

DELAWARE BAY REPORT SERIES

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THE BIOLOGY OF THE OYSTER COMMUNITY
AND ITS ASSOCIATED FAUNA
IN DELAWARE BAY

by

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ABSTRACT

The purpose of this study was to describe the composition of the fauna of Delaware oyster beds. The local oyster beds are termed the bay beds, which include planted and natural populations, and the river beds. From 1967 to 1971 approximately 800 samples were collected and the majority of these were from the bay beds. In 1968 and 1969, 132 samples were systematically collected from the river beds and 19 from the bay beds. These were returned to the laboratory for special care in identification. Samples from monthly fouling panels and oyster rafts provided additional species. One hundred fifty-two species were identified. In order of decreasing frequency of occurrence the top 23 species were: Sabellaria vulgaris, Conopeum tenuissimum, Panopeus herbsti, Nereis succinea, Palaemonetes vulgaris, Crassostrea virginica, Nassarius obsoletus, Polydora websteri, Membranipora tenuis, Garveia franciscana, Balanus improvisus, Diadumene leucolena, Aiptasiomorpha luciae, Melita nitida, Obelia longicyatha, Alcyonidium polyomm, Sertularia argentea, Crangon septemspinosa, Hydroides dianthus, Eurypanopeus depressus, Modiolus demissus, Parapleustes sp., and Hartlaubella gelatinosa. The diversity of species decreases up the estuary with decreasing salinity. Substrate can alter this pattern in particular cases. Within a given salinity range the presence of any firm substrate or mud influenced the nature of the community from epifaunal to infaunal. Four faunal units were recognized: the planted and natural beds; the four

southern rivers; the Leipsic River; the Woodland Beach area. The Leipsic River area marks a critical transition zone with a rapid reduction in species. North of Woodland Beach mesohaline conditions begin to prevail. The fauna was more diverse in late spring than in the fall but seasonality was not as marked as expected. The faunal composition of Delaware oyster beds agrees with the cosmopolitan view of estuaries. The stability time hypothesis proposed by Sanders provides a theoretical basis to explain faunal distributions in the Delaware oyster community. The variable but hardy nature and geologic history of an oyster community makes it a sensitive indicator of environmental degradation in the estuary.

INTRODUCTION

The purpose of this report is to describe the composition of the fauna of local oyster beds and to discuss the effects of salinity, substrate, temperature and season on this fauna. The distribution of the oyster beds, their potential value for commercial harvesting and their utilization have been reported elsewhere (Maurer et al. 1971). During the course of our survey of the oyster population it was observed that there was a well defined associated fauna. A detailed analysis of this associated fauna is described in Maurer and Watling (1973).

Research on benthic communities in this region has been restricted to the ocean side and Cape May region of New Jersey (Richards 1929, Dean and Haskin 1964, Phillips 1967), the river portion of the Delaware estuary (Schuler et al. 1970 a, b) and work in progress by our laboratory. Most studies on invertebrates in this area were concerned with a single species, a specific taxonomic group or a special problem (Fowler 1911, Stauber 1945, Carriker 1951, McDermott and Flower 1953, Cronin 1954a, Porter 1956, Hulburt 1957, Cronin et al. 1962, Haskin 1964, Bousfield 1969, Watling and Maurer 1972a, b, 1973).

The classic work on the oyster community was conducted by Mobius (1877). This was followed in Europe by Caspers (1950), Korringa (1951) and Mistakidis (1951).

Hedgpeth (1953) provides one of the most comprehensive

descriptions of oyster associations in the United States. In a later paper Hedgpeth (1957) asserts that oyster reefs are the most significant aggregations in estuaries since they are a major feature influencing patterns of sedimentation and at the same time they provide habitats for a variety of smaller organisms. This latter point was well documented in a survey of the fauna of oyster beds in Beaufort, North Carolina by Wells (1961) who reported 303 species. He referred to surveys of organisms associated with the American oyster, Crassostrea virginica, in the Potomac River (Frey 1946) and Apalachicola, Florida (Pearse and Wharton 1938). In Odum et al. (1969) oyster reefs are reviewed, and the importance of such structures as substrate for an abundance of associated forms is indicated. In Chesapeake Bay, Beaven (1947) and Andrews (1953) report on important fouling organisms of oysters, Merrill and Boss (1966) describe an oyster fauna from deep water in the Patuxent, and Calder and Brehmer (1967) describe a monthly fouling study from the lower Chesapeake. Cory's (1967) fouling study in the Patuxent is also pertinent. Parker (1969) comments that large natural oyster reefs do not occur in the Cape Cod region, although Thomas (1970) recognizes oyster associations in a study of the benthos on Prince Edward Island. Gunter (1969) described the gross features of oyster reefs, including old buried ones. Gunter and Geyer (1955) described associations of oysters and other organisms on artificial structures in the northwestern Gulf of Mexico. These studies delineate rather clearly some depth and salinity relationships of three oyster species and associated organisms.

The first part of this report presents a description of Delaware Bay, its hydrographic condition, and collecting methods. Then follows a list of the species with their local geographic distribution and notes on their ecological preferences. Finally the overall view of the community is presented in a discussion section.

DESCRIPTION OF STUDY AREA

Delaware Bay, a major estuary along the Atlantic seaboard of the United States, is geographically situated between Long Island to the north and Chesapeake Bay to the south (Figure 1). The morphometry of Delaware Bay was described in detail by Shuster (1959) and its coastal geology by Kraft (1971). Biggs (1972) studied sedimentation in the shell beds. In brief, the shape of the Delaware Basin is essentially that of a flattened funnel with extensive intertidal flats along the New Jersey shore. The deepest areas lie in the western portion of the bay with a maximum depth of 151 feet (46.0 m.) and mean depth of 31.7 feet (9.7 m.). The length of the bay is 46.7 miles (75.2 km.) with mean and maximum widths of 15.3 miles (24.6 km.) and 27.1 miles (43.6 km.) respectively. The bay encompasses approximately 720 square miles (2779.92 sq. km.) and volume of about 4.7×10^{12} gallons (1.74×10^{13} litres). Tides are of the irregular semi-diurnal type and their range at the mouth of the bay is 4.1 feet (1.25 m.).

Within the study area nine tributaries flow into Delaware Bay from

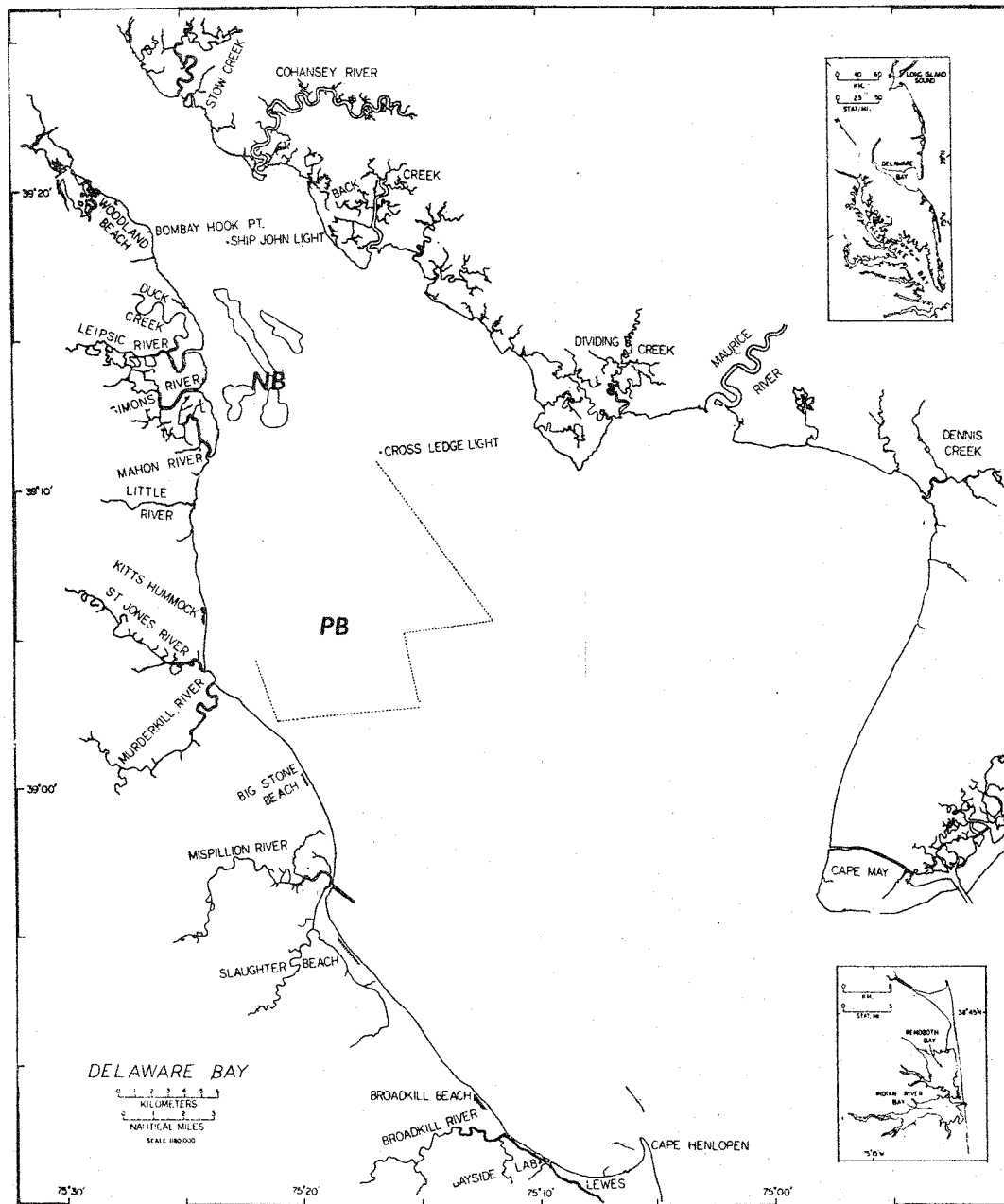


Figure 1. Map of Delaware Bay and Tributaries. NB= natural beds; PB= planted beds.

the west (Figure 1). These meandering rivers are, in general, less than ten miles (16.6 km) long with the widest cross section (600 feet; 180 m) occurring at the mouth of the Leipsic River. The depth in the rivers is very shallow, ranging from 2-12 feet (0.6 - 3.6 m) in the majority of rivers, to 22-25 feet (6.6 - 7.5 m) in the Leipsic River at mean low water.

Hydrographic data are summarized in Table 1. Stauber (1943), Cronin (1954b), Shuster (1959), Aulenback and Kaplovsky (1961), Rasmussen et al. (1966), DeWitt (1968), Daiber and DeWitt (1968), Daiber and Beattie (1969), and Maurer et al. (1971) provide hydrographic data for the rivers, the planted and the natural beds in the Delaware Bay area. Woodland Beach, the northern most extension of Delaware's natural beds, has the lowest salinity range (2-16 o/oo). The southern most extension of Delaware's oyster beds is the southern margin of the planted beds, immediately north of Big Stone Beach. Here the salinity ranged as high as 28 o/oo and an annual average of 25 o/oo has been recorded (Daiber and Wockley 1968). On the New Jersey side of the bay oyster beds extend to Cape May where they are exposed to salinity of 28-30 o/oo. Water temperature is, in general, more uniform than salinity throughout Delaware's oyster beds. In the Woodland Beach area water temperature increases earlier in the spring, attains higher levels in the summer, decreases later in the fall and cools faster in the winter than on the other bay beds. For example, lowest water temperatures occur in January up-bay, and in March in the lower bay (Daiber and Wockley 1968). In the winter ice

TABLE 1

Observed Hydrographic and Substrate Characteristics of Delaware's Oyster Beds

Bed	Range Temp. C	Range Sal. o/oo	Range O ₂ mg/l	Range Depth Ft.(m.)	Substrate Remarks
Woodland Beach	2.0-29.0	2.0-16.6	6.4-15.3	8-12(2.5-3.7)	Intercalated mud and shell bottom.
Natural	1.0-26.0	18.0-25.0	6.0-8.0	20-25(6.2-7.8)	Hard shell bottom intercalated with muddy shells and mud, some newly planted surf clam shells.
Planted	3.6-26.5	14.7-28.5	5.8-11.4	20-25(6.2-7.8)	Hard shell bottom intercalated with muddy shells.
Leipsic	-1.0-29.0	2.0-18.0	2.0-11.0	20-25(6.2-7.8)	Hard shell bottom first 2000 yds. (1800m); then scattered shell, mud and marsh grass debris.
St. Jones	-1.5-28.5	2.0-26.0	0.8-12.5	2-8(0.6-2.5)	Scattered shell and mud; intertidal oyster bars near mouth.
Murderkill	-1.5-28.5	2.0-27.0	1.8-11.1	14-20(4.3-6.2)	Hard shell bottom first 2000 yds. (1800m); then intercalated shell and mud; intertidal oyster bar near mouth.
Misphillion	-1.0-29.0	2.5-29.0	2.0-11.0	8-16(2.5-5)	Hard shell bottom first 1500 yds. (1350m); then intercalated shells with mud and grass debris.
Broadkill	-1.8-28.9	3.5-33.0	0.7-9.5	8-14(2.5-4.3)	Mostly newly planted surf clam shells.

(From various sources)

flows are normally restricted to January and February. Dissolved oxygen values are lowest (5 ppm.) in August and highest (12.00 ppm.) in April.

In the rivers the highest maximum salinity (33 o/oo) was recorded in the Broadkill River and the lowest maximum (18 o/oo) in the Leipsic River. It deserves repeating that the oyster bars occur within 4,000 yards (3600 m) of the river mouths so that they essentially live in the region of the maximum salinity for each river. The oyster bars in the Broadkill River are an exception, however. In 1939 the river mouth was rerouted through a canal to Delaware Bay, thus in effect moving the oyster bars 1 1/2 miles (2.4 km) from Delaware Bay. Seasonal water temperatures in the rivers tend to reflect air temperatures and are therefore cooler (fall) and warmer (spring) than on the bay beds. One consequence of this is earlier spawning in the rivers than in the bay.

In contrast to the bay beds the river beds experience wide fluctuation in oxygen levels. During July, August, and early September low oxygen values may be a limiting factor in the setting of oyster larvae. This may be particularly true for the St. Jones River whose oxygen values are consistently lower than the Murderkill River located less than a quarter mile away. The St. Jones River, which has been a main outlet for domestic sewage from central Delaware for the past 20 years, also has the least amount of oysters of all the rivers (Maurer et al. 1971).

Since the hydrography of the Broadkill River has been studied

more than any of the other oyster producing tributaries, it may be informative to discuss it in some detail. Although there are some specific differences among Delaware's tidal rivers in terms of depth, cross section and drainage, conditions in the Broadkill River are representative of the general features of local rivers. The following account is based mainly on the report of Daiber and DeWitt (1968).

The Broadkill River is subjected to a semi-diurnal tidal flow over its entire course. The lower estuarine portion has salinities ranging from 20-33 o/oo for most of the tidal cycle. This area appears to be vertically and laterally homogeneous except for the presence of a salt wedge at the beginning of each flooding cycle. The highest mean current velocity (1.65 ft./sec.; 0.5 m/sec.) was found in this portion of the system. Current velocities of the ebb tide were usually stronger than the corresponding velocities of the flood tide. Net movement of water was seaward at all levels. The pH was 7.7 and the mean dissolved oxygen concentration was 6.1 mg-at/l.

The upper estuarine portion of the Broadkill River showed a vertically stratified salinity distribution. Salinity ranged from 1 o/oo to 14 o/oo over a tidal cycle. Mean current velocity was 1.10 ft./sec. (0.3m/sec.) with ebbing currents affecting the water column at all depths.

The freshwater section of the Broadkill system was the region where salinity variations were not directly related to the tidal flow. Mean current velocity, pH, and dissolved oxygen concentration was 0.51 ft./sec. (0.15 m/sec.), 6.2, and 0.2 mg-at/l respectively.

Low pH values and oxygen concentrations in this region appeared to be directly related to each other and to the tidal flow. The flushing time of the entire system varied between 7 and 14 days.

OYSTER POPULATION

Although the oyster ranges from the mouth of Delaware Bay (33 o/oo) to Hope Creek, (3-6 o/oo) the major beds (in terms of density, area occupied, and size of individuals) are located south of the Cohansey River on both sides of the bay, with extensive intertidal flats on the New Jersey side along Cape May (Figure 1). Nelson (1947) presented a map of New Jersey's oyster beds. Those oyster beds within the jurisdiction of the Delaware Department of Natural Resources are the main target area of this report.

Previous work on Delaware's oyster beds was conducted by Moore (1911), Engle (1953), Hess (1967), Keck (1969), Maurer et al. (1971) and Keck et al. (1973). The following summary is taken from those sources. The oyster beds discussed herein can be divided into three types: (1) the natural beds; (2) the planted beds in Delaware Bay and; (3) the adjacent river beds. The natural beds are seed areas from which oysters are dredged and normally placed on beds leased from the state, termed planted beds (Figure 1). Oysters occurring in the tributaries are called river beds and have been harvested or used as seed depending on their size and supply. In recent years river oysters have been exclusively transferred to planted beds for

purposes of depuration.

Distribution in the lower bay is in large part due to the hydrographic conditions which apparently do not favor oyster setting on the west side of Delaware Bay (Nelson 1954), but do favor setting on the Cape May flats (Haskin 1964, Hidu and Haskin 1971). Hydrography together with submarine topography (deep, elongate channels), predation, and the lack of continuous shell bottom thus makes the west side of the bay a difficult site for oyster larvae to colonize. Exclusive of rivers the southern margin of Delaware beds is 16 miles (25.6 km) from the mouth of the bay, where salinity ranges from 14 to 28 o/oo. This is in contrast to the New Jersey situation: along Cape May extensive tide flats bathed in salinity of 25-28 o/oo and heated by summer temperatures of 28°C receive heavy oyster sets. Distribution in the upper bay is influenced by low salinity, low numbers of brood stock and lack of suitable substrate. The effect of lower salinity can be seen in oysters from Woodland Beach, where two year old oysters and mid-bay oysters were compared. The latter were almost twice as large as the former (Maurer - unpublished data). Similar reductions in bivalve size due to salinity have been reported from other estuaries (Pearse and Gunter 1957, Muus 1967).

The natural oyster beds are exclusively subtidal and are primarily parallel to the axis of the bay. Those beds which lie within 3 miles (4.8 km) of shore are locally called oyster rocks, and may be several miles long. The substrate varies widely within beds and from bed to bed. For example, the southern portions of the Silver

and Ridge beds consist of hard shell bottoms which grade northward to mud-shell deposits. There have been recent efforts to improve the condition of the natural beds by regular dumping of shucked surf clam shells. The planted beds range in size from a few to several acre plots and are commonly lenticular or polygonal in outline. Shells of oysters, surf clams, and hard clams make up the bottom. Since there had been almost no oystering from 1961-1970, the shells for the most part have become silted. In the rivers the size, shape, and distribution of oyster bars is even more irregular than bay beds. The oyster beds extend from the mouth of the rivers to a maximum of 4,000 yards (3600 m) upstream. Each river has a characteristic distribution of shell-mud interfaces. Some of the river bars are narrow and elongate and are located in mid-channel. Others are located on meanders or the inside curve of a meander and grow towards mid-stream by accretion at the edges (Keck et al. 1973). Two of the rivers, the St. Jones and Murderkill, contain intertidal oyster flats within, and outside of, their mouths. Jetties, pilings, bulkheads and other hard substrates found throughout the rivers are commonly occupied by clusters of oysters.

Following the mass mortalities from MSX in the late 1950's and 1960's it was necessary to determine the condition of Delaware oyster beds. Estimates of standing crop yielded a total of approximately 55,000 bushels in 237 acres of river beds and 65,000 bushels in 941 acres of natural beds (Maurer et al. 1971). Both sources were considered depleted but certain rivers showed immediate potential as

seed areas. The association of high oyster production with a hard substrate was demonstrated. Since there had been practically no oystering in Delaware since 1961, an experimental planting of seed was carried out. Although the experimental plots were not particularly productive, results indicated that with proper management Delaware oyster beds can be rehabilitated. Shell planting in the summer of 1970 coupled with a late warming period in September yielded the heaviest set in almost fifteen years. Results of monitoring the beds in April 1971 indicated that survivorship was high over the winter. Certain areas in the Ridge bed were dredged in May 1971 which resulted in 42,000 bushels of seed, with another 80,000 bushels of seed taken in the spring of 1972. The seed was placed on the planted beds. Several years of heavy set similar to that of 1970 will be required to make the bay beds the main source of seed in Delaware they once were. Surveys in progress indicate that the acreage of natural beds is greater than in 1967, but, unfortunately, setting is irregular; for example, the set in the summer of 1971 was very light. Finally, examination of histological sections for MSX revealed that the incidence of this oyster parasite was not as serious as it was in the late fifties and sixties.

DESCRIPTIVE BIOLOGY

From 1967 to 1971 approximately eight hundred oyster dredge samples were collected in river and bay oyster beds. These collections include systematic quantitative samples (Maurer et al. 1971) and

random qualitative samples. Maurer and Watling (1973) contains the details of sampling. An extensive review of the literature revealed that there were no comprehensive taxonomic sources for the Mid-Atlantic region comparable to the Woods Hole Key (Smith 1964) for the New England area or Light's key (1961) for central California. Gosner's (1971) guide was published after the taxonomic work of the authors on this study was completed. Because of the labor involved in searching the literature and collating those references most applicable to the Middle Atlantic region, it was considered valuable to include them in this presentation. This list stresses references most useful for the local biota and is not intended as an exhaustive review of any taxon.

Porifera: Old (1941), McDougall (1943), de Laubenfels (1947), Hartman (1958), Wells (1959b), Wells et al. (1960, 1964), Hopkins (1962)

Coelenterata: Nutting (1915), Fraser (1944), Woods Hole Oceanographic Institution (W.H.O.I., 1952), Christensen (1967), Humphries (1970), Jensen (1970), Calder (1971), Watling and Maurer (1972b)

Turbellaria: Hyman (1939, 1940, 1944, 1952)

Nemertea: Coe (1943), McCaul (1963)

Mollusca: Johnson (1934), Smith (1951), Abbott (1954), Russell-Hunter and Brown (1964), Moore (1964), Kraeuter (1966), Stanley (1970, 1972)

Polychaeta: Hartman (1945, 1951, 1959, 1965), Pettibone (1963), Smith (1964), Wells and Gray (1964), Wass et al. (1966), Blake (1971)

Amphipoda: Holmes (1905), Fowler (1911), Künkel (1918), Crawford (1937),

Shoemaker (1947), Feeley (1967), McCain and Feeley (1965), McCain (1965, 1968), Barnard (1969), Bousfield (1969, 1972), Watling and Maurer (1972a)

Isopoda: Richardson (1905), Bowman (1955), Smith (1964), Wigley (1961), Menzies and Frankenberg (1966), Burbanck (1967), Schultz (1969)

Decapoda, Mysidacea, Cirripedia, Pycnogonida and Xiphosurida: Rathbun (1930), Stauber (1945), Hedgpeth (1948), McDermott and Flower (1953), Ryan (1956), Menzel and Hopkins (1956), Shuster (1957), Hulburt (1957), Price (1962), Hopkins (1965), Zullo (1963, 1964), Williams (1965), Fleming (1969), Haefner (1969), Wigley and Burns (1971).

Ectoprocta: Osburn (1944), Maturo (1957), Rogick (1964), Powell and Crowell (1967), Powell (1968)

Urochordata: Smith (1964)

Pisces: Robinson and Schwartz (1965)

The 154 species found associated with oyster beds are listed in Table 2. This total includes: 4 sponges, 17 coelenterates, 4 flatworms, 5 nemerteans, 21 annelids, 44 molluscs, 1 sipunculid, 44 crustaceans, 1 pycnogonid, 1 xiphosurid, 8 ectoprocts, 1 urochordate and 3 vertebrates. No attempt was made to identify protozoans, copepods, ostracods or nematodes.

TABLE 2

Occurrence and Distribution of Species From
Oyster Bars

	BK	MS	MK	SJ	LC	PB	NB	WB
Phylum Porifera								
<u>Cliona celata</u> (Grant)						x	x	
<u>Microciona prolifera</u> (Ellis and Solander)				x		x	x	
<u>Prosuberites microsclerus</u> (Lamarck)							x	
* <u>Halichondria bowerbanki</u> (Burton)								
Total	0	0	0	1	0	2	3	0
Phylum Coelenterata								
Class Hydrozoa								
<u>Ectopleura dumortieri</u> (Van Beneden)					x			
<u>Tubularia crocea</u> (L. Agassiz)			x		x	x	x	
<u>Hydractinia echinata</u> (Fleming)				x				
<u>Garveia franciscana</u> (Torrey)	x	x	x	x	x		x	
<u>Obelia commissuralis</u> (McCrady)	x							
<u>O. longicyatha</u> Allman	x	x	x	x	x		x	
<u>Gonothyrea loveni</u> (Allman)						x	x	
<u>Hartlaubella gelatinosa</u> (Pallas)	x	x	x	x	x	x	x	x
<u>Eulaomedeia angulata</u> (Hincks)			x					
<u>Campanulina</u> spp.	x	x	x		x		x	
<u>Sertularia argentea</u> Linné	x	x	x	x	x	x	x	
* <u>Obelia biscuspidata</u> Clark								
* <u>O. longissima</u> (Pallas)								
* <u>Schizotricha tenella</u> (Verrill)								
Class Anthozoa								
<u>Aiptasiomorpha luciae</u> (Verrill)	x	x	x	x			x	
<u>Diadumene leucolena</u> (Verrill)	x	x	x	x	x	x	x	
<u>Metridium senile</u> (Linné)			x	x		x		
Total	8	7	10	8	8	6	9	1
Phylum Platyhelminthes								
Unidentified species	x	x			x			
* <u>Bdelloura candida</u> (Girard)								
<u>Notoplana atomata</u> (Muller)						x		
<u>Stylochus ellipticus</u> (Girard)						x		
Total	1	1	0	0	1	2	0	0
Phylum Rhynchocoela								
<u>Zygeupolia rubens</u> (Coe)	x							
<u>Micrura rubra</u> Verrill		x	x	x			x	
<u>Tetrastemma elegans</u> (Girard)		x			x			
* <u>Cerebratulus lacteus</u> (Leidy)								
* <u>Malacobdella grossa</u> (Muller)								
Total	1	2	1	1	1	0	1	0

TABLE 2 (cont.)

	BK	MS	MK	SJ	LC	PB	NB	WB
Phylum Annelida								
Class Polychaeta								
<u>Hypaniola grayi</u> Pettibone	x	x	x	x			x	
<u>Heteromastus filiformis</u> (Claparede)	x	x	x					
<u>Glycera dibranchiata</u> Ehlers	x	x	x	x			x	
<u>Nereis succinea</u> (Frey and Leuchkart)	x	x	x	x	x	x	x	x
<u>Scoloplos fragilis</u> (Verrill)	x		x					
<u>Owenia fusiformis</u> Delle Chiaje							x	
<u>Pectinaria gouldii</u> (Verrill)			x	x				
<u>Eteone heteropoda</u> Hartman	x	x	x	x	x			
<u>E. lactea</u> Claparede						x		
<u>Eumida sanguinea</u> (Oersted)						x		
<u>Harmothoe extenuata</u> (Grude)		x	x		x		x	
<u>H. imbricata</u> (Linné)						x		
<u>Lepidonotus sublevis</u> Verrill						x		
<u>Sabellaria vulgaris</u> Verrill	x	x	x	x	x	x	x	
<u>Hydroides dianthus</u> (Verrill)	x	x	x	x		x	x	
<u>Polydora ligni</u> Webster	x	x	x	x		x	x	
<u>P. websteri</u> Hartman	x	x	x	x	x	x	x	
<u>Streblospio benedicti</u> Webster		x	x					
* <u>Glycera americana</u> Leidy								
* <u>Paraprionosyllis longicirrata</u> (Webster and Benedict)								
* <u>Spiochaetopterus oculatus</u> Webster								
Total	10	11	13	9	5	9	9	1
Phylum Mollusca								
Class Gastropoda								
<u>Epitonium rupicolum</u> (Kurtz)			x	x			x	
<u>Crepidula fornicata</u> (Linne)	x	x	x	x		x	x	
<u>C. plana</u> Say		x	x	x		x		
<u>Eupleura caudata</u> (Say)		x						
<u>Polinices duplicatus</u> (Say)	x						x	
<u>P. immaculatus</u> Totten							x	
<u>Urosalpinx cinerea</u> (Say)			x	x		x	x	
<u>Anachis avara</u> (Say)						x		
<u>Mitrella lunata</u> (Say)		x	x			x		
<u>Busycon canaliculatum</u> (Linné)						x	x	
<u>B. carica</u> (Gmelin)				x			x	
<u>Nassarius obsoletus</u> (Say)	x	x	x	x	x	x	x	
<u>N. trivittatus</u> (Say)		x		x		x		
<u>N. vibex</u> (Say)		x						
<u>Acteon punctostriatus</u> C. B. Adams							x	
<u>Haminoea solitaria</u> (Say)			x					
<u>Retusa canaliculata</u> (Say)				x			x	
<u>Odostomia impressa</u> Say			x	x			x	
<u>Turbonilla interrupta</u> Totten	x		x				x	

TABLE 2 (cont.)

	BK	MS	MK	SJ	LC	PB	NB	WB
<u>Doridella obscura</u> (Verrill)	x	x	x	x		x	x	
<u>Tergipes despectus</u> (Johnston)		x	x	x	x			
<u>Eubbranchus exiguus</u> (Alder and Hancock)							x	
* <u>Anachis translirata</u> Ravenel								
* <u>Melampus bidentatus</u> Say								
Class Bivalvia								
<u>Nucula proxima</u> Say						x		
<u>Modiolus demissus</u> (Dillwyn)	x	x	x	x	x			x
<u>Amygdalum papyria</u> (Conrad)	x	x			x	x	x	
<u>Mytilus edulis</u> Linné	x	x	x	x	x	x		
<u>Crassostrea virginica</u> (Gmelin)	x	x	x	x	x	x	x	x
<u>Mysella planulata</u> Stimpson			x					
<u>Mercenaria mercenaria</u> (Linné)	x		x	x		x		x
<u>Gemma gemma</u> (Totten)	x	x	x			x	x	
<u>Petricola pholadiformis</u> Lamarck	x	x		x	x	x		
<u>Tellina agilis</u> Stimpson	x					x		
<u>Macoma balthica</u> (Linné)	x	x		x	x			x
<u>Tagelus divisus</u> (Spengler)	x							
<u>Solen viridis</u> Say				x			x	
<u>Mulinia lateralis</u> (Say)	x	x	x	x		x	x	
<u>Mya arenaria</u> (Linné)	x	x	x	x			x	
<u>Cyrtopleura costata</u> (Linné)				x				
<u>Barnea truncata</u> (Say)			x	x	x			
<u>Lyonsia hyalina</u> (Conrad)	x		x					
* <u>Anomia simplex</u> d'Orbigny								
* <u>Spisula solidissima</u> (Dillwyn)								
Total	18	20	19	22	9	18	20	4
Phylum Arthropoda								
Subphylum Chelicerata								
Class Merostomata								
<u>Limulus polyphemus</u> (Linné)				x		x	x	
Class Pycnogonida								
<u>Callipallene brevirostris</u> (Johnston)	x	x						
Subphylum Mandibulata								
Class Crustacea								
Subclass Cirripedia								
<u>Balanus improvisus</u> Darwin	x	x	x	x	x	x	x	x
<u>B. eburneus</u> Gould	x				x			
* <u>B. balanoides</u> (Linné)								
Subclass Malacostraca								
Order Mysidacea								
<u>Neomysis americana</u> (S. I. Smith)	x					x	x	
Order Isopoda								
<u>Cyathura polita</u> (Stimpson)	x	x	x					
<u>Edotea triloba</u> (Say)	x	x	x	x				
* <u>Chiridotea nigrescens</u> Wigley								

TABLE 2 (cont.)

	BK	MS	MK	SJ	LC	PB	NB	WB
Order Amphipoda								
<u>Ampelisca abdita</u> Mills	x	x	x	x	x			x
<u>A. vadorum</u> Mills	x	x						
<u>A. verrilli</u> Mills			x					
<u>Ampithoe valida</u> Smith					x			
<u>Cymadusa compta</u> (Smith)			x		x			
<u>Microdeutopus gryllotalpa</u> Costa		x		x				
<u>Cerapus tubularis</u> Say	x							x
<u>Corophium acherusicum</u> Costa	x		x		x			
<u>C. insidiosum</u> Crawford	x	x		x		x	x	
<u>C. lacustre</u> Vanhoffen	x							
<u>C. tuberculatum</u> Shoemaker			x			x		
<u>Unciola serrata</u> Shoemaker			x			x	x	
<u>Gammarus daiberi</u> Bousfield								x
<u>G. mucronatus</u> Say	x	x						
<u>G. tigrinus</u> Sexton	x							
<u>Elasmopus levis</u> (Smith)			x	x				
<u>Melita nitida</u> Smith	x	x	x	x				
<u>Monoculodes edwardsi</u> Holmes				x				
<u>Microprotopus raneyi</u> Wigley								x
<u>Parapleustes</u> sp.	x	x	x	x	x	x		
<u>Parametopella cypris</u> (Holmes)			x		x		x	
<u>Orchestia grillus</u> Bosc								x
<u>Paracaprella tenuis</u> Mayer	x	x	x	x		x		
* <u>Batea catharinensis</u> Muller								
* <u>Corophium acutum</u> Chevreux								
* <u>Gammarus palustris</u> Bousfield								
Order Decapoda								
<u>Palaemonetes pugio</u> Holthuis				x				
<u>P. vulgaris</u> (Say)	x	x	x	x	x	x		
<u>Crangon septemspinosa</u> (Say)	x	x	x	x	x		x	
<u>Pagurus longicarpus</u> Say			x	x	x		x	x
<u>Callinectes sapidus</u> Rathbun	x	x	x	x	x			
<u>Eurypanopeus depressus</u> (Smith)			x	x	x	x	x	
<u>Neopanope texana sayi</u> (Smith)	x	x					x	x
<u>Panopeus herbsti</u> H. Milne-Edwards	x	x	x	x	x	x	x	
<u>Rhithropanopeus harrisi</u> (Gould)	x	x		x	x			x
<u>Pinnotheres ostreum</u> Say	x	x	x		x		x	
* <u>Hexapanopeus angustifrons</u> (Benedict and Rathbun)								
Total	24	24	19	18	15	13	17	2
Phylum Ectoprocta								
<u>Alcyonidium polyoum</u> (Hassall)	x	x	x	x	x	x	x	
<u>A. verrilli</u> Osborn		x					x	
<u>Anguinella palmata</u> Van Beneden		x		x			x	x
<u>Amathia vidovici</u> (Heller)			x					

TABLE 2 (cont.)

	NK	MS	MK	SJ	LC	PB	NB	WB
<u>Bowerbankia gracilis</u> Leidy	x	x	x	x		x		
<u>Membranipora tenuis</u> Desor	x	x	x	x	x	x	x	x
<u>Conopeum tenuissimum</u> (Canu)	x	x	x	x	x	x	x	x
* <u>Bugula californica</u> Robertson								
Total	4	6	5	5	3	6	4	2
Phylum Sipunculida								
<u>Golfingia gouldi</u> (Pourtales)							x	
Total	0	0	0	0	0	0	1	0
Phylum Chordata								
Subphylum Urochordata								
<u>Molgula manhattensis</u> (DeKay)	x			x	x	x	x	
Subphylum Vertebrata								
Class Pisces								
<u>Gobiosoma bosci</u> (Lacepede)	x	x	x	x	x			
<u>Opsanus tau</u> (Linnaeus)	x							
<u>Sygnathus fuscus</u> (Storer)							x	
Total	3	1	1	2	2	1	2	0
TOTAL SPECIES	69	72	69	66	43	57	67	9

* These are species which have been occasionally collected on the oyster beds, but they were not collected during the systematic survey (Maurer and Watling 1973). These species are not included in the numerical total. Watling and Maurer (1973) contains the most complete listing of Delaware Bay benthos.

BK=Broadkill River, MS=Mispillion River, MK=Murderkill River, SJ=St. Jones River, LC=Leipsic River, PB=Planted Beds, NB=Natural Beds, WB=Woodland Beach.

The species typically associated with oysters and shells include: coelenterates, Aiptasiomorpha luciae, Diadumene leucolena, Garveia franciscana, Obelia spp., Sertularia argentea, Tubularia crocea; molluscs, Crepidula fornicata, C. plana, C. convexa, Mytilis edulis, Amygdalum papyria; polychaetes, Sabellaria vulgaris, Hydroides dianthus, Polydora websteri; amphipods, Cerapus tubularis, Corophium acherusicum, C. insidiosum; barnacles, Balanus eburneus, B. improvisus; ectoprocts, Membranipora tenuis, Conopeum tenuissimum; and the tunicate, Molgula manhattensis.

A number of the remaining animals live among these sessile forms, usually depending on them for attachment or food: nemerteans, Micrura rubra, Zygeupolia rubens; nudibranchs Tergipes despectus, Eubranchus exiguus; polychaetes, Eumida sanguinea, Eteone heteropoda; amphipods, Paracaprella tenuis, Cymadusa compta; and the pycnogonid, Callipallene brevirostris. Many of the above animals may be found in crevices between shells as well as those which find shelter in the oyster bed; bivalves, Petricola pholadiformis, Mysella planulata; xanthid crabs, Panopeus herbsti, Eurypanopeus depressus; isopod, Edotea triloba; amphipod, Parapleustes sp.; and the polychaete, Nereis succinea.

Cliona celata and Polydora websteri actively burrow into oyster shells. Active predators of adult oysters and spat and other molluscs include: gastropods, Urosalpinx cinera, Eupleura caudata, Busycon carica, B. canaliculatum, Polinices duplicatus, P. immaculatus; xanthid crabs; blue crab, Callinectes sapidus; flatworm, Stylochus

ellipticus. The oyster crab, Pinnotheres ostreum, and the pyramidellid snails, Odostomia impressa and Turbonilla interrupta, can be added to this list of oyster pests.

In the substrate between oysters and shells or under them in mud are found: polychaetes, Scoloplos fragilis, Glycera dibranchiata, Hereromastus filiformis; bivalves, Mercenaria mercenaria, Lyonsia hyalina, Tellina agilis, Mulinia lateralis, Solen viridis, Tagelus divisus, Macoma balthica; hermit crab, Pagurus longicarpus, horseshoe crab, Limulus polyphemus; naked goby Gobiosoma bosci and northern pipefish Sygnathus fuscus. In addition to typical inhabitants of oyster beds there are species more characteristic of other habitats: molluscs, Modiolus demissus, Melampus bidentatus, Littorina irrorata from the marsh; the polychaete Hypaniola grayi, the amphipod Ampelisca abdita, and the gastropod Nassarius obsoletus from nearby mud bottoms; the gastropod, Nassarius vibex and the polychaete Pectinaria gouldi from surrounding sandy areas; and the shrimp Crangon septemspinosa and Palaemonetes vulgaris and the blue crab Callinectes sapidus as vagile transients. The shrimp may be considered semi-permanent inhabitants in that they may also find shelter and food among the oysters.

A. Porifera:

Four species of sponges were collected: Halichondria bowerbanki, Microciona prolifera, Prosuberities microsclerus, and Cliona celata. Halichondria bowerbanki is a common sponge in our region (Watling and Maurer, 1973) but it was collected only once on the oyster beds (in

the St. Jones River). Dead colonies are frequently found washed ashore along the bay. Microciona prolifera was essentially restricted to the bay beds but it was also collected at two stations in the St. Jones River in the winter. We did not find this species to be particularly associated with oysters, however McDermott and Flower (1953) commented that M. prolifera was common enough on the Delaware Bay oyster beds to be a frequent hiding-place for mud crabs. Recent sampling has shown this species to be quite abundant in isolated areas. Microciona prolifera is considered a common oyster associate throughout New Jersey planted beds and lower seed beds (Kunkel-personal communication). Hartman (1958) reported this sponge to grow abundantly on oysters in Long Island Sound as did de Laubenfels (1947) on oysters in Beaufort, North Carolina. Hartman also reported collections of M. prolifera from Great Egg Harbor, New Jersey and off the New Jersey coast but not from Delaware Bay. Microciona prolifera is perennial in growth in Long Island Sound (Hartman 1958) and appears to be so in Delaware Bay. Merrill and Boss (1966) considered this sponge to be the dominant epizoic organism on oysters in a deep basin of the Patuxent River. In the same river, Cory (1967) reported M. prolifera to attach during the period July to September. Locally M. prolifera is most commonly observed in colder months (November-February). Its most usual structure is a fusion of erect lobes, a structure which is characteristic of estuarine conditions (Wells et al. 1960). Wells et al. (1964) commented that in North Carolina M. prolifera has been commonly observed and collected

from hard, clean sand bottoms. This has also been noted in Rehoboth and Indian River Bays (Maurer - unpublished data). This genus has not been reported commonly with oysters on the gulf coast but it can occur so thickly on oyster trays as to appear like red paint (Gunter-personal communication). Prosuberites microsclerus was collected from planted and natural beds in the spring and fall. Wells et al. (1960, 1964) described the seasonal occurrence and production of gemmules in some detail. Hartman (1958) does not include P. microsclerus in his list of marine sponges of southern New England.

Cliona celata was commonly found on the Delaware Bay oyster beds. Galtsoff (1964) considered this genus of boring sponge the most common animal associated with oysters. Cliona celata is not restricted to oysters but locally has also been found infesting shells of dead and live Mercenaria mercenaria. Apparently the calcareous substrate afforded by molluscs in general can be colonized. This sponge was found more frequently in the planted beds than in the natural beds and was infrequently collected live in the rivers. Shuster (1959) listed a salinity range of 15-36 o/oo for this species in Delaware Bay. We found huge growths of gamma stage C. celata in channels and sloughs within 7 miles (11.2 km) of the bay mouth to north of the St. Jones River. In a three-minute tow with a commercial hydraulic dredge, 30 bushels of sponge were collected. Hartman (1958) reported that detached stages are termed "bay pumpkin" or "whale dung." While large colonies have been obtained from Delaware Bay, a colony from East Haven, Connecticut reached 35 cm x 16 cm x 8 cm (Hartman

1958). In the planted and natural oyster beds the alpha or boring stage is most prevalent with some occurrence of the beta or overgrowing stage. The gamma stage, so conspicuous in the channels of the lower bay, has been infrequently collected in the oyster beds. Wells (1959b) recorded the gamma stage in North Carolina but noted its absence in Hatteras Harbor. Cliona celata can be found locally all year but appears to be more abundant in the fall months. Hartman (1958) lists several recorded occurrences of C. celata in Delaware Bay and suggests that additional searching would probably reveal the presence of Cliona vastifica Hancock. In view of the presence of five species of Cliona in Chesapeake Bay (Old 1941) and four species in Long Island Sound (Hartman 1958), other species of Cliona should be expected to occur in Delaware Bay. In fact, Kunkel (personal communication) has found Cliona lobata Hancock in parts of the bay where the salinity ranges from 15 to 25 o/oo. The incidence of infection by species of Cliona on Crassostrea virginica (both living and dead) in Long Island Sound ranges from 80 to 90 percent (Hartman 1958). Based on our observations on Delaware natural beds, estimates of infection would be less than 50 percent but on the planted beds estimates would be as high as 80%. In fact, infection among living oysters is considerably lower than in dead shells. Kunkel (personal communication) considers that infection is equally common in living oysters if not more common in some areas. Although C. celata is an oyster pest on Delaware beds, it does not appear to be as serious a pest as in Long Island Sound, Chesapeake Bay, or

Beaufort, North Carolina.

B. Coelenterata:

Among the coelenterates the anemones, Aiptasiomorpha luciae and Diadumene leucolena, were conspicuous throughout the study area. Metridium senile is most common near the mouth of Delaware Bay whereas the other two anemones are more common up bay and in the rivers. These species are similarly distributed over a wide salinity range in the Chesapeake Bay (Andrews 1953). Diadumene leucolena and A. luciae occurred together in all the rivers except the Leipsic, where the latter species was missing. These species are two of the most characteristic oyster associates, but are not restricted to the oyster community. As with many other members of the oyster community these species require only a tolerable salinity and a firm substrate. For this reason they are also considered common fouling organisms, and were found in the Patuxent fouling community from May through September (Cory 1967).

The following discussion of the hydroids draws heavily on Watling and Maurer (1972b) who identified 18 species from Delaware waters. In terms of diversity the hydroids were well represented in the oyster beds. One species, Obelia longicyatha was numerous and widely distributed. It was most common on the oyster beds in the rivers from April to June and September to January 1968-1969. This species was found growing on stalks of Garveia franciscana and Sertularia argentea as well as on oyster shells.

New colonies of Tubularia crocea set during June and September.

This hydroid was one of the most abundant and frequently collected species during the winter. Tubularia and Obelia are the commonest genera of coelenterates recognized as fouling organisms (WHOI 1952). In the fall of 1968 Garveia franciscana was collected only in the upper reaches of the Broadkill and Leipsic Rivers and at Woodland Beach. The following spring it was collected on pilings, jetties, oyster shells and other hard substrates from Woodland Beach to the mouth of the Bay. Colonies bearing sporosacs each with a single planula were found in the rivers during late May and early June 1969. By the fall of 1969 it has replaced O. longissima and O. longicyatha as the dominant hydroid fouling surfaces at the mouth of the Broadkill River. Again in January 1971 it was the most common hydroid in the Broadkill and other rivers but has since decreased in abundance. Bimeria franciscana, a synonym of G. franciscana, was cited as the most dominant fouling hydroid in San Francisco Bay (WHOI 1952).

Gonothyrea loveni was only found in autumn on oyster shells on the natural beds. It was considered a winter form in Chesapeake Bay by Calder (1971). Hartlaubella gelatinosa was collected during autumn and spring throughout the oyster beds. New colonies set on the planted and natural beds in April and May. This species is found in the polyhaline zones of Delaware Bay. Eulaomedeia angulata occurred once in May 1969 on oyster shells in the Murderkill River. Two species of "Campanulina" were taken from oyster shells in the Broadkill, Mispillion and Murderkill Rivers. Until gonophores of these species

can be examined their generic affinities will remain in doubt. Another winter species, Sertularia argentea was commonly collected from all the oyster beds except the St. Jones and Woodland Beach. This species and T. crocea are important local winter species whose habits have been described for other areas (McDougall 1943, WHOI 1952, Calder 1971). Hydractina echinata was never collected from oyster shells but was characteristically found on shells of the moon snail, Polinices duplicatus and mud snail, Nassarius obsoletus inhabited by hermit crabs. In this study H. echinata was found to be rare in the oyster beds and more characteristic of the lower bay. Merrill and Boss (1966) has reported this hydroid attached to a variety of molluscs occupied by hermit crabs but primarily in areas where the substrate consists of clean sand or other more coarse material.

C. Turbellaria:

Three species of Turbellaria were recognized: Bdelloura candida, Stylochus ellipticus and Notoplana atomata. Bdelloura was the characteristic commensal of the horseshoe crab, Limulus polyphemus. Stylochus ellipticus is considered a serious oyster predator, particularly of spat (Galtsoff 1964). The incidence of Stylochus ellipticus and its effect as a predator seems to vary geographically (Landers and Rhodes 1970). This species is harmful in Chesapeake Bay (Cory 1967, Shaw 1967, Merrill and Hanks 1969), but the same intensity of predation was not observed in Delaware Bay. This species was not collected in the systematic sampling program but it has been

collected at other times. Gunnell (1971) has studied the feeding behavior of S. ellipticus in Delaware Bay: his preliminary findings about predation pressure from this flatworm seem to corroborate ours. The third species, Notoplana atomata, was collected in dredge hauls and from strung cultch on oyster culture rafts in the rivers. It was easily washed from hydroids attached to the strung cultch. At present its effect on oyster populations is unknown. In addition, Kunkel (personal communication) has found Hoploplana inquilina Pearse to be locally common in recent years as a commensal in oyster drills. Stauber (1941) has reported on this earlier.

D. Nemertea:

The nemertines Micrura rubra, Tetrastemma elegans, Zygeupolia rubens, and Cerebratulus lacteus were minor elements of the oyster bars and showed no preference for bay beds or the high salinity areas of the river beds. They were most common in intercalated mud-shell or in thick mud sediment traps provided by hydroids and fleshy ectoprocts. Zygeupolia rubens was reported to occur abundantly in intertidal sand and sandy bottoms, M. rubra from muddy bottoms, and T. elegans from eel grass in Chesapeake Bay (McCaul 1963). Cerebratulus lacteus is locally more abundant than the other nemertines and it is more frequently associated with soft muddy bottoms or mud bottoms with scattered rocks. Another species, Malacobdella grossa (Müller) was taken from the gills of live Mercenaria mercenaria south of the planted oyster beds. Its commensal relationship with bivalves is well known (Ropes 1963, Gibson 1968).

E. Mollusca, Pelecypoda:

Among the species of pelecypods, few show any direct ecological association with the oyster. Bivalves such as Amygdalum papyria, Mytilus edulis, Mysella planulata, Modiolus demissus were collected with their byssal threads attached to the oysters. Stanley (1972) has proposed that M. demissus is an endobyssate bivalve living attached but partly or entirely buried in soft sediment. We have treated this species as epifaunal in this paper. In the rivers M. demissus and A. papyria were most commonly attached to marsh vegetation. For example, in the Broadkill River area the former species was more common intertidally on roots of Spartina alterniflora than subtidally (Lent 1967). The latter species was always far less abundant than M. demissus and occurred subtidally. Chanley and Andrews (1971) reported that adults of A. papyria occur in salinity above 5 o/oo in Chesapeake Bay and its tributaries. The ribbed mussel was uncommon on the bay beds except at Woodland Beach. Here the reduced salinity and proximity of the marshes as a source of brood stock favor heavy setting on any firm substrate. Kunkel (personal communication) reports that the hooked mussel, Brachidontes recurvus Rafinesque formerly was frequently found on upper bay beds (above the Cohansey River) and is now very rare. The reason for its decline is unknown but it was coincident with the mid-60's drought. Cory (1967) reported this mussel as a prominent member of the oyster bed community. Allen (1954) found a similar relationship with plants for M. demissus and also reported (Allen 1955a) that A. papyria

was uncommon in the Maryland part of Chesapeake Bay but when it occurred it was usually attached to the grass, Ruppia maritima Linnaeus. On the other hand, Mytilus edulis and Mysella planulata were frequently found with subtidal populations of oysters. In some cases (e.g., Broadkill River) M. edulis forms small lenticular reefs. This species occurred in inlets between barrier islands and the mouth of Chesapeake Bay (Chanley and Andrews 1971).

Both in the bay and rivers the hard clam, Mercenaria mercenaria was commonly collected in fine sands with clay, near and in, oyster bars. Local oystermen consider old, noncultivated oyster beds as productive sites for harvesting hard clams. We found this to be true while surveying for hard clams in abandoned planted oyster beds. Castagna (1970) has suggested that juvenile hard clams survive predation better in certain shell fragment sizes than others. Apparently shell fragments afford the young clams a protection site until they attain a critical size when they are no longer susceptible to predation from crabs. Surveys in progress will provide additional information on the biology of the hard clam. Mercenaria mercenaria is considered abundant in salinities above 15 o/oo in Chesapeake Bay (Chanley and Andrews 1971).

Infaunal species such as Macoma balthica, Mya arenaria, Solen viridis, Tagelus divisus, Tellina agilis and Nucula proxima were mainly collected in mud, fine sand, and shelly-mud bottoms between oyster bars. In most cases only dead valves or juveniles of these species were taken because these bivalves are excellent burrowers and

could not be reached by the oyster dredge. Solen viridis, Tagelus divisus, Tellina agilis, and Nucula proxima commonly occurred in the bay and river mouths whereas Macoma balthica and Mya arenaria also ranged into and beyond the limits of the oyster bars in the rivers. These latter two species are known to occur in salinity as low as 5 o/oo and show preference for sediments with some silty mud (Allen 1963, Chanley and Andrews 1971). The presence of many valves of the razor clam and the soft clam in the planted beds probably indicates a high abundance of those species.

A few bivalves showed an affinity for a specific substrate. Cyrtopleura costata, Barnea truncata, and Petricola pholadiformis were characteristic in sections of rivers (e.g., Leipsic, St. Jones) with clay and peat moss (marsh debris) substrate. The association between P. pholadiformis and clay has been noted many times (Abbott 1954, Ansell 1970). Cyrtopleura costata was more abundant than B. truncata and was also collected more commonly with P. pholadiformis than with B. truncata. Andrews (1953) reported this pholad to occur primarily in the deep waters of Chesapeake Bay proper and Chanley and Andrews (1971) limit its distribution to waters of greater than 10 o/oo salinity.

Bivalves such as Gemma gemma, Mulinia lateralis, and Lyonsia hyalina showed no particular association with the oyster. Mulinia lateralis prefers a sandy substrate (Allen 1955b). It occurred in considerable numbers in the river mouths. This distribution agrees with the field salinity ranges (8-25 o/oo) reported by Castagna and

Chanley (1966) for M. lateralis. Further, based on experimental data, these authors suggested that the coot clam's distribution is primarily controlled by factors other than salinity. The local distribution and abundance of M. lateralis indicates that this species is ecologically significant. Calabrese (1969) cites a number of fish, invertebrates, and birds which feed on this clam. In contrast to M. lateralis, which seems to thrive near the river mouths, Gemma gemma occurred locally in small numbers in salinity less than 20 o/oo, but has been reported as commonly occurring in waters above 10 o/oo in the Chesapeake (Chanley and Andrews 1971). The gem clam is extremely abundant in Rehoboth and Indian River Bays, where counts of subtidal populations have totaled 280,000/m² (Maurer - unpublished data). In his comprehensive study of Gemma gemma, Sellmer (1967) recorded 200,000 or more per square meter on an intertidal beach. Gemma gemma also serves as a source of food for many bottom feeding animals, although it is more significant in sand-mud bottoms than the harder oyster bottoms. Lyonsia hyalina occurred infrequently and sporadically throughout the oyster beds and is similar to G. gemma in its preference for soft bottoms and in its salinity tolerances (Chanley and Andrews 1971).

Anomia simplex d'Orbigny occurs widely throughout the Delaware Bay region in salinity primarily above 15 o/oo but was not collected in this study. Kunkel (personal communication) reported that this species was formerly locally abundant in New Jersey planted grounds, frequently occurring in all higher salinity (20+o/oo) areas.

It has been cited as an oyster pest in Long Island Sound where its rapid growth is known to smother spat (Loosanoff and Engle 1941). Mackenzie (1970) noted that a light set of A. simplex in the same area caused little mortality. These two sources emphasize how populations can fluctuate widely from year to year. Our experience with A. simplex is primarily restricted to Rehoboth and Indian River Bays where it is attached to algae and occurs in moderate numbers. It is found commonly in waters above 10 o/oo in Chesapeake Bay (Chanley and Andrews 1971).

F. Mollusca, Gastropoda:

In contrast to the bivalves the gastropods show strong association with oysters. Among 22 species of snails collected, 10 are known to be oyster predators or bivalve pests. The economic and ecologic significance of species like Urosalpinx cinera, Eupleura caudata, Busycon canaliculatum, B. carica, Polinices duplicatus, P. immaculatus, Turbonilla interrupta and Odostomia impressa is well documented (Stauber 1943, Hanks 1953, Loosanoff 1956b, Carriker 1951, 1955, Wells 1959a, Wood 1968, Mackenzie 1970, and Manzi 1970). Although relatively common on the southern margin of the natural oyster beds whelks are not considered limiting predators here. On the other hand, most mortality of 1971 spat was attributed to drills on the Ridge and Silver Beds. Local oystermen consider both drills and whelks as a serious problem in the planted beds. In an oyster transplant study (Maurer - unpublished data) 800 whelks per acre were estimated for a bed near the southern margin of the planted beds. Planted beds farther north yielded lower counts. In New

Jersey planted beds and intertidal flats, drills prey heavily on the oysters. In Delaware, drills and whelks extend farther upstream in the southern rivers than in the northern rivers. Distribution of drills in the rivers is spotty and unpredictable; for example, the Broadkill, St. Jones, and Leipsic rivers have low numbers whereas the Mispillion and Murderkill rivers contain appreciable numbers.

A great deal has been made about the ectoparasitic habit of pyramidellids (Loosanoff 1956a, Wells 1959a, Fretter and Graham 1949). For example, Wells (1959a) found Odostomia impressa primarily on oyster beds in Newport, North Carolina and Hopkins (1956) described how O. impressa parasitizes southern oysters. Locally, two pyramidellids, Odostomia impressa and Turbonilla interrupta were collected from oysters. During the fall of 1971 as many as five pyramidellids were observed on a single adult oyster. In most instances these snails occurred on the bay beds and rarely in the rivers. Kunkel (personal communication) reports that Odostomia has a spotty distribution over a wide salinity range and that it may be locally abundant at one time and place and be absent there a few months later. These species together with other pyramidellids occur in Rehoboth and Indian River Bays where there are no natural oyster beds. The abundance of these pyramidellids without this commonly cited host suggests another mode of feeding. Many pyramidellids are not specific in their host selections (Scheltema 1965). Moreover, pyramidellids include a variety of bivalves, coelenterates and tubicolous polychaetes in their diet and these are

locally abundant. Odostomia impressa has been recorded as feeding on Crepidula convexa, Urosalpinx cinera, and Molgula manhattensis and is not host specific for oysters (Allen 1958). We agree with Sanders (1958, 1960) that certain pyramidellids may not be obligate ectoparasites. Perhaps they become deposit feeders when hosts are missing. In the oyster beds this situation does not often arise. But exceptions like those mentioned indicate a much greater range in feeding habit for certain taxonomic groups than previously recognized. Certain bivalves traditionally considered deposit feeders are known to function as suspension feeders when they are confronted with a non-deposit feeding environment (Maurer 1967a, 1967b). This type of feeding flexibility has all kinds of ramifications when applied to trophic levels and energy flow. It becomes increasingly difficult to simply categorize the feeding type of marine invertebrates, which in turn makes energy modelling more tenuous than it is.

The effect of predation by the moon snails, Polinices duplicatus and P. immaculatus, on oysters appears negligible. In fact our impression is that P. duplicatus exerts a greater effect on other bivalves, specifically Spisula solidissima Dillwyn and M. mercenaria, than on oysters. Evidence of predation by moon snails is particularly clear on the Cape Henlopen tide flats. Carriker (1951) cites a number of examples of predation by P. duplicatus and refers to the high incidence of predation on the Cape May, New Jersey tide flats. The smaller naticid, P. immaculatus, is more frequent subtidally.

Common oyster associates are the slipper shells, Crepidula

fornicata, C. plana, and C. convexa. These snails can become oyster pests when they attach in great numbers, thus competing for space and food with oyster spat (Loosanoff and Engle 1941) and possibly overgrowing the spat (Mackenzie 1970). On Delaware beds C. plana and C. fornicata are frequently found in separate clusters on the same substrate. Franz (1970a) described the shell shape of C. convexa in relation to substrate diversity. In addition to oysters, horseshoe crabs and whelks are favorite sites for attachment of slipper shells. Distribution of Crepidula is most abundant in salinity above 20 o/oo. Andrews (1953) considered them of minor importance as a result of predation by oyster drills.

Two species which occur sporadically in the rivers but are more common in the bay are Anachis avara and Mitrella lunata. These gastropods are considered carnivores and are particularly effective in preying on small sessile invertebrates (Russell-Hunter and Brown 1964).

These species, plus Anachis translirata (Ravenel) occur in great numbers on the algae in the smaller bays. Despite its commonplace occurrence little is known of the ecology of A. avara (Scheltema and Scheltema 1963). Anachis avara and A. translirata live on different substrates but are commonly confused. The former was collected by Scheltema (1968) from Cape May, New Jersey and Little Creek, Delaware. According to Scheltema A. translirata favors firm substrates and A. avara favors eel grass. These species, together with M. lunata, Haminoea solitaria, Retusa canaliculata, and Acteon punctostriatus

are not abundant and widespread in the oyster beds but are extremely abundant in the smaller bays which have greater algal growth than Delaware Bay.

The remaining species of gastropods fall into two habitat groups; first, the marsh and mud snails, and second, the hydroid feeders. Melampus bidentatus is particularly abundant on the high marsh and was only occasionally washed into the rivers. This species hibernates and is generally absent from the marsh surface during the winter (Hauseman 1932, Allen 1954, Apley 1970). In Delaware, the mud snail Nassarius obsoletus ranges from the mouth of the bay to Woodland Beach. The mud snail is particularly common on the low marsh and the clay mud banks of the rivers proper. This species has been studied extensively and its ecology is now better known than most common gastropod species along the Atlantic Coast (Scheltema 1964a). This species is abundant intertidally; it lives upon a variety of substrates but prefers silt and mud. In estuaries it is restricted to the seaward end, generally to waters with a salinity exceeding 15 o/oo. Carriker (1951) suggested that accidental consumption of newly set hard clams by browsing snails deserved further study; however, Scheltema (1964a) considered the mud snail primarily a scavenger. Other nassariids such as N. trivittatus and N. vibex were also taken inside the river mouths. Nevertheless, these species are more characteristic of bay beds on sand or silty-sand bottoms. Nassarius trivittatus is most often found subtidally but may also occur intertidally (Scheltema 1964b, Scheltema and Scheltema 1965).

An interesting feeding habit for N. vibex has been reported where in aquarium studies this snail fed on eggs of polychaetes in preference to carrion and detritus (Hurst 1965). Preliminary laboratory studies (D. Palmer - personal communication) on lethal temperatures provides experimental evidence to explain the intertidal distribution of N. obsoletus compared to the subtidal distribution of N. vibex and N. trivittatus. The latter species suffered greater mortalities as higher temperatures were approached. The resistance of the mud snail to high temperature was also studied by Nagabhushanam and Sarojini (1963).

The nudibranchs, Tergipes despectus, Eubranchus exiguus, and Doridella obscura were usually found on hydroids and algae attached to oysters. Franz (1970b) includes these species in his list of nudibranchs from New Jersey. Franz (1967) considers Corambella depressa Balch a synonym of Doridella obscura Verrill. This species was the most abundant nudibranch found in this study and appeared to be less dependent on the presence of hydroids than the other nudibranchs. This would suggest a type of feeding habit other than browsing on hydroids. Franz (1967) reported large populations of D. obscura in lower Delaware Bay, particularly in deep water [20-25 feet (6.2-7.8m)] oyster beds and in the intertidal zone. He always found the nudibranch in association with and feeding on encrusting ectoprocts, including Membranipora crustulenta [= Conopeum tenuissimum (Canu)] in the intertidal and Acanthodesia tenuis (= Membranipora tenuis Desor) in deep water. Even though our study was confined to

subtidal oyster populations, we found the same association between D. obscura and the ectoprocts. Swennen (1961) reported that Tergipes despectus occurs on mud flats and is very resistant to fluctuations in temperature and ranges from marine to 10 o/oo salinity. Further he commented that colonies of the hydroid Laomedea (Obelia of this study) without T. despectus were rare in the Netherlands. In fact T. despectus has the same salinity range cited by Swennen (1961). However, this species has not as yet been collected intertidally. Although T. despectus was collected from species of Obelia attached to oysters in the rivers and bay, it was also collected from other species of hydroids, principally Garveia franciscana. This nudibranch has also been taken from Sertularia in the New England area (Moore 1950). It is our impression that T. despectus is not restricted to feeding on species of Obelia alone and probably includes other hydroids in its diet. Confirmation of this will have to wait until field or laboratory observations can be made. Swennen (1961) commented that Eubranchius exiguus penetrates far into brackish waters (5-7 o/oo). He also observed it feeding on Laomedea longissima, L. geniculata, L. dichotoma, and L. loveni. Our findings essentially agree with Swennen's except they include other species of Obelia (Laomedea of his study) and species from other genera of hydroids.

G. Polychaeta:

Among the 20 species recorded only four, Hydroides dianthus, Polydora websteri, P. ligni, and Sabellaria vulgaris show a positive association with oysters and only 5 species, Harmothoe extenuata,

Lepidonotus sublevis, Eteone heteropoda, E. lactea, and Eumida sanguinea are associated with the mud and debris accumulated by epifaunal organisms. Species like Scoloplos fragilis, Spiochaetopterus oculatus, Owenia fusiformis, Pectinaria gouldi, Hypaniola grayi, and Streblospio benedicti occur more commonly in substrates with other than a shell bottom. All these species are usually dependent on a specific substrate to burrow into, to construct tubes in, or to feed upon. Populations of these species are commonly found in the sandy-mud bottom of the smaller bays. Nereis succinea is a special case in that it occurs in almost every substrate type we have encountered. Even though it was abundant in crevices among oysters and shells, this species was also found in mud, hard clay, and peat bottoms where no other macroscopic species were collected. Shuster (1959) lists the range of salinity tolerance for this species as 8-31 o/oo. Based on our work and the literature this range would extend from 1-31 o/oo [M. Taylor, personal communication, and Goerke (1971)]. Thus, to indicate N. succinea as a specific oyster associate would be misleading. Among errant polychaetes Nereis was cited as the most frequent genus of fouling organism and Harmothoe was second (WHOI 1952). Andrews (1953) asserted that N. succinea is probably the most abundant polychaete in Chesapeake Bay and was found almost anywhere some mud or debris was collected. We are unsure whether this species is the most abundant in Delaware Bay, but consider it one of the most abundant and widely distributed polychaetes in the area.

Although not exclusively restricted to oysters, the tube dwellers Hydroides dianthus and Sabellaria vulgaris were commonly found on oyster shells. The former species (a serpulid) secretes a calcareous tube whereas the latter species (a sabellariid) builds tubes by cementing together sand grains and/or shell fragments. Populations of both species are most common in high salinities (Andrews 1953) and occurred in greater abundance at the river mouths rather than in the upper reaches. Both species occurred in all the bay beds and rivers except the Leipsic River, which did not contain the serpulid. Hydroides dianthus locally requires a hard substrate such as shell, pilings, and sunken boats to settle on. Among sedentary worms serpulids have been cited as the most abundant fouling group with Hydroides as the most abundant genus (WHOI 1952).

This is not the case with the sabellariid. Sabellaria vulgaris may grow in great numbers and size to form reefs (Kirtley and Tanner 1968, Gram 1968). Such reefs occur along the western side of Delaware Bay (Wells 1970). Sabellaria vulgaris occurs both subtidally and intertidally. While some specimens occur in all the rivers, optimum reef development appears to occur between the Mispillion and Broadkill Rivers. Although salinity is a limiting factor for the distribution of this species in an estuary, the substrate must also be critical. At the upper boundary of the oyster beds in the Murderkill River massive developments of this species were found (tube aggregations one foot long). Normally the substrate is shelly mud or mud in this portion of the rivers. However, a nearby

land fill operation resulted in excess sand being deposited in the river at that site. The inordinately rapid growth of S. vulgaris in the river is directly attributable to the source of sand. Wilson's extensive work over the years (1929, 1968a, 1968b, 1970a, 1970b) has documented the ecological significance of substrate to the settling and growth of sabellariids. In some cases S. vulgaris occurred so densely that it created a hard bottom between oyster beds. Local oystermen consider S. vulgaris a pest. However, Kunkel (personal communication) reports that New Jersey oystermen claim that Sabellaria overgrowing oyster spat protects spat from drills. He has found many more living spat in an area of heavy Sabellaria overgrowth than on several adjacent areas lacking appreciable overgrowth. This polychaete actively competes for setting space with oyster larvae thereby reducing the spat set. This problem was particularly noticeable during the summer of 1971. Based on its number of occurrences in samples, Sabellaria vulgaris ranked highest as an oyster associate in the rivers.

Species of Polydora were also characteristic of the oyster beds, which is normally the case (Galtsoff 1964). In Delaware Bay both P. websteri and P. ligni were found. Nelson and Stauber (1940, 1941) stated that New Jersey oyster beds harbored great numbers of P. ligni. These species together with P. ciliata (Johnston) have frequently been confused and the names have been used interchangeably (Haigler 1969). This in turn has lead to confusion about their ecology. Our work indicates that P. websteri infests oyster shells to form mud

blisters and that P. ligni normally forms mucilaginous tubes of silt. The latter species is very selective in its choice of particle size for tube construction. A few specimens of P. ligni were taken from mud blisters in oyster shells, but we agree with Haigler (1969) that P. websteri is the principal shell-boring polychaete in the Chesapeake-Delaware Bay region. Existing data on P. ligni have been summarized by Orth (1971) who reports it as the most abundant polychaete in the Chesapeake Bay area.

Examination of several hundred oysters picked at random indicates that P. websteri can be a serious oyster pest locally. The frequency of incidence and degree of activity of this polychaete vary from river to river and is most intense from July through September. Work in the laboratory on growth of spat at continuous, elevated temperatures (25-30°C) produced some unexpected side-lights. During the experiment, which lasted six months (March-August), P. websteri reproduction was almost continuous. The high temperatures apparently promoted the high productivity of the polychaetes. In turn the oysters were continually reinfested giving a very high level of incidence. This experiment may, on a gross level, simulate boring activity under natural conditions during the summer.

Galtsoff (1964) reported that on several occasions the reproduction of P. ligni on oyster bottoms of Delaware Bay was so rapid that almost every live oyster in the affected area was killed by the accumulation of mud consisting of hordes of live worms and their tubes several inches thick.

H. Arthropoda:

In the oyster beds, the most frequently collected amphipod was Melita nitida. This species, unlike many epifaunal non-tube dwellers, also occurred on oyster shells which lacked other epifaunal organisms. It was taken in Delaware Bay in both the marine and polyhaline zones in fall and spring. In terms of abundance and distribution M. nitida was particularly characteristic of river oyster bars. In Chesapeake Bay M. nitida was also found in mesohaline regions (Feeley 1967). The corophiids, Corophium insidiosum, C. lacustre, C. acherusicum, Unciola serrata, the gammarids, Gammarus daiberi, G. tigrinus, G. mucronatus, and Parametopella cypris and Parapleustes sp. were taken more frequently from the oyster beds than elsewhere. The corophiids, in particular, use the hard substrate afforded by oysters as a site of attachment for their tubes. Wells (1961) commented that amphipods were usually numerous among shells with Corophium, building mud tubes upon shells and thus further adding to the accumulation of sediment. In the series of oyster growing experiments at elevated temperatures in our laboratory, C. insidiosum showed the same pattern of continuous reproduction as P. ligni. Cerapus tubularis attached its chitinous tube to asbestos plates in similar experiments. Corophium insidiosum was collected almost exclusively from the Broadkill and Mispillion Rivers and bay beds. A more uncommon corophiid, Unciola serrata, was found in the sand tubes of the polychaete Sabellaria vulgaris. Although we have recognized a strong association between corophiids and a hard

substrate, corophiids are not restricted to hard substrates and may also be found on algae and hydroids. Species of Corophium have been commonly recorded as important elements of fouling studies and among the Amphipoda are second only to species of Caprella (WHOI 1952).

Ampeliscids were found in crevices between oyster shells. This group of amphipods normally occurs on soft bottoms (Mills 1967). In some cases (Broadkill River) their tubes were found in such great numbers as to rival the abundance recorded in Rehoboth and Indian River Bays (Watling and Maurer 1972a). Occurrences on the oyster beds were usually associated with mud-shell and mud bottoms. Exclusive of the tube dwelling Ampeliscidae and Corophiidae the remaining amphipods occurring on the oyster bars were non-tube dwelling epifaunal species. These species were extremely abundant among hydroids. The occurrence of Parapleustes sp., Parametopella cypris, and Paracaprella tenuis seemed to be influenced by the presence of large colonies of the hydroid Hartlaubella gelatinosa with Parapleustes sp. being found primarily in the sediment at the base. Parametopella cypris and Parapleustes sp. were also found in the tangled masses of the hydroid Tubularia crocea. Parapleustes sp. was the second most abundant amphipod in this study: as one moves up bay it becomes gradually more numerous in the area of the bay beds and Leipsic River. Gammarus daiberi was collected on the natural beds and G. tigrinus from the Woodland Beach area. The latter species was also collected from the upper boundary of the Broadkill oyster beds. Both species should be expected to occur in the upper reaches of the rivers as

they are mesohaline in distribution (Bousfield 1969).

The isopods collected were Edotea triloba, Chiridotea nigrescens, and Cyathura polita. None of the species were particularly abundant. Edotea triloba and Cyathura polita occurred in all the rivers except that the latter was not taken from the Leipsic. Edotea triloba was also collected from the bay. Cyathura polita was associated with sediment consisting largely of coarse, clean sand. Burbanck (1962) speculated whether populations of Cyathura can become associated with oysters or whether their occurrence with oysters was due to animals being temporarily lodged there following transportation from other locations. Finally Burbanck (1967) has frequently found C. polita with benthic animals such as Nereis, Hypaniola, Macoma, Nassarius, Gammarus tigrinus and Corophium, which certainly mirrors conditions in Delaware's estuarine rivers.

Among the decapods, the mud crabs, Panopeus herbsti, Eurypanopeus depressus, Neopanope texana sayi, and Rhithropanopeus harrisi were most common. Neopanope texana sayi was primarily restricted to the bay beds, the more southern rivers (i.e., the higher salinity rivers). It appears to be the most abundant xanthid on the intertidal Henlopen sand flats at the mouth of Delaware Bay. Shuster (1959) lists a salinity range of 15-31 o/oo for this species. McDermott and Flower (1953) found it scarce in the littoral area and regions of low salinity in Delaware Bay. Ryan (1956) reported that in Chesapeake Bay N. texana sayi may have declined in numbers in recent decades. McDermott and Flower (1953) stated that P. herbsti was most common in the area

of the bay where it was condominant with N. texana sayi. We found P. herbsti to be common in the bay and also abundant in the rivers. Schwartz and Cargo (1960) reported the salinity range of P. herbsti as 10-34 o/oo. As the abundance of P. herbsti declines progressively in the northern rivers another mud crab, Rhithropanopeus harrisi becomes more important. Although R. harrisi occurs on the bay beds, this species was most common in the rivers, particularly at the upper reaches of the bars. It has been found in salinities as low as 1.0 o/oo (M. Taylor, personal communication.) McDermott and Flower (1953) considered this the dominant species in the upper part of the natural beds in Delaware Bay. In the Leipsic River this species almost rivals P. herbsti in numbers.

Cory (1967) collected R. harrisi from panels thick with hydroids that had been placed in the Patuxent River. This crab was most numerous during June and August. Still another species of mud crab, Eurypanopeus depressus, was abundant in the river and oyster beds. McDermott and Flower (1953) found it to be abundantly distributed in the middle portions of Delaware Bay. Ryan (1956) commented that this species was collected at salinities ranging from 5-20 o/oo although he cited Cowles (1930) as catching this species in offshore waters of Chesapeake Bay. This would suggest a higher salinity range than 20 o/oo. Based on our work this salinity range can be extended to at least 28 o/oo, since E. depressus was found in the Broadkill River with P. herbsti. Indeed these two species were the most abundant species of mud crabs in the rivers. A noteworthy

omission from our collection was Hexapanopeus angustifrons (Benedict and Rathbun). This species was identified by McDermott and Flower (1953) who considered it the least common of local mud crabs. Ryan (1956) states that H. angustifrons was an uncommon species in his study and that its salinity range was 18-32 o/oo. The same author reported that E. depressus showed a high coincidence with oysters and was the most abundant mud crab followed by R. harrisi. In Delaware Bay McDermott and Flower (1953) regarded N. texana sayi as the most abundant mud crab with E. depressus, P. herbsti, and R. harrisi equally important in certain areas. Ryan (1956), McDermott and Flower (1953), and McDermott (1960) state that mud crabs can be significant predators on oysters. Under laboratory conditions they are size selective, preferring thin shelled individuals. In field studies Mackenzie (1970) found N. texana sayi to be an oyster spat predator. Throughout our survey almost every oyster box contained at least one crab. We do not attribute the mortality of the oyster to the resident crab, but this indicates the abundance of these crabs and their potential predation on oyster spat. Among decapods, several species of xanthids are dominant fouling organisms (WHOI 1952).

The remaining crabs collected include Callinectes sapidus, Pagurus longicarpus, and Pinnotheres ostreum. In addition, Kunkel (personal communication) reports Pagurus pollicaris Say as occurring frequently in high salinity (25+ o/oo) portions of the bay. Pagurus longicarpus was also primarily restricted to the higher salinities of the bay beds or the mouths of the southern rivers. However, Roberts

(1971) reports that mortality of developing larvae is unaffected in salinities from 18.5 o/oo to 30 o/oo. We do not consider P. longicarpus to be an important oyster associate. However, Roberts (1968) has shown in laboratory experiments that P. longicarpus is capable of feeding on large pieces of oyster tissue and Mackenzie (1970) suggested that this hermit crab could be a possible predator of oyster spat.

Because of its wide salinity tolerance Callinectes sapidus was found everywhere. In most cases specimens were juveniles, adults presumably avoiding the oyster dredge. During the late fall some adults were found to have burrowed into the mud in the rivers. This was surprising in view of the often stated pattern which has them migrating to the deeper waters of Delaware Bay for winter hibernation (Shuster 1960). The blue crab is known to be an oyster enemy (Galtsoff 1964), particularly of spat (Menzel and Hopkins 1956), but we have been unable to locally document this.

Extremely large numbers of the oyster crab, or pea crab, Pinnotheres ostreum, have been reported in some New Jersey oyster beds (Stauber 1945, Flower and McDermott 1952, McDermott 1961, Christensen and McDermott 1958). This species is also abundant enough to reduce yields of meat in oysters from Chesapeake Bay (Haven 1959, Andrews et al. 1968). Stauber (1945) demonstrated that the pea crab was an oyster parasite, providing data to show that the incidence of parasitism ranged from a high of 80% in 1941 to 55% in 1942. Christensen and McDermott (1958) recorded infestations ranging from 12-69% in the lower bay with lower incidence in the upper parts of New Jersey's natural seed beds.

After opening approximately 1000 oysters for various studies, fewer than 25 specimens of P. ostreum were found. These oysters equally represented river and bay oysters. This species has become rare in recent years throughout the New Jersey oyster areas (Kunkel - personal communication). He suggests that this may be a result of the drastically reduced oyster population caused by MSX. It is possible that salinity may be limiting infestation of pea crabs on Delaware's oysters and promoting it among New Jersey's beds. Christensen and McDermott (1958) suggested that salinity may limit molting in the pea crab. Since the greater part of our survey was in a salinity range of 12-25 o/oo, and their work was mainly in salinity of 20-30 o/oo, the difference in degree of infestation may be explained on that basis. Stauber (1945) emphasized the fluctuation of pea crab incidence as another example of the cyclic nature of marine populations. This suggestion together with the slightly lower salinity range we were working with leads us to conclude that the pea crab is not now a pest on Delaware oyster beds.

The shrimp, Crangon septemspinosa and Palaemonetes vulgaris were collected abundantly in the rivers and bay. In the majority of samples P. vulgaris outnumbered C. septemspinosa. Another species of shrimp P. pugio was collected at a few stations in the St. Jones River. In the Delaware Bay region the distribution of species of Palaemonetes suggests that it may be controlled by salinity. Palaemonetes vulgaris is more common in higher salinity than P. pugio which is more common in the upper bay (Ferrante - personal communication). A third

species, P. intermedius (Holthius), was identified near the freshwater limit of the Broadkill River (Price - personal communication). Fleming (1969) suggests that P. vulgaris and P. intermedius are conspecific but that this should be supported by detailed populational and ecological data. Although shrimp are considered as transients and not oyster associates, Price (1962) identified juveniles of Mytilus edulis, Gemma gemma, polychaetes, isopods, and amphipods from the gastric mill of the sand shrimp C. septemspinosus. Further he suggested that C. septemspinosus may derive benefit secondarily from the great quantities of detritus emitted from salt marshes bordering Delaware Bay by consuming mysids, small bivalves nourished by decaying detritus or bacteria associated with the detritus. Perhaps this species and other shrimp may find an oyster bed with its many residents a productive place for foraging and scavenging (Dales 1957).

The mysid, Neomysis americana was rarely collected. This species is one of the most abundant members of the zooplankton in the bay area (Hulburt 1957, Hopkins 1965). We consider this mysid as a transient species throughout the oyster beds. The mysids, sand-shrimp, and xanthid crabs are major food items for the weakfish and northern sea robin (Daiber and Smith 1968).

Two species of barnacles were collected: Balanus improvisus and B. eburneus. The former species was three to four times more abundant than the latter. Balanus eburneus was not taken in the bay beds. Zullo (1963) reported that B. eburneus is seldom found subtidally. In Chesapeake Bay B. eburneus was of little importance as a fouling

organism on oyster cultch but is the most serious fouler of pilings in the intertidal areas (Andrews 1953). On the other hand, B. improvisus caused nearly all the barnacle fouling of oyster cultch in the same area. It was distributed throughout the bay and up the rivers almost to fresh water, but was most abundant in salinity of approximately 15 o/oo where it was the chief fouling organism (Cory 1967). Both species are known to withstand extreme variations in salinity but Gordon (1969) found B. improvisus distributed in lower salinity in Chesapeake Bay than B. eburneus. Andrews' (1953) discussion of B. improvisus distribution in Chesapeake Bay holds for Delaware Bay except that in this case it was not readily observed in salinity lower than 10 o/oo. Balanus improvisus was one of the most characteristic oyster associates found in this study. This association varies geographically in that B. eburneus was cited as the most serious fouling pest of the Beaufort region with B. improvisus much more rare (McDougall 1943). Among acorn barnacles, species of Balanus are most often reported as fouling organisms (WHOI 1952).

One species each of pycnogonid and xiphosurid was collected. The pycnogonid, Callipallene brevirostris, was rare and then exclusively taken from hydroids and fleshy ectoprocts. Because of its rareness, this species probably has little influence on the oyster bar community. In contrast the xiphosuran, Limulus polyphemus, may exert a great deal of influence. This arthropod is abundant throughout the Delaware Bay area. During the spring sampling period it occurred in such great numbers as to inconvenience the dredging

operation. It was taken at almost every sampling station. It was rare only when hard bottom ("sand coral," shell deposits, sand) was encountered. Considerable predation of molluscs such as juvenile soft clams and hard clams has been demonstrated for L. polyphemus (Turner et al. 1949, Carriker 1951, Smith 1953, Shuster 1952). Because of its local abundance and molluscan feeding habit it is suggested that L. polyphemus may be a predator on oyster spat. This predation may be masked by the combined effects of the mud crabs.

I. Ectoprocta:

The major ectoprocts in the oyster beds are Membranipora tenuis and Conopeum tenuissimum. Both species occurred abundantly in the bay and especially in the rivers. Although both species occur at Woodland Beach, the almost complete absence of M. tenuis from the Leipsic River substantiates the salinity tolerance observations of Osburn (1944). He found that Membranipora crustulenta (Pallas) (= Conopeum tenuissimum of this study) is more serious as an oyster pest in low salinity water whereas M. tenuis favors salinities of approximately 15-20 o/oo. Galtsoff (1964) also lists these species as serious competitors for space. In the lower salinities of the Patuxent Cory (1967) showed that new colonies of C. tenuissimum were always more abundant on fouling panels than M. tenuis. The same pattern of occurrence has been found in Delaware Bay. Species of Membranipora have been cited as the most common encrusting ectoproct (WHOI 1952). In addition to their effect on oysters these ectoprocts commonly overgrow worm tubes of S. vulgaris and H. dianthus. However, we are unsure whether

this fouling causes death to the polychaetes since the association was found with both inhabited and uninhabited tubes. Mackenzie (1970) commented that calcareous bryozoans were extremely common on oysters and other hard surfaces in Long Island Sound. According to him they kill spat by growing either between their two open valves or completely over both valves and sealing them. We have observed both types of fouling. These ectoprocts are among the most characteristic oyster associates on Delaware beds.

Fleshy ectoprocts like Alcyonidium verrilli, Amathia vidovici and Anguinella palmata occurred rarely. Kunkel (personal communication) considers all three species as common. Alcyonidium verrilli is common in high salinity (23+ o/oo) areas, and Anguinella palmata has wide distribution and is often very abundant on shallow grounds of Maurice River Cove. Amathia vidovici is very common in late summer-fall on New Jersey seed beds. In contrast Osburn (1944) reported that A. verrilli appeared to grow larger and more profusely in Long Island Sound than in Chesapeake Bay. Curiously Williams and Porter (1964) found A. verrilli the most common ectoproct on blue crabs in Delaware Bay. Amathia vidovici and Anguinella palmata were considered brackish water species which occur abundantly in Chesapeake Bay (Osburn 1944). Locally Bowerbankia gracilis occurred sporadically and appeared to be best developed in high salinity although Osburn (1944) indicated that it can withstand a considerable range in salinity. Mackenzie (1970) suggested that an unidentified species of Bowerbankia may kill by strong acid secretions, although this was not confirmed

in the laboratory.

One of the most interesting ectoprocts was Alcyonidium polyoum. This species was limited to higher salinities and occurred only once in the Leipsic River. Alcyonidium polyoum showed a strong association with the mud snail, N. obsoletus. Approximately 4,000 specimens of the mud snail were collected from eight localities differing progressively in salinity. The percentage of association between the ectoproct and the snail ranged from 90% in salinity of 30 o/oo to less than 5% in salinity of 10 o/oo. There was also a trend related to sediment type within the same salinity range. Gastropods in sand had lower numbers of ectoprocts than did snails living in mud. Osburn (1944), Maturo (1959), Rogick (1964), and Williams and Porter (1964) indicate a variety of substrates (eg. barnacles, rocks, algae, shells, oysters, Libinia, P. longicarpus, Crepidula fornicata, Callinectes sapidus, Busycon spp.) to which A. polyoum may attach. Another specific association of this ectoproct with a mollusc was cited by Powell (1968). He indicated that A. polyoum showed a high incidence of encrustation on the ocean scallop Placopecten magellanicus (Gmelin). In those areas shells of P. magellanicus were the principal substrate. On Delaware beds, oysters, oyster shells, and surf clam shells are the main substrate. Nevertheless, A. polyoum was rarely recorded from those substrates. At present the association between N. obsoletus and A. polyoum and the generalizations involving salinity and substrate are not without exceptions but they deserve additional study to confirm them.

J. Tunicates and Pisces:

One species of tunicate, Molgula manhattensis, the commonest of large simple ascidians along the Atlantic Coast of the United States (McDougall 1943), was collected. Setting of M. manhattensis occurs locally in August, and is so heavy that spat are hidden under masses of tunicates. Early in our work we were fooled by the appearance of such cultch and thought that oyster setting was poor or impossible under those conditions. Fortunately for the oysters, the "sea grapes" die and slough off in the fall apparently leaving the spat unharmed (Galtsoff 1964). On New Jersey beds it is often extremely abundant on shells and oysters mostly in upper seed beds, salinity less than 15 o/oo (Kunkel, personal communication). Molgula is found there most abundantly in late fall into winter and occasionally is abundant in summer. It can accumulate mud and smother spat. We have found that tunicate fouling becomes more serious in oyster raft culture than under natural conditions. The tunicates serve as traps for sediment and setting surfaces for other organisms. The accumulated weight can add significantly to the load on oyster strings. Molgula manhattensis must certainly be ranked locally as an important oyster associate particularly on a seasonal basis.

Gobiosoma bosci, Sygnathus fuscus, and Opsanus tau were the only fishes taken. This association was particularly prevalent in the river beds. The occurrence of Opsanus tau with oysters is well known. From stomach analyses McDermott (1964) found that O. tau consumed large numbers of mud crabs, perhaps controlling one of the major

oyster spat predators.

The other two species are bottom dwelling fish amenable to collection with a dredge. Further they were probably foraging on shrimp, amphipods, and polychaetes living amidst the hydroids and ectoprocts (Cory 1967). Sygnathus fuscus was commonly associated with the alga Ulva attached to oyster shells. On New Jersey beds the goby is common throughout the oyster areas except above the Cohansey. It uses oyster boxes for shelter and for deposition. The pipefish, away from Ulva, is far less numerous than the goby but equally widespread. Hippocampus erectus and Trinectes maculatus are commonly caught on oyster bottoms, the former an amphipod feeder, the latter a polychaete feeder (Kunkel - personal communication). All three fish species were also collected in an oyster faunal study in the Patuxent River (Merrill and Boss 1966).

GENERAL COMPARISONS OF THE FAUNA

The composition of the fauna by phylum for the river beds and bay beds is summarized in Table 3. Several trends can be seen. There is a significant difference in the number of species between the Leipsic River and the other rivers. A similar relationship can be demonstrated for the Woodland Beach area compared to the planted and natural beds. Molluscs and arthropods constitute the majority of taxa for almost all the beds. Coelenterates, rhynchocoels, and ectoprocts are relatively evenly distributed throughout the beds. The annelids are evenly represented in all rivers except the

TABLE 3

Composition of Fauna by Group

		BK	MS	MK	SJ	LC	PB	NB	WB
Porifera	#	--	--	--	1	--	2	3	--
	%*				1.5		3.6	4.4	
Coelenterata	#	8	7	10	8	8	6	9	1
	%	11.5	9.7	14.4	12.1	18.1	10.9	13.4	10
Platyhelminthes	#	1	1	--	--	1	2	--	--
	%	1.4	1.3			2.2	3.5		
Rhynchocoela	#	1	2	1	1	1	--	1	--
	%	1.4	2.7	1.4	1.5	2.2		1.4	
Annelida	#	10	11	13	9	5	9	9	1
	%	14.4	15.2	18.8	13.6	11.3	16.3	13.4	10
Mollusca	#	18	20	20	22	9	18	20	4
	%	26.0	27.7	28.9	33.3	20.4	32.7	30.3	40
Arthropoda	#	24	24	19	18	15	13	17	2
	%	34.7	33.3	27.5	27.2	34.0	23.6	25.3	20
Sipunculida	#	--	--	--	--	--	--	1	--
	%							1.4	
Ectoprocta	#	4	6	5	5	3	6	4	2
	%	5.7	8.3	7.2	7.5	6.8	10.9	5.9	20
Chordata	#	3	1	1	2	2	1	2	0
	%	4.3	1.3	1.4	3.0	4.5	1.8	2.9	-
Total number Species		69	72	69	66	44	57	66	10

* Percent of the total species at each location

Legend: See Table 2.

Leipsic and the Porifera are more evident in the bay beds than in the river beds. The fauna of the Woodland Beach area seems to be exceptional in almost every regard.

A trellis diagram of Jaccard coefficients for the fauna on the oyster beds, including combined fall and spring samples, is presented in Table 4. The diagram shows the greatest similarity among the Broadkill, Mispillion, Murderkill, and St. Jones beds. Oyster bars in the Leipsic, planted beds, and the natural beds do not show even moderate affinities with any other area. In brief, we see four faunal units: 1) Broadkill, Mispillion, Murderkill, and St. Jones Rivers; 2) planted and natural beds; 3) Leipsic River and; 4) Woodland Beach. In reality certain western portions of the planted beds, for example, may be very similar to oyster bars in the mouths of the Murderkill and St. Jones Rivers, or the fauna in the western portions of the natural beds may have some affinity with the fauna in the mouth of the Leipsic. Since an estuary is a continuum one would expect this type of gradation or transition from one bed to the next. Nevertheless, the four faunal units mentioned above have a characteristic grouping of species which makes these units identifiable. The relationships will be described further in the discussion section.

The number of species in various percentages of the total samples was determined. Based on this, 23 species occurred in 20% or more of the samples. Although the 20% level is somewhat arbitrary it has been used before in an oyster fauna study (Wells 1961). The 23 species in descending order of occurrence are included in Table 5. Nineteen of

TABLE 4

Jaccard Coefficient for Fauna on Oyster Bars
Fall and Spring Samples Combined

Number species in common/number species involved								
	BK	MS	MK	SJ	LC	PB	NB	WB
BK		52/88	46/90	43/91	33/79	32/93	37/98	10/69
MS	59.0		52/88	50/88	34/80	37/92	38/99	9/73
MK	51.1	59.0		49/85	34/78	32/93	39/96	8/70
SJ	47.2	56.8	57.6		31/77	36/85	40/90	10/63
LC	41.7	42.5	43.6	40.3		21/81	26/86	9/46
PB	34.4	40.2	34.4	42.4	25.9		35/87	7/58
NB	37.7	38.4	40.6	44.4	30.2	40.2		6/71
WB	14.4	12.3	11.4	15.9	19.6	12.1	8.5	

$$\text{Jaccard Index} = \frac{\text{No. pairs}}{\text{total A} + \text{Total B} - \text{No. pairs}} \times 100$$

TABLE 5

Species that Occur in 20% or more of all Samples

	% of Samples		% of Samples
<u>Sabellaria vulgaris</u>	86.2 E	<u>Diadumene leucolena</u>	43.5 E
<u>Conopeum tenuissimum</u>	79.0 E	<u>Aiptasimorpha luciae</u>	43.5 E
<u>Panopeus herbsti</u>	72.5 E	<u>Melita nitida</u>	42.7 E
<u>Nereis succinea</u>	69.3 I	<u>Obelia longicyatha</u>	40.3 E
<u>Palaemonetes vulgaris</u>	64.5 VT	<u>Alcyonidium polyoum</u>	35.4 E
<u>Crassostrea virginica</u>	63.7 E	<u>Sertularia argentea</u>	32.3 E
<u>Nassarius obsoletus</u>	57.2 E	<u>Crangon septemspinosa</u>	31.4 VT
<u>Polydora websteri</u>	49.1 I	<u>Hydroides dianthus</u>	27.4 E
<u>Membranipora tenuis</u>	47.5 E	<u>Eurypanopeus depressus</u>	25.0 E
<u>Garveia franciscana</u>	46.7 E	<u>Modiolus demissus</u>	24.1 E
<u>Balanus improvisus</u>	45.1 E	<u>Parapleustes</u> sp.	22.5 E
		<u>Hartlaubella gelatinosa</u>	21.7 E

E = Epifaunal
 I = Infaunal
 VT = Vagile Transient

the species are normally categorized as epifaunal. Two species of shrimp are vagile transients. Because of the wide tolerance range in salinity and substrate for N. succinea one would expect to find it anywhere in the estuary. However, it does commonly live in the mud accumulated in the cracks and crevices of oysters. In general this group of species is locally very representative of the oyster community and for this reason can be used as an indication of the relative development of that community in Delaware waters. Notable exceptions from the list are species of Crepidula and Anomia simplex.

The 23 species which occurred in 20% or more of the total number of hauls can be considered the dominant members of that river's community. Based on these species the fauna of the Murderkill and St. Jones Rivers have the most parallel community structure, with the fauna of the Murderkill and Mispillion the next closest. The Broadkill fauna has a weaker association with the above three and the Leipsic has essentially no association within this frame of reference with any area.

SUBSTRATE

The number of stations with a given substrate per river in fall and spring is listed in Table 6. This table shows the distribution of sediment types in each river. The sediment types were listed in order of presumed increasing suitability for members of the oyster community; marsh debris, mud, shelly mud, muddy shell, "sand coral," and shell. The Mispillion and Leipsic Rivers have the most clean shell stations and the Murderkill has the highest frequency of

TABLE 6

Number of Stations with a Given Substrate in each River, Fall and Spring

River		MD	M	SM	MSh	SC	SH
BK	F	-	-	3	2	-	4
	S	-	-	3	2	-	4
	Rank	6	5	2	3	4	1
MS	F	2	1	2	3	1	6
	S	-	2	-	3	1	8
	Rank	6	3	5	2	4	1
MK	F	-	2	2	3	2	4
	S	-	-	1	4	5	4
	Rank	6	5	4	3	2	1
SJ	F	1	-	5	2	-	3
	S	-	2	3	5	-	1
	Rank	5	4	1	2	6	3
LC	F	4	5	1	1	-	4
	S	1	2	4	1	-	6
	Rank	4	2	3	5	6	1

Legend

MD = Marsh Debris
M = Mud
SM = Shelly Mud
MSh = Muddy Shell
SC = "Sand Coral"
SH = Shell

F = Fall
S = Spring

"sand coral" bottom. The St. Jones River has the least amount of clean shell bottom and the highest proportion of mixed mud and shell bottom. In addition to containing stations with clean shell, the Leipsic also has many soft or mixed bottom stations (Maurer et al. 1971). The lack of correlation with the substrate of the Leipsic is probably due to the high proportion of soft bottom (especially mud) in the Leipsic. Similarly the difference between the Murderkill and St. Jones is probably because of the lack of sand coral and high proportion of shelly mud in the St. Jones River. It appears that most of the epifaunal species here can tolerate some degree of muddy conditions. That is, substrates of clean shell, muddy shell, or shelly mud may yield similar faunal compositions. Gradations of mixed shell to clean shell does not influence the faunal composition but the presence or absence of a hard or soft bottom does. On the other hand gradations of substrate definitely affect the relative abundance of individuals.

A summary of the percent of all species in each river occurring on a given substrate is listed in Table 7. In almost all cases most of the species found per river occur on shell. In some cases, for example, in the St. Jones and Leipsic Rivers, high percentages of the species occur on mixed bottoms. There appears to be a positive trend in the mean percent of species occurring on soft bottoms through hard bottoms. The relatively low mean percent of species for sand coral may be an artefact of its limited occurrence in only two rivers. In other words if "sand coral" was present in sufficient

TABLE 7

Percent of All Species in Each River Occurring on a Given Substrate in
the Fall and the Spring

			MD	M	SM	MSh	SG	SH	TOTAL
BK	F	#	--	--	29	20	--	45	55
		%	--	--	52.7	36.3		81.8	
	S	#	--	--	22	28	--	37	51
		%	--	--	43.1	54.9		72.5	
MS	F	#	21	15	21	25	13	31	46
		%	45.6	32.6	45.6	54.3	28.2	67.3	
	S	#	--	5	--	27	23	51	62
		%	--	8.0	--	43.5	37.0	82.2	
MK	F	#	--	20	26	30	23	44	55
		%		36.3	47.2	54.5	41.8	80.0	
	S	#	--	--	19	38	35	42	57
		%	--	--	33.3	66.6	61.4	73.6	
SJ	F	#	6	--	27	24	--	23	36
		%	16.6	--	75.0	66.6	--	63.8	
	S	#	--	23	30	47	--	21	59
		%	--	38.9	50.8	79.6	--	35.5	
LC	F	#	22	19	7	8	--	25	32
		%	68.7	59.3	21.8	25.0	--	78.1	
	S	#	17	16	28	19	--	30	37
		%	45.9	43.2	75.6	51.3	--	81.0	
Mean	%		44.2	36.4	49.5	53.3	42.1	65.1	

quantities to be considered a definite type of substrate in all rivers, we believe that the mean percent of species would range from around forty-five to fifty-five percent.

SALINITY AND SEASON

In terms of salinity the position of the river beds and the bay beds are located along typical estuarine gradients. As far as the fauna is concerned there is a general similarity in the number of species of the four southern rivers with a marked difference at the Leipsic (Table 7). The same relationship can be observed when the faunas of the planted and natural beds are compared to Woodland Beach (Table 4). The classic pattern of decreasing diversity of marine organisms as one moves up the estuary is evident. Local modifications of this pattern will be discussed later.

The effect of season on the number of species can also be seen in Table 7. In general the highest number of species occurred in the late spring compared to fall. This trend is reversed for the fauna of the Broadkill River.

DISCUSSION

Research on oysters has been intensive and undoubtedly was undertaken to determine the necessary biology for prudent exploitation of a food source (Galtsoff 1964). This in turn led to studies of the associated fauna (Möbius 1877, Caspers 1950, Korrington 1951,

Mistakidis 1951, Gunter and Geyer 1955, Hedgpeth 1953, and Wells 1961) which exerted some influence on the oyster population. These studies included predation, parasitism, and aspects of the biology of other "pests" (Carriker 1951, Sinderman 1968, Loosanoff 1956a). Fouling studies (WHOI 1952, McDougall 1943, Fuller 1946, and Calder and Brehmer 1967) have also contributed to our knowledge of oyster communities. Research on the oyster and other commercial shellfish began a long time ago, but most of the ensuing work on benthic ecology has primarily been on soft level-bottom communities (Petersen 1918, Thorson 1957, Sanders 1958, 1960, Barnard 1970, Lie and Kelley 1970, Johnson 1970). Although epifaunal communities found on oyster grounds have been quantified (Caspers 1950, Mistakidis 1951, Richards and Riley 1967), it is a difficult undertaking which may explain some of the emphasis on research with the infauna of soft bottom communities.

As we interpret it, the formation of oyster beds is initially dependent on hydrography and substrate. After a certain period the oyster bed has grown to the point where it exerts its own effect on the local hydrography and substrate. The oyster bed is much more than just a substrate to which other species can attach. It is significant that the fundamental, community concept of ecology began with Möbius' (1877) work on the oyster reef biocenose. The oyster community is truly organic, sending chemical signals which attract organisms (Hidu 1969, Keck et al. 1971, Veitch and Hidu 1971), and evolving through time and space. Since the geological

development of this community has required millions of years and is characteristic of estuarine environments (Hedgpeth 1957), changes in community size and structure offer a yardstick in assessing man's effects on the estuary. It would seem that its commercial importance, biological influence, environmental location, and ecological sensitivity should make research on the total oyster community relevant today.

There is a striking resemblance among faunas of estuaries throughout the world. Many genera and species are cosmopolitan, or their congeners occupy similar ecological niches. On a world-wide basis Hedgpeth (1957) listed Nereis, Idotea, Gammarus, Palaemonetes, Membranipora, and Neomysis as cosmopolitan estuarine genera. In addition he included Diadumene (=Aiptasiomorpha) luciae and the tubicolous amphipod Corophium acherusicum as cosmopolitan species. Carriker (1967) referred to Balanus improvisus, Mya arenaria, Modiolus demissus and Crassostrea virginica as dominant benthic estuarine organisms. Thus on a broad geographic scale the fauna of Delaware oyster beds conforms to an estuarine fauna observed throughout the world. Comparison of the Delaware Bay oyster community with Chesapeake Bay (Andrews 1953, Merrill and Boss 1966, and Cory 1967) shows a strong similarity. Based on the oyster community, the Delaware Bay fauna belongs to the same biogeographic province as Chesapeake Bay.

The planted beds and the southern portion of the natural beds occur in the same salinity range as the four southern rivers. However, larger areas of varied substrate make the bay beds a more

heterogeneous environment. This faunal unit may be less distinct than it presently appears. Its distinctness may, in fact, be an artifact of the lower systematic collecting effort it received in comparison to the rivers. At this time we believe that the fauna of the four southern rivers reflects the diversity of the bay beds and that together they comprise a more reasonable faunal unit.

In contrast to the bay beds and the four southern rivers, the faunal breaks at the Leipsic River and at Woodland Beach are firmly based. The region from the middle portion of the natural beds to the Leipsic River shows the steep gradient from marine to brackish water in terms of species diversity. Our data (Figure 2) correspond well with the hypothetical diagram of Remane (1934) which depicts the rate at which the number of species decreases as one progresses from marine to brackish waters. The Woodland Beach fauna marks the base of this curve.

Animals living at Woodland Beach and farther up the estuary are living in mesohaline to oligohaline waters (Venice System 1959). The presence of small oyster rocks and other euryhaline marine organisms north of the Woodland Beach area has been reported (Schuler et al. 1970a, b, Kunkel personal communication). This kind of penetration of organisms on the left-hand side of estuaries (looking down estuary) in the northern hemisphere has been attributed to the shift in isohalines caused by the earth's rotation (Nelson 1947). The present study has emphasized the epifauna. Any faunal boundaries established on the basis of this research would have to be reevaluated

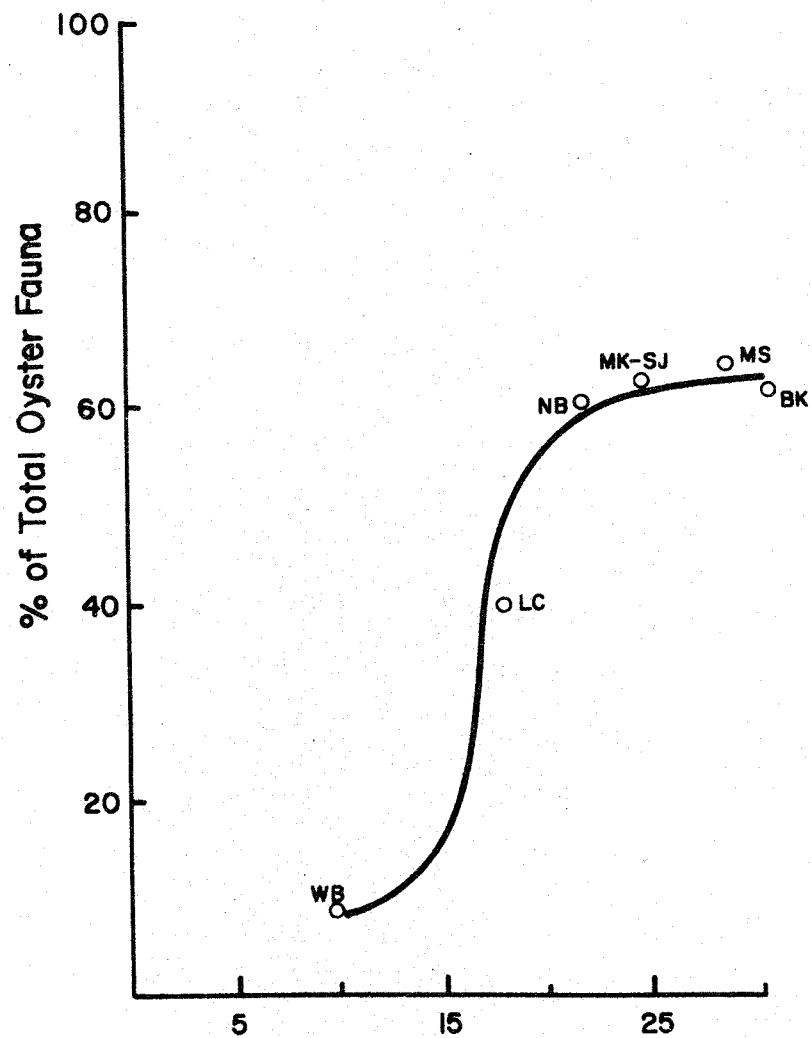


Figure 2. The relationship between the maximum salinity and species abundance on the oyster bars of Delaware Bay.

when dealing with the infauna since it has been shown that infaunal marine species occur farther up the estuary than marine epifaunal species (Sanders et al. 1965, Carriker 1967). For example, the infaunal species Mya arenaria, Nereis succinea, and Cyathura polita and the epifaunal species Crassostrea virginica, Balanus balanoides, B. eburneus and Rhithropanopeus harrisi have been collected approximately 2.5 miles north of Woodland Beach where the salinity is as low as 3 o/oo (Schuler et al. 1970b). Also, the infaunal species N. succinea, Streblospio benedicti, Rangia cuneata Gray have been collected as far up the Delaware estuary as the Chesapeake and Delaware Canal where the salinity is as low as 1 o/oo (M. Taylor - personal communication).

The significance of a firm substrate in controlling the nature of a benthic fauna has been noted many times (Thorson 1957). In addition, rates of sedimentation and turbidity, especially in estuaries, affect the development and composition of the community (Glude 1954, Carriker 1961). For soft level-bottom communities Rhoads and Young (1970) suggested the instability of the bottom and the frequent resuspension of biogenically reworked sediments was limiting for most suspension feeders. The dominant species in the oyster community are epifaunal suspension feeders. The turbid conditions of an estuary are well documented and most solid surfaces possess a thin layer of sediment (Carriker 1961, 1967). Regardless of this heavy rate of sedimentation populations of oysters continue to maintain themselves through regular recruitment (Korringa 1951, Hidu and

Haskins 1971). The oysters, in turn, provide the substrate for the development of the associated fauna. Circumstantially then, the oyster and its associated community must have very broad tolerances to turbidity. It appears, in fact, that the stability provided by the oyster shell is the main determining factor for the distribution of estuarine suspension feeders. This may be supported by the fact that there was no gradual increase in epifaunal species from mud through shell substrates (Table 7). Almost any substrate which contained a trace of shell, be it muddy-shell, shelly-mud, or shell yielded similar faunal compositions. The presence of any firm substrate offered a site of attachment. In contrast mud bottoms normally provided infaunal species or admixtures of infauna and remains of epifauna.

In terms of abundance of organisms there is strong evidence to support the premise that an increase in abundance is associated with a gradual increase in clean, hard shell substrate. This is particularly true of the oyster itself (Maurer et al. 1971). We tentatively suggest that the abundance of the epifauna appears to be a more sensitive indicator of the response to substrate and turbidity than occurrence alone.

Seasonality of biotas in north temperate estuaries is quite distinct (Hedgpeth 1957). Table 7 shows that, in general, in Delaware Bay the highest number of species occurred in the late spring rather than in the fall. The oyster community appears to be quite responsive to the changing seasons. That this may be due to the epifaunal

nature of the community is suggested by Thorson (1957), who showed that epifauna in shallow water situations in middle and higher latitudes can be greatly depressed by winter temperatures. Locally, there seems to be more activity among the infauna than the epifaunas during the winter. Conspicuous epifaunal exceptions include Microciona prolifera, Tubularia crocea and Sertularia argentea.

The oyster community of Delaware Bay is in the classic mold. It consists of large geological structures developed through thousands of years of evolution. The oyster beds provide not only a major source of sea food for man but also a major substrate for the attachment of the diverse estuarine epifauna. The epifaunal organisms are adapted to and thus are able to respond to the myriad complex of factors which characterize the estuarine environment. Any sizeable changes or disruptions in the oyster beds produce serious consequences of both a commercial and ecological nature. In the latter case this could lead to interruptions of major links in the estuarine food web. In view of the geologic time required to develop this community, it would be extremely difficult to rehabilitate or duplicate it. Because of its stability a serious disruption of this community may also be merely a symptom of the biological state of an estuary already irretrievably lost.

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