species.

Species	Number occurring in Fall	Winter	Spring	Summer	Total
Microciona prolifera	+	+	+	+	
Cliona truitta	+				
Sponge a		+			
Cordylophora caspia			+	+	
Garvela franciscana			+	+	
Clytia hemisphaerica				+	
Obelia bicuspidata		+			
Gonythyraea loveni	+	+			
"Campanulina"				+	
Sertularia argentea	+	+			
Chrysaora quinquecirrha				1	1
Edwardsia elegans		2	1		3
Diadumene leucolena	1971	1110	972	81	4134
Stylochus ellipticus	46	3	271	16	336
Euplana gracilis	2		2	25	29

Appendix II. (Cont'd)

Species	Number occurring in Fall	Winter	Spring	Summer	Total
Zygeupolia rubens	2	2	1		5
Amphiporus bioculatus	1		1	1	3
Tetrastemma jeani	1				1
Zygonemertes virescens	47	65	85	2	199
Species d	16	7	7	44	74
Species e		2			2
Species f		2			2
Victorella pavida	+				
Anguinella palmata	+	+	+		
Aeverrillia armata	+	+	+	+	
Membranipora tenuis	+	+	+	+	
Electra crustulenta	+	+	+	+	
Pedicellina cernua				+	
Phoronis architecta		1			1

Appendix II. (Cont'd.)

Species	Fall	Number occurring in Winter	Spring	Summer	Total
Pseudeurythoe sp.	195	141	74	76	486
Drilonereis filum		2			2
Heteromastus filiformis	708	746	584	323	2361
Spiochaetopterus oculartus	2				2
Paleanotus heteroseta	2		1		3
Tharyx setigera	14	30	30		74
Glycera americana	2				2
Glycera dibranchiata	2	7	3		12
Glycinde solitaria	120	54	29	2	205
Gyptis vittata	45	50	40	4	139
Parahesione luteola	3	1	11	1	16
Clymenella torquata	2				2
Nereis succinea	967	935	499	963	3364
Scoloplos fragilis	44	19	41	4	108
Pectinaria gouldii	3	1			4
Eteone heteropoda	41	133	582	13	769

Appendix II. (Cont'd.)

Species	Number occurring in Fall	Winter	Spring	Summer	Total
Nereiphylla fragilis	17	18	9		44
Ancistrosyllis jonesi			1		1
Sabellaria vulgaris	22	6	9		37
Fabricia sabella	3	2			5
Sabella microphthalma	26	8	1		35
Hydroides dianthus	15	2	12		29
Boccardia hamata	467	203	197	1085	1952
Polydora ligni	345	887	2298	342	3872
Polydora websteri	298	218	319	147	982
Polydora sp.		1			1
Prinonospio?		3			3
Paraprionospio pinnata	1	1			2
Scolecolepides viridis	7	6	6	8	27
Spio?		1			1
Streblospio benedicti	224	720	2558	60	3562
Spionid a	1				1

Appendix II. (Cont'd.)

Species	Fall	Number occurring in Winter	Spring	Summer	Total
Syllid a	17	2	1		20
Terebellid?	1				1
Peloscolex spp.	2931	3135	1915	542	8532
Anadara transversa	5	1	5		9
Brachidontes recurvus	884	1020	575	1087	3566
Anomia simplex	1				1
Crassostrea virginica	232	136	111	73	552
Congeria leucophaeta	4	1	3	1204	1212
Mercenaria mercenaria			2		2
Mulinia lateralis			95	19	114
Rangia cuneata		4	3	21	28
Tellina agilis	5			2	7
Macoma balthica	3	9	9	2	23
Macoma mitchelli		1			1
Mya arenaria	92	591	283	6	972

Appendix II. (Cont'd.)

	Number occurring in				
Species	Fall	Winter	Spring	Summer	Total
Lyonsia hyalina	5	3	40	14	63
Bivalve a	1				1
Skeneopsis planorbis	4	17	2		23
Epitonium rupicolum	30	30	7	2	69
Hydrobia sp.	2		9	14	25
Cerithiopsis greeni	2				2
Triphora nigrocincta	1				1
Crepidula convexa	19	4	13		36
Eupleura caudata		1			1
Urosalpinx cinerea	3	2			5
Mitrella lunata	111	38	14		163
Nassarius vibex	21	1	28	9	59
Mangelia plicosa	12	7	5		24
Odostomia impressa	594	370	374	20	1358
Odostomia dux	1				1
Pyramidella fusca	15	13	29	3	60

Appendix II. (Cont'd)

	Number occurring in				
Species	Fall	Winter	Spring	Summer	Total
Rictaxis punctostriatus	1				1
Acteocina canaliculata	23	13	14		50
Doridella obscura	25	15	62	7	109
Cratena pilata	5				5
Centropages hamatus		1			1
Acartia sp.	1				1
Cyclopoida	4		1		5
Balanus eburneus	48	23	7	1	79
Balanus improvisus	6705	4629	15,775	1846	28,955
Neomysis americana	159	1	5	2	167
Cyclaspis varians	2	2			4
Leucon americanus			5		5
Oxyurostylis smithi			1		1
Cyathura polita	67	16	10	12	105
Cyathura burbancki	16	27	35	17	95

Appendix II. (Cont'd.)

Species	Number occurring in Fall	 Winter	 Spring	 Summer	 Total
Cassidinidea lunifrons	1430	553	298	483	2764
Edotea triloba	68	27	47	6	148
Ampelisca abdita	5				5
Ampithoe longimana			1		1
Cymadusa compta	1				1
Leptocheirus plumulosus	1	15	120	4	140
Corophium lacustre	487	222	1656	939	3304
Unciola irroratus	7				7
Elasmopus levis		2			2
Gammarus daiberi	115	374	115	1	605
Gammarus mucronatus		4			4
Melita nitida	933	290	1239	597	3059
Monoculodes edwardsi		1			1
Pleusymtes glaber			3	1	4
Stenothoe minuta	3		7		10
Paracaprella tenuis	33		31	5	69

Appendix ii. (Cont'd.)

Species	Fall	Number occurring in Winter	Spring	Summer	Total
Palaemonetes pugio	7				7
larval shrimp		1	2		3
Crangon septemspinosus			8	2	10
Upogebia affinis	3	1		1	5
Callinectes sapidus	1			5	6
Neopanope sayi	10	2	2	2	16
Panopeus herbstii	8	1	2	4	15
Rhithropanopeus harrisii	30		2	3	35
Pinnotheres ostreum	19	3	9	5	36
Trichoptera			1		1
Baetidae	1	1		1	3
Cryptochironomus sp.			4		4
Procladius sp.		1		1	2
Coelotanypus sp.	1				1

Appendix II. (Cont'd.)

Species	Number occurring in Fall	Winter	Spring	Summer	Total
Molgula manhattensis		1	1	878	880
Opsanus tau	1				1
Micropogon undulatus	1				1
Gobiosoma bosci	31	13	11	25	80

Appendix III. Life form code for noncolonial species. First digit represents feeding type, second digit purchase type and third digit reporductive type.

<u>Chrysaora quinquecirrha</u>	123
<u>Diadumene leucolena</u>	122
<u>Edwardsia elegans</u>	133
<u>Stylochus ellipticus</u>	111
<u>Euplana gracilis</u>	111
<u>Zygeupolia rubens</u>	133
<u>Amphiporus bioculatus</u>	131
<u>Tetrastemma jeani</u>	111
<u>Zygonemertes virescens</u>	111
Nemertean Species d	131
Nemertean Species e	131
Nemertean Species f	131
<u>Phoronis architecta</u>	543
<u>Pseudeurythoe</u> sp.	133
<u>Drilonereis filum</u>	133
<u>Heteromastus filiformis</u>	343
<u>Spiochaetopterus oculatus</u>	543
<u>Paleanotus heteroseta</u>	113
<u>Tharyx setigera</u>	433
<u>Glycera americana</u>	243

Appendix III. (Cont'd.)

Glycera dibranchiata	243
Glycinde solitaria	133
Gyptis vittata	113
Parahesione luteola	113
Clymenella torquata	343
Nereis succinea	243
Scoloplos fragilis	331
Pectinaria gouldii	443
Eteone heteropoda	113
Nereiphylla fragilis	113
Ancistrosyllis jonesi	143
Sabellaria vulgaris	523
Fabricia sabella	541
Sabella microphthalma	521
Hydroides dianthus	522
Boccardia hamata	453
Polydora ligni	453
Polydora websteri	453
Polydora sp.	453
Prinonospio?	443
Paraprionospio pinnata	443
Scolecolepides viridis	443
Spio?	441
Streblospio benedicti	443

Appendix III. (Cont'd.)

Spionid a	443
Syllid a	113
Terebellid?	441
Peloscolex spp.	331
Anadara transversa	523
Brachidontes recurvus	523
Anomia simplex	523
Crassostrea virginica	523
Congeria leucophaeta	523
Mercenaria mercenaria	533
Mulinia lateralis	533
Rangia cuneata	533
Tellina agilis	433
Macoma balthica	433
Macoma mitchelli	433
Mya arenaria	533
Lyonsia hyalina	533
Bivalve a	533
Skeneopsis planorbis	211
Epitonium rupicolum	111
Hydrobia sp.	211
Cerithiopsis greeni	213
Triphora nigrocincta	213

Appendix III. (Cont'd)

Crepidula convexa	511
Eupleura caudata	111
Urosalpinx cinerea	111
Mitrella lunata	211
Nassarius vibex	213
Mangelia plicosa	133
Odostomia impressa	111
Odostomia dux	113
Pyramidella fusca	113
Rictaxis punctostriatus	431
Acteocina canaliculata	431
Doridella obscura	113
Cratena pilata	113
Centropages hamata	513
Acartia sp.	513
Cyclopoida	413
Balanus eburneus	523
Balanus improvisus	523
Neomysis americana	511
Cyclaspis varians	431
Leucon americanus	431
Oxyurostylis smithi	431
Cyathura polita	241

Appendix III. (Cont'd.)

Cyathura burbancki	241
Cassidinidea lunifrons	211
Edotea triloba	411
Ampelisca abdita	441
Ampithoe longimana	421
Cymadusa compta	421
Leptocheirus plumulosus	531
Corophium lacustre	521
Unciola irrorata	441
Elasmopus levis	411
Gammarus daiberi	211
Gammarus mucronatus	211
Melita nitida	211
Monoculodes edwardsia	431
Pleusymtes glaber	211
Stenothoe minuta	411
Paracaprella tenuis	111
Palaemonetes pugio	213
Larval shrimp	213
Crangon septemspinosa	113
Upogebia affinis	543
Callinectes sapidus	113
Neopanope sayi	113
Panopeus herbstii	113

Appendix III. (Cont'd.)

Rhithropanopeus harrisii	113
Pinnotheres ostreum	213
Trichoptera	211
Baetidae	211
Cryptochironomus sp.	411
Procladius sp.	411
Coelotanypus sp.	411
Molgula manhattensis	522
Opsanus tau	111
Micropogon undulatus	113
Gobiosoma bosci	111

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