RELATIVE EFFECTS OF HARVEST PRESSURE AND DISEASE MORTALITY ON THE POPULATION DYNAMICS OF THE EASTERN OYSTER (*CRASSOSTREA VIRGINICA*) IN DELAWARE BAY

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SUMMARY

We used data sets generated by the Haskin Shellfish Research Laboratory for management of New Jersey's Delaware Bay seed oyster fishery from 1953 to the present to assess which of several factors play important roles in determining the abundance of oysters on natural beds - specifically, whether removal of oysters due to harvesting of seed has had a greater or lesser impact on oyster population dynamics on the beds than has loss due to disease. The data sets encompass the following: 1) hydrographic measures; 2) annual estimates of live and dead spat, yearling, and oyster abundance, 3) annual and seasonal patterns of oyster mortality, 4) the prevalence and intensity of MSX disease, and 5) estimates of the volume of oysters removed from the seed beds. These data sets are first described and then used to generate multivariate regressions assessing physical and biological factors important to adult seed oyster abundance.

Hydrography

Bottom temperatures and salinites were obtained from nearly 5500 collections over oyster seed beds from 1953 to 1990 and from Delaware River flow rates at the Trenton, NJ. These two data sets were utilized to 1) describe temporal patterns, 2) partition the seed beds into four regions of similar salinity regime, and 3) establish the relationship between salinity data and the more extensive river flow data. Grouping of seed beds increased statistical power of various analyses. Average annual river flow was highly correlated with the measured salinities. Because the river flow data were more complete than the salinity data, they were used in subsequent correlation and regression analyses. The 1960s and the early 1980s were periods of below average flow. The ten years from 1961 through 1970 were consistently below average; the next nine years, from 1971 through 1980 were consistently above average. From 1980 through 1992, seven years were below average, two were average, and 4 were above average.

Seed Bed Condition

The Delaware Bay New Jersey oyster seed beds were surveyed every year from 1953 to 1993. Abundances of live and dead spat, yearlings, and adult oysters per sample volume were recorded from a stratified random sampling pattern on each bed. The abundance of yearlings was highly dependent (r^2=0.73) on the abundance of spat in the preceding year; likewise, adult oyster abundance was related, although less strongly ($r^2 = 0.31$), to yearling abundance in the previous year. Temporally, adult oysters were least abundant prior to the early 1970s, most abundant from 1974 to 1984, and about average since 1985. Spatially, oysters were most abundant on the upper beds and least abundant and most variable on the lower beds. Oyster drill-caused spat mortality was highest on the lower beds; however, the data suggested that spat and yearlings had somewhat reduced survival on the upper beds, perhaps due to extreme, short-term salinity depressions.

A single year class, 1972, was numerically dominant during the study period, especially on the lower beds. Along with succeeding sets, it increased mean adult oyster abundances until the mid 1980s. Trend analysis showed that oyster abundances had increased several years in a row prior to 1972, indicating that factors affecting oyster survival had changed before that year. Both oyster and spat mortality rates decreased in the late 1960s at a time when MSX disease prevalence and drill predation decreased. At the same time, Delaware River flows changed from a long period of below average flow to one of above average flows.

Mortality

After the advent of MSX disease in 1957, a sampling program was initiated to provide oysters for infection and mortality determination. Annual and seasonal mortality rates, separated into predation and nonpredation causes, were estimated from samples collected 6-10 times per year from 1958 to 1987. Mortality patterns described by these samples was similar to that found from the seed bed condition samples, in which mortality was judged from samples taken only once a year. High death rates occurred on all beds in the mid 1960s and mid 1980s, which were periods of low Delaware River flow and high MSX disease prevalence. Predation was heaviest on the lower beds and occurred predominantly in the fall. Very little predation was recorded on the upper beds, where mortality occurred in the spring except when MSX disease was prevalent. Higher unexplained losses on the upper beds,

probably associated with spring freshets, just about balanced the higher predation on the lower beds. Consequently, there was no particular upbay-downbay trend in total mortalities.

MSX Disease

Live oyster samples were collected from 1958 to 1992 and examined at late fall/early winter and late spring prevalence peaks. Dead oysters were collected and examined throughout the year. Infections were prevalent on the uppermost beds only in the mid 1960s, mid 1980s, and early 1990s - which were also peaks in other areas also. Prevalences increased in a downbay direction; infections were found in most years on the lowermost beds. There were no significant correlations between succeeding fall and spring, and spring and fall, peaks indicating that the disease process was being affected by different factors at the different seasons. Although fewer live and dead oysters were found to be infected with MSX on the upper beds compared to the lower beds, the proportion of infections that were systemic (most advanced) was similar throughout the seed bed area. Most oysters dying with MSX disease had systemic infections, regardless of bed.

Seed Bed Harvest

Data relating the quantities harvested from individual seed beds by boat, by day ,were compiled and analyzed for each of the 27 seed harvest seasons during the study period. The numbers of boats registered in the fleet varied considerably until the imposition of limited entry in 1981 and then stabilized at about 100 vessels. Numbers of vessels actually harvesting seed has remained around 50 since the middle 1970s. Catch per unit effort was more variable during the years prior to 1970, but has remained relatively constant at nearly 60% efficiency throughout the 34 years of record. Harvests were concentrated on the upper half of the beds during the first part of the study period, but later shifted to the lower half as oysters became more numerous there. Overall, however, the large central regions, encompassing parts of both the upper and lower sections, has provided the greatest harvests. There was no evidence of overharvesting at any time, perhaps because beds were closed when the relative oyster volume reached 40%, and sometimes well before. Through the past 34 years, a tripartite system of state regulation, strong industry leadership, and a consistent independently collected (by the laboratory) data base has allowed continuation of a resource despite variable recruitment, changes in harvesting techniques, and the incursion of epizootic disease.

Relationships

The prevalence of MSX disease was highly correlated to oyster abundance (negatively) and to oyster mortality (positively) when all beds were considered together. No such relationships were apparent when the beds were examined individually, probably because number of replicates was too small. Correlations produced no evidence that harvests reduced oyster abundance or increased mortality. A highly significant general regression model was developed for the beds as a whole that explains almost two-thirds of the variance in adult oyster abundance and includes only three variables:

$$\mathbf{OYS = -3.55 + 0.44(YRL\ ) + 0.74(FLO) - 0.64(MSX)}$$

where OYS = mean adult abundance$_{(\text{year } t)}$, YRL = mean yearling abundance$_{(\text{year } t-1)}$, FLO = mean annual Delaware River flow$_{(\text{year } t)}$, and MSX = mean proportion of oysters infected with MSX disease in the spring$_{(\text{year } t)}$. Yearling abundance in the preceding year was the independent variable with the greatest influence on adult abundance. River flow and the proportion of spring infections were the next two most important independent variables with flow having a positive effect and spring disease infections having an equal, but negative, effect on adult abundance.

GENERAL INTRODUCTION

Conceptual Approach

Effective fishery management requires understanding the roles played by various natural and anthropogenic factors in determining the year-to-year abundances of the fishery species. Most fisheries regulate and attempt to preserve future harvests without the benefit of such insights. Many impediments exist to gathering the needed data. Funding that supports research or monitoring rarely lasts long enough or occurs in sufficient size to permit addressing fisheries' problems at adequate spatial and temporal scales. Many fishery species exhibit life-history stages (e.g., planktonic larvae), behaviors, or morphological characteristics that pose severe logistical and technical hurdles to collecting unconfounded, representative data. Fishery species interact with their environment in complex ways. Their populations can increase or decrease, often in non-linear ways, in response to a range of biological and environmental factors that may or may not interact with each other. These interactions can be further confounded when man induces additional complexity by harvesting and managing the resources.

Some fisheries have benefited from great-enough scientific and public interests to provide the means for attaining substantial amounts of biological data. The large revenues historically produced by, and the high public demand for, the eastern oyster (*Crassostrea virginica*, Gmelin) has enabled the accumulation of extensive information on this species and the associated fishery. Unfortunately, gathering of data frequently addresses just local or immediate problems in the oyster fishery. Relating this temporally and spatially fractured information into a comprehensive, meaningful story presents several methodological and interpretational challenges. Such an effort is being attempted to provide a general model representing oyster life-histories in the Gulf of Mexico and Chesapeake Bay (Powell *et al*. 1992, Hofmann *et al*. 1992, 1994) using a "bottom-up" approach. A population model of this type combines an array of basic characteristics of the oyster's biology that affect population dynamics. Once the characteristics have been related by algorithms, substitution of local values for those characteristics allows estimation of which factors are most important to producing changes in oyster abundance. The critical aspect of this procedure is relating the characteristics in a manner that is biologically meaningful and realistic.

In Delaware Bay extensive (>40 years), continuous, synoptic data have been collected on several parameters of oyster biology over most of the region where oysters occur. These data provide an alternative means for estimating the importance of various factors to oyster population dynamics. This is a "top-down" approach, in which direct comparison of changes in the oyster population to changes in an array of measured factors suspected of inducing those changes can reveal the relative importance of the factors as determinants of oyster population size. Few *a priori* assumptions are necessary about the mechanisms of interactions between potential determining factors and the population dynamics. The relationships among the independent and dependent factors are examined statistically to uncover any patterns of association inherent in the data. Once the patterns are identified, they can be tested in the field to determine the mechanisms involved and they can serve as guidelines to "bottom-up" models that relate the enormous array of specific biology to population change.

We have used data sets generated through the management of New Jersey's Delaware Bay seed oyster fishery from 1953 to the present to assess which of several factors play important roles in determining the abundance of oysters on natural beds. Specifically, we are interested in determining whether removal of oysters due to harvesting of seed has had a greater or lesser impact on oyster population dynamics on the beds than has loss due to disease.

History of the Seed Fishery in Delaware Bay

Oysters grow in Delaware Bay from its mouth to Bombay Hook, on the western (Delaware) side of the estuary, and to just below Artificial Island on the eastern (New Jersey) side, a distance of about 80 km (50 miles) along a salinity gradient that decreases from about 30^{o}/oo to 5^{o}/oo. Most of the extant beds lie in the upper half of the bay, largely in the eastern half of the basin (Fig. 1; Nelson 1947, Maurer *et al*. 1971).

Commercial oystering probably began in Delaware Bay in the first half of the 18th century (Smith 1765, Rolfs 1971). Natural beds occurred throughout the bay at this time and harvested oysters were transported directly to markets in Philadelphia (Ingersoll 1871). Oystermen recognized, however, that oysters in the lower estuary grew faster and attained a better meat quality than did those taken from the upbay beds. In New Jersey, legislation enacted in 1846 legalized the planting of oysters (i.e., private ownership of the shellfish). Gradually, a natural division arose between the upper bay seed beds, where low salinity protected the young oysters from major predators and the lower bay, where seed oysters could be planted for a period before marketing.

In 1899, at the request of the planters, the state of New Jersey took control of the industry and all of the oyster growing areas in the eastern half of Delaware Bay. The organization established at that time exists, essentially unchanged, to the present time. The state manages and controls the seed beds, and leases grounds in the lower bay to individual planters. Seed dredging occurs at some time between 1 May and 30 June during what is known as "Bay Season". Once planted on the leased grounds, seed oysters become the property of the oysterman , and can be marketed at any time after planting. Direct marketing of oysters from the seed beds is prohibited. A similar management structure exists on the Delaware side of the Bay. Since 1961, the seed beds have provided the only seed used by planters; consequently, maintaining the health of the beds is crucial for the industry.

In the first published survey of the oyster industry in Delaware Bay, Ingersoll (1881) estimated that in 1879-80 that nearly 1,400 vessels (about 300 of them sloops and schooners greater than 5 tons) planted 2,400,000 bushels (9.6×10^{7}L) of oysters from the seed beds. Between then and 1956, sporadic records exist of seed harvests from Delaware Bay (Nelson, 1889; Hall, 1894; Fiedler, 1931, 1932, 1934, 1936, 1938), although it is usually not clear how the data were obtained. In several of the reported years (1888, 1892, 1901, 1931, 1937, and 1938) the volume equalled or slightly exceeded one million bushels (4×10^{7} L); in 1930, two million bushels (8×10^{7}L) were planted. In nearly all other reported years, the amount was at least half a million bushels (2×10^{7}L).

Throughout this time, the demand for seed was frequently greater than the supply, and oystermen began importing seed from the Chesapeake. During the 1830s, an average of 150,000 bushels (6 x 10^6L) per year passed through the Chesapeake and Delaware Canal. Each decade thereafter, the volume increased until during the 1880s, it averaged nearly half a million bushels (2 x 10^7L) a year. Ingersoll (1881) estimated that in 1879-80, the total was nearly 940,000 bushels (3.8 x 10^7L), 700,000 (2.8 x 10^7L) of which were destined for planting in the bay and the remainder for market in or through Philadelphia. Over the next 70 years, imported seed continued to supplement the native supply in Delaware Bay. In the early 1950s, hundreds of thousands of bushels were imported from the seaside bays of the Virginia, especially Chincoteague Bay (N. Jeffries, Sr. and H. Bickings, Sr., personal communication to SEF). The practice ended shortly after the outbreak of MSX disease in 1957, when all imports and exports were banned.

Deterioration of the seed beds, reported since the turn of the century (NJ Bureau of Shellfisheries, 1905), was accelerated during World War II when the requirement for sail dredging was eliminated. Motorized boats were much more efficient at harvesting seed: they could be operated in most weather, and could dredge in smaller and shoaler areas. Unexplained mortalities of seed oysters in the early 1940s and again in 1950 (Miller, 1962), and a series of set failures in the late 1940s and early 1950s, and left the natural beds in a condition that had never before "been so uniformly bad for so long a period as at present, and it is highly probable that the present oyster population of the Natural Beds represents an all time low" (New Jersey Oyster Research Laboratory 1953). Only continued importation of seed from Maryland and Virginia allowed the industry to market an average one million bushels (4 x 10^7L) per year until 1956. In New Jersey, Rutgers University's Department of Oyster Culture, under Dr. Harold Haskin, began studies of factors influencing oyster seed-bed recruitment. Annual surveys of oyster populations were started in 1953. In 1956, an annual census of boats involved harvests of seed bed oysters, including an estimate of the volumes of seed removed, was started. These studies provide the data for much of this report.

In 1957, the oyster industry suffered its most serious blow yet. That spring, heavy mortality was discovered in oysters planted the previous year on the New Jersey leased grounds (Ford and Haskin, 1982). The cause, soon discovered to be a protozoan parasite, had never been seen before. It was initially given the acronym "MSX", standing for "multinucleated sphere unknown" and was later classified *Hasplosporidium* (formerly *Minchinia*) *nelsoni* (Haskin et al., 1966). The parasite spread rapidly over most of the bay, limited only by the fresher waters of the creeks, rivers, and upper bay (Haskin and Ford, 1982). By the end of 1959, 90-95% of the oysters on the planted grounds and about half of those on the seed beds had died. Beginning in 1958, the Oyster Laboratory added to its seed bed studies a regular program of sampling both seed beds and leased grounds for the presence of *H. nelsoni* and for related mortalities. Results of this long-term project form the second component of the data reported here. In addition to the biological data obtain from both sampling programs, hydrographic data were collected each time a sampling station was visited. These form a third component of the overall data set.

Delaware Bay New Jersey - Oyster Seed Beds

Our analysis of the relative effects of harvest pressure and disease mortality on population dynamics of oysters in Delaware Bay deals exclusively with the seed beds because these are the only areas where a fishery exists and where there is an attempt to maintain and enhance the *natural* population. Planted grounds, on the other hand, can be considered temporary holding areas that are harvested in their entirety to produce market oysters. Further, our study is restricted to the New Jersey beds. Reference to "baywide" in the analysis is to all the New Jersey oyster seed beds.

Traditional names have been used to identify the historically most productive areas of the seed beds (Fig. 2). The beds vary in size, proximity to the shore, average water depth, and average salinity regimes (Table 1). Oysters are not distributed uniformly within any of the beds. This variation in oyster abundance within the beds has been used as the basis for identifying the strata used in the stratified random sampling described below. Areas that have oysters, but in abundances well below commercial densities have been characterized as "low". Areas that have marginal or highly variable commercial densities of oysters have been characterized as "medium". Areas that consistently have relatively high commercial densities have been characterized as "high".

The data sets used in this analysis encompass the following: 1) measures of several physical factors such as bottom salinities, water temperatures, and Delaware River flow; 2) annual estimates of live and dead spat, yearling, and oyster abundance on the seed beds, 3) annual and seasonal patterns of oyster mortality on representative seed beds, 4) the prevalence and intensity of MSX disease on representative seed beds, and 5) estimates of the volume of oysters removed from the seed beds.

Integrity of the Data Sets

The data sets exist because of the seed bed rehabilitation program established in 1953 by Harold H. Haskin, and by his successful efforts to have it continuously funded by State (New Jersey) and Federal governments. The integrity and consistency of the data are due largely to the constant oversight of Donald E. Kunkle, biologist in charge of the program from its inception to his death in 1989.

Organization of the Report

The report is organized into three sections: 1) descriptive statistics of each of the five data sets and the methods used to obtain and analyze them ; 2) an analysis of the statistical relationships among the data sets, including a general model; and 3) principal conclusions of the study.

HYDROGRAPHY

Hydrography - Introduction

Hydrographical data concerning the Delaware Bay oyster seed beds were obtained from two sources: 1) surface and bottom salinities and temperatures routinely measured from the *R/V Julius Nelson* of the Rutgers Oyster (now Haskin Shellfish) Research Laboratory, as part of all field studies in Delaware Bay; and 2) fresh water flow rates into the Delaware River, recorded at Trenton, New Jersey by the U. S. Geological Survey (Water Resources Data for New Jersey, USGS, US Department of the Interior and NJ Department of Environmental Protection), as part of its national surface-water monitoring program.

Hydrographical data are of interest to this project because of the documented effects that physical parameters, particularly temperature and salinity, have on the survival, growth, and reproduction of oyster populations. Delaware River flow measured at Trenton provides about 60% of the gauged fresh water input into the Delaware estuary. It has a major influence on salinity, especially over the seed beds, and also influences oysters by affecting sedimentation and bottom scouring.

Hydrography - Methods

Surface and Bottom Salinities and Temperatures**.** Bottom water samples for salinity determination were collected using a Nansen bottle. Surface water was collected using a bucket. From 1953 through 1986, samples were returned to the laboratory in screw-cap glass bottles. Until 1978, salinities were determined by silver nitrate titration (Knudsen, 1901). From 1978 through 1986, salinities were determined using an Autosal Model 8400 salinometer. After 1986, salinity measurements were made on board using a hand-held refractometer. In extremely shallow water (< 1m), a single sample was collected as representative of both surface and bottom water. The time and location of each sample was recorded to allow later calculation of local tidal stage at the time of collection. Surface water temperatures were measured directly from the bucket sample with a hand-held thermometer. Bottom water temperatures were recorded from a reversing thermometer attached to the Nansen bottle. For this study, only bottom salinity and temperature measurements were used.

From 1953 through 1990, physical data were collected at a total of 5493 stations. In most years, 100 or more stations were visited, but this rate decreased after 1987 (Tables 2 and 3). More stations were made during the summer than during the winter (Table 2). The major seed beds were better represented than the minor beds (Table 3).

Delaware River flow at Trenton, NJ. An extensive data set concerning the hydrology of the Delaware River and its drainage basin has been collected by the USGS, in cooperation with the NJ Department of Environmental Protection, and published in annual Water Resources Data Reports. The records from Trenton, NJ begin in the late 1800s. The methods by which these data were collected and calculated are presented in each of the USGS annual reports.

The data of interest to this study are the mean daily flow rates, measured in cubic feet per second (cfs), at Trenton. Regularly collected data are available from 1913. Our analysis includes data through 1992. All flow rate measurements have been converted into cubic meters per second (m^3s^{-1} = cfs x 0.02832). These data were plotted in several ways to determine long-term trends before and during the study period. Relationships between freshwater flow and salinity on the seed beds were investigated, and the flow rates were used in regression analysis to determine their influence on seed bed populations.

Hydrography - Results

Bottom Water Temperatures. Two features of bottom water temperatures over the seed beds are apparent from the 36-year record. First, a relative constancy from year to year is suggested by the low year-to-year fluctuation in annual means (Fig. 3); and the small variation in monthly (Fig. 4a) and daily (Fig. 4b) means. Second, within an annual cycle, temperatures are almost always increasing or decreasing (Fig. 4). There are only two relatively brief periods of steady bottom water temperatures: the winter months of January and February, and the summer months of July and August.

Baywide Bottom Salinity Patterns. The average salinity over all seed beds between 1953 and 1990 was 15.6 ppt (S.D. = 4.3, n = 4988). Average annual salinities (Fig. 5) on the oyster beds ranged from 12.4 ppt (1972) to 19.0 (1963). Standard deviations were typically about 25% of the mean. Slightly higher salinities occur in early autumn and late winter months (Fig. 6). Lower salinities occur in spring months. The highest monthly mean occurred in October (= 18.1 S.D. = 3.56, n = 228) and the lowest in April (= 10.48, S.D. = 4.36, n = 196).

Use of Bottom Salinities to Cluster Seed Beds. Bottom salinity was used as a variable in correlation analyses with other factors affecting oyster abundance. For some statistical analyses, it was necessary to combine the data from more than one seed bed to achieve a sample size adequate for the statistical operations. Bottom salinity data was used as a parameter to group seed beds together. By combining bottom salinity data collected since 1953, it was possible to calculate average bottom salinities for the major oyster seed beds. Cluster analysis was then used to group the major seed beds into four main seed bed regions: the Upper, Upper Middle, Lower Middle, and Lower regions (Fig. 7, Table 5).

Region Bottom Salinity Patterns. Mean monthly bottom salinities for the regions show the same pattern as the baywide values (Figs. 8 and 9). Average salinities are highest in autumn and late winter months, and lowest in the spring. Because the clustering of seed bed into regions was made according to bottom salinity regimes, the difference in mean salinity values is similar - about 3 ppt - for each set of adjacent regions (Table 5) and about the same differential is apparent in nearly all months (Fig. 9). Salinities in the Upper region are always the lowest of the four regions, followed by those in the Upper Middle, and then Lower Middle. Salinities in the Lower region are always the highest.

Delaware River Flow at Trenton, NJ. The average annual flow rate of the Delaware River at Trenton NJ between 1913 and 1992 was 329 m^3s^{-1} (S.D. = 74.8, n = 80). Between 1950 and 1992, a span that approximates the study period, the mean was considerably lower at 326 m^3s^{-1} (S.D. = 84.6, n = 43). The maximum average flow rate was 497 m^3s^{-1}(1952) and the minimum was 142 m^3s^{-1}(1965) (Figure 10a). These were 50% and 58%, respectively, above and below the long-term mean. The early 1950s and the 1970s were periods of above average flow. The 1960s and the early 1980s were periods of below average flow (Fig. 10b). The ten years from 1961 through 1970 were consistently below average; the next nine years, from 1971 through 1980 were consistently above average. From 1980 through 1992, seven years were below average, two were average, and 4 were above average. The extremes in Delaware River flow during the study period, compared to the preceding 40 years, are particularly well illustrated by plots of absolute and cumulative deviations from the long-term monthly mean flow rates (Fig. 11). In the cumulative plot, steep downward and upward slopes such as occurred in the 1960s and 1970s, respectively, indicate long periods in which successive month's flows were consistently below or above average (Fig. 11a). These periods were far more extreme than earlier dry periods in the 1920s and early 1930s, the wet years in the late 1920s and mid to late 1930s, or the shorter wet/dry periods in more recent years.

Delaware River flow patterns vary throughout the year. Highest average flow rates typically occur in March and April. Lowest flow rates usually occur during July, August, and September (Fig. 12). Standard errors are usually 10-15% of the mean monthly flow rates.

<u>Relationships between Delaware River flow and seed bed salinities</u>. There is an inverse relationship between the flow rate of the Delaware River at Trenton, NJ and bottom salinities measured on the oyster seed beds. Using annual averages, the correlation coefficient between average annual flow rate at Trenton and the average bottom salinities measured on all seed beds is -0.81 (Fig. 13). When flow rates and salinities are grouped by month, and correlations are measured for each of the four seed bed regions, the overall pattern persists (Table 6). Higher flow rates result in lower salinities, with the magnitude of the correlation greatest in the Upper region, and least in the Lower region.

Hydrography - Discussion.

Bottom temperature data, at the scale examined, did not provide sufficient information to be of use in our analysis. On the other hand, the relatively low-salinity regime of the upper Delaware Bay has long been recognized as important to the seed beds (Haskin and Ford 1982). The record of salinity measurements is incomplete, however, both spatially and temporally. This effect is magnified when salinity data are compared with other data sets, which are not necessarily contemporaneous. The high correlation between salinity and Delaware River flow is especially important to our study because the flow record is complete since 1913. Therefore, it can be used as an indicator of gross changes in salinity on the oyster seed beds. For this reason, correlation analysis involving oyster population data include Delaware River Flow data, rather than salinity data.

SEED BED CONDITION

Seed bed condition - Introduction.

Direct determination of temporal and spatial variation in the abundance of the various life-history stages is the cornerstone of any study attempting to understand oyster population dynamics. Unfortunately the logistics and costs associated with obtaining this information frequently exceed the capacity of researchers to gather abundance data on temporal or spatial scales large enough to reveal meaningful patterns. We are fortunate to have a continuous, oyster population data set that was collected, largely by the same individuals, over several decades and throughout much of the region where natural oyster beds occur in the Delaware estuary.

Every year from 1953 to 1993, on the larger oyster seed beds in the upper half of eastern Delaware Bay, estimates were made of the relative abundances of several oyster life-history stages and of recent oyster mortality. Here we report on abundances of spat (0-year class), yearlings (1-year class), adult oysters (>1 year old); mortality of oysters and yearlings; mortality of spat; the relationships of spat with yearlings the following year; and the relationships of yearlings with adult oysters the following year.

Seed bed condition - Methods.

Basic procedure. The estimates were based on material collected in oyster dredge samples. For each sample, the oyster dredge (71.1 cm tooth bar with a bag capacity of approximately 80L) was hauled on the bottom for one minute at a constant boat speed (i.e., constant effort). The sample was deposited on deck and a 13 - 14L subsample of the mixed dredge contents was retained. This procedure was repeated two more times. The three subsamples from each of the one-minutes hauls were combined to form a composite sample and returned to the laboratory for further analysis.

In the laboratory the samples were stored in a cold room until they could be processed. For each sample the following were determined by direct inspection: 1) total number of oysters 1-year old or older, 2) total number of oysters approximately 1 year old (yearlings), 3) total number of spat, 4) total number of boxes (articulated but empty oyster valves; this includes both "new" and "old" boxes as defined in Mortality section), 5) total number of gapers (oysters that do not close their valves completely), and 6) total number of dead spat . The articulated valves of the dead spat were examined for evidence of damage by crabs and drills. Separate tallies were kept for these sources of spat mortality, Generally, most samples were processed within several days of their collection in the field.

Sampling regime. For sampling purposes, the area of each oyster seed bed was subdivided into a grid of contiguous 275 m x 370 m rectangles (approximately 0.2 min of longitude x 0.2 min of latitude, respectively: the area of each grid equals 10.2 hectare or 25 acres). The grid pattern for a given seed bed was unique and remained constant from year to year. The grids selected for sampling in a given year were chosen in a stratified random manner. The strata were defined on the basis of long-term oyster abundance (see Oyster Seed Beds above) and randomly selected grids were chosen from each stratum in each year. The total number of grids sampled varied from seed bed to seed bed, and occasionally, from year to year within a seed bed (Table 7). Not all seed beds were sampled in all years (Fig. 14).

Temporal scope. In most years the samples were taken using a boat that could retrieve a maximum of 10-12 samples per day and that was limited in the range of sea conditions in which it could operate. More importantly, only two individuals were available to analyze the samples, which needed to be processed within a week or so of collection. As a result, the samples were retrieved over a period of several months. Sampling generally occurred between the beginning of November and the end of April (Table 8). Several factors, especially mortality, could change during this lengthy time interval over which the samples were taken, confounding our ability to make within or between bed comparisons. However, little biotic activity (predation, disease, oyster feeding, etc.) occurs during the winter months and temporal changes in the beds are likely to be small. The total number of samples collected varied among years, but was generally >90 and from at least 15 seed beds (Fig. 15).

Spatial scope. Within each sampling season approximately 10% of the total number of grids were sampled. Over the forty sampling seasons more than three quarters of the grids (729 of 941) have been sampled at least once, about one quarter of the grids have been sampled at least five times, and one tenth of the grids have been sampled at least 10 times (Table 7). Nonsampled grids are considered to be largely on nonproductive sections of the beds. Over the course of the study, areas of high, medium, and low density remained fairly constant.

Changes in sampling since 1989. Modifications to the sampling scheme described above were made at the start of the 1989 sampling season and have been utilized since. The time frame in which all samples have been collected has been reduced to less than one week (usually in the latter half of October). Use of a commercial oyster boat and equipment along with recruitment of more people to assist in collecting and processing samples made this change possible. The number of samples taken from most beds was altered based on the accumulated data. Beds that exhibited high variability in adult oysters in preceding years received greater sampling effort while beds that were more homogeneous in adult oyster abundance have been sampled less intensively. Comparison of the data between the beds within a given year can now be made with greater confidence. However, our ability to compare the data collected since 1989 to that collected before is reduced. For some of the analyses described below, the post-1989 data have not been included.

Standardization of the data. Relative oyster abundance data derived from dredge samples cannot be used to estimate the number of oysters per unit area of bottom, the dispersion of oysters on the bottom, or the total number of oysters present. Changes in water depth, sediment compaction, and the boat's land speed (cruising speed plus any tidal current speed) alter a dredge's effectiveness (Kunkle and Ford 1986). Even with the attempt to standardize sampling effort in this study (see above), the dredge certainly undersampled the number of oysters present to varying degrees both within and between hauls. Attempts to relate dredge hauls to actual bottom densities (collected by divers or patent tongs) have indicated that dredges capture 2% to 7% of the oysters present (Kunkle, HSRL unpub. data). The use of the dredge in this study continued for two reasons: 1) the dredge requires less time than diving or using patent tongs and 2) the results of this study have been used primarily to inform fishery managers and oyster fishermen, who would be using dredges, what they could expect if harvest occurred.

The dredge data represent an index of oyster abundance on the oyster beds. Records indicate that the total volumes obtained during the three one-minute tows varied considerably from one location to another. To standardize all the samples, the counts were divided by the respective number of liters actually collected and then converted to a standard volume of 20L (arbitrarily chosen to produce most count data in the range of 1 - 400, this volume is about half the size of a standard New Jersey bushel used by the fishery as a standard measure of harvest). Some dredge samples (<10 %) never filled the dredge and consisted of 25L or less of material in total. Using the above transformation would artificially increase the apparent numbers of these low-density samples. Consequently, we assumed that the counts made for these samples represented all of the individuals that were present, regardless of the exact volume of dredge material that would have been collected. These counts were not modified. Baywide, region, and individual seed bed means were computed using all samples from the relevant area; when a mean was computed from other means, it is specifically noted.

The derived variables computed for analysis of seed bed condition and for the regression analyses that were used to develop the general model (see General Model section) are listed here:

Oyster Abundance = Mean number of live oysters $20L^{-1}$

Yearling Abundance = Mean number of live yearling $20L^{-1}$

Spat Abundance = Mean number of live spat $20L^{-1}$

Oyster Change = Mean live oysters $20L^{-1}$ $year_{(t)}$ – Mean live oysters $20L^{-1}$ $year_{(t+1)}$

Oyster Mortality = Mean number of Gapers + Boxes $20L^{-1}$

Total Spat Mortality (TSM) = nondrilled spat $20L^{-1}$+ drilled spat $20L^{-1}$

Total Drilled Spat Mortality (TnDSM) = drilled spat $20L^{-1}$

Total nonDrilled Spat Mortality (TnDSM) = nondrilled spat $20L^{-1}$

Relative Oyster Mortality (ROM) = $\frac{\text{Total Boxes (B) + Gapers (G)}}{\text{Total Boxes (B) + Gapers (G) + Oysters (O)}}$

Relative Spat Mortality (RSM) = $\frac{\text{Total Dead Spat (DS)}}{\text{Total Dead Spat (DS) + Total Live Spat (S)}}$

Relative Drilled Spat Mortality (RDSM) = $\frac{\text{drilled spat } 20L^{-1}}{\text{Total Dead Spat (DS) + Total Live Spat (S)}}$

Relative nonDrilled Spat Mortality (RnDSM) = $\frac{\text{nondrilled spat } 20L^{-1}}{\text{Total Dead Spat (DS) + Total Live Spat (S)}}$

The mean precision of the annual means of oyster abundance is 20% (range 11% to 31%, S.D. = 5.33%). This was determined by finding the distribution that best fit the data (negative k binomial in this case) and using the formula relating sample size to precision for the appropriate distribution (Krebs 1989). This indicates that sampling was adequate in most years to provide moderately good precision in the annual means of the counts of oyster abundance. All abundance data were ln-transformed, and all proportional data were subjected to angular transformation, before statistical analysis.

Seed bed condition - Results.

Baywide results pool the data from all nineteen beds examined in this study. Because not all beds were sampled in some years examination, of regional patterns within the bay cannot be done by examining the results from the beds alone. Several of the beds lie in close proximity to each other and experience very similar bottom salinities. We clustered (using K-means, Wilkinson *et al*. 1992) the beds into four regions on the basis of bottom salinities retrieved from cruise data (see Hydrography section) collected from 1953 to 1992 (Fig. 7, Table 5). Clustering improved temporal continuity and increased sample sizes within a given region, mediating some of the spatial and temporal gaps in the original data set.

<u>Baywide annual changes in abundances (1953 - 1992)</u>. In most years the mean abundance of spat ranged between 100 - 400 individuals $20L^{-1}$ (Fig. 16a). In six of the nine years from 1953 to 1961, annual mean abundances of spat remained less than 100 individuals $20L^{-1}$. Another interval of low recruitment of equal length occurred in the last years of the study when six of nine years show means of less than 100 spat $20L^{-1}$. The greatest mean abundance of spat occurred in 1972.

Mean yearling abundances ranged between 50 - 200 individuals $20L^{-1}$ in most years. The magnitude of yearling abundances frequently varied in the same direction and degree as the mean spat abundances observed in the preceding year (Fig. 16b). Regression of abundance data revealed a significant ($P<0.001$) relationship in which 73% of the variation in yearling abundance resulted from variation in spat abundance in the preceding year (Table 9).

A weaker association existed between adult oysters and yearlings; 30.5% of adult oyster variation in abundance in any year was explained by variation in yearling abundance in the preceding year (Table 10). Mean adult abundances remained low (around 50 individuals $20L^{-1}$) from 1953 until the mid 1960s (Fig. 16c). After this time, oyster abundances began to increase. From 1974 to 1984 oyster abundances generally exceeded 150 individuals $20L^{-1}$. Since 1985 oyster mean abundances have stayed near 100 individuals $20L^{-1}$. The 1972 year class dominates all three histograms (Fig. 16), although the relative size of this year class decreased with time.

Spat mortality (RSM) showed little year to year variation although the figure before 1967 was generally twice that occurring thereafter (Fig. 17a). The amount of spat mortality attributable to oyster drills (RDSM) did vary from year to year , in some cases by three to four fold (Fig 17b). Drill-caused mortality was highest during two intervals, the early 1960s and, except for 1987, the late 1980s. The ROM also showed considerable annual variation (Fig. 17c). Several intervals of successive high mortality (>40%) years occurred from 1957 - 1958, 1985 - 1987, and 1991 - 1992. In contrast, the interval from 1974 - 1984 had only one year in which mortality exceeded 20%.

<u>Changes in abundances (1953 - 1992) in the Upper region</u>. In most years the numbers of spat, yearlings, and adult oysters $20L^{-1}$ exceeded those found in the three other regions. A large amount of annual variability existed in spat abundance on the uppermost beds (Fig. 18a). Very little recruitment (<50 spat $20L^{-1}$) occurred in one quarter of the years (10 of 40) while relatively

large recruitment (>300 spat $20L^{-1}$) occurred in 9 of the 40 years. The 1972 set of spat was the largest.

Yearling abundances are a function of spat abundances from the preceding year (r^2 = 0.785, Table 9). Adult abundances were not strongly related to preceding yearling abundances (r^2 = 0.253, Table 10 , Fig. 18b). The temporal patterns in yearling and oyster abundances differed from the baywide pattern in that the 1972 year class, though relatively large, was not the largest year class present throughout the period. Several year classes, both before and after, were as large or larger in numbers of yearlings or oysters than the 1972 year class (Fig. 18). The greatest abundances of adult oysters occurred in the early 1980s.

Low RSM and ROM occurred in most years (<10% and <20%, respectively, Fig. 19a and c). Drill-caused spat mortality (RDSM) was observed in only two years (Fig. 19b).

Changes in abundances (1953 - 1992) in the Upper Middle region. The annual changes in abundance of spat, yearlings, and adult oysters were similar to the baywide patterns of each respective life-history stage (Fig. 20). Yearling abundance still resulted largely from the preceding year's spat abundance (r^2 = 0.661, Table 9). Similar to the relationship in the Upper region, adult abundance was weakly related to the preceding year's yearling abundances (r^2 = 0.272, Table 10). The 1972 year class was the dominant year class in the study period.

The RSM and ROM patterns reflect the baywide patterns (Fig. 21a and c). Substantial (>25%) drill-caused spat mortality (RDSM) occurred in two periods from 1961 to 1967 and in 1989. From 1972 to 1988 RDSM was largely absent.

Changes in abundances (1953 - 1992) in the Lower Middle region. The annual changes in abundance of spat, yearlings, and adult oysters were similar to those seen in the Upper Middle region except the overall mean numbers of each life-history stage were lower (Fig 22). Yearling success remained strongly dependent on the previous year's spat success (r^2 = 0.778, Table 9). The relationship of adult oyster abundance to the preceding year's yearling abundance was moderate (r^2 = 0.499, Table 10) but substantially higher than occurred in the upper two regions. Once again, the 1972 year class numerically dominated the other year classes in this region.

The RSM generally exceeded twice that seen in the Upper Middle region in most years (Fig. 23a). Except for a short interval in the late 1970s, a large percentage of spat mortality within each year resulted from drill predation (Fig 23b). As in the Upper Middle region, ROM was high in most of the late 1950s, late 1960s, late 1980s, and first two years of 1990s (Fig 23c). As with the RSM, the ROM was higher in the Lower Middle region within a given year than it was in the Upper Middle region.

Changes in abundances (1953 - 1992) in the Lower region. No sampling occurred in either of the two beds in the Lower region from 1965 - 1968. This gap in the data does not obscure the near absence of spat, yearlings, and adult oysters in the Lower region from 1953 to the early 1970s (Fig 24). Several intervals of spat recruitment from 1969 -1974, 1978 - 1982, and, to a lesser degree, 1988 - 1991 produced subsequent increases in yearling abundance (r^2 =

0.740, Table 9) and adult oyster abundance ($r^2 = 0.632$, Table 10). Even when spat, yearlings, and adult oysters were present, their abundances within this region were the lowest of all four regions.

The very low numbers of oysters of any life-history stage from 1953 to 1971 make comparisons of the relative mortality estimates of both spat and oysters to the mortality of the other regions less meaningful because variation associated with sampling live and dead oysters will affect proportions more than if the oysters were abundant. In the years after 1971, when greater numbers of oysters were present and relative mortality estimates are more robust, RSM and ROM figures were similar in magnitude to those in the Lower Middle region (Fig. 25a and c). Once again, drill predation accounted for the majority of spat mortality in most years (Fig. 25b).

Presence of temporal trends within the data. Inspection of the annual means for all of the seed beds and each of the regions suggests that trends exist in the data where intervals of several years are characterized by fairly constant magnitudes of the respective variables. To examine this issue more carefully, runs tests were performed on the ln-transfomed (count data) or angular-transformed (proportional data) means to determine whether the occurrence of runs above and below the median value of the data set could be explained by random variation alone (Siegel and Castellan 1988).

Several patterns are revealed by this procedure (Table 11). In all regions, oysters were low in abundance prior to 1970, high in abundance from 1970 to 1984, and variable but near the median abundances after 1984 (Fig. 26). In contrast, yearling and spat abundances display no temporal trends except in the Lower region where alternating four to six year intervals of above median and below median abundances occurred after 1969 (Figs. 27 and 28). In the two Middle regions, but not the Upper and Lower regions, RSM and ROM occurred in annual groupings (Fig. 29 and 30). Three intervals of low relative mortality occurred in these regions from 1960 to 1962, 1970 to 1984, and 1989 to 1990. The proportion of spat killed by drills changed from 1969 to 1970 in the two Middle regions (Fig. 31). With few exceptions, drill-induced spat mortality was considerably lower there after 1969 than before.

Changes in abundances (1953 - 1992) in individual seed beds. The annual mean abundances of spat, yearlings, and oysters as well as the mean relative mortality measures for the individuals beds generally follow the patterns observed at the respective regional levels (Figs. 32 to 36). The greatest variability among beds within a region occurred within the Lower Middle region. It is not clear whether this diversity in abundance and mortality patterns results from the greater variation in location of the beds in this region relative to the shore (Table 1) or the decreased sampling effort that had been made on several of the beds in this region (Table 7).

Between year relationships of spat, yearlings, and adult oysters. The general patterns of high dependency of yearling mean abundances on the preceding year's spat mean abundance and moderate dependency of oyster mean abundances on the preceding year's yearling mean abundances continue within each of the seed beds (Table 9 and 10). Regardless of spatial scale, model II regressions reveal that generally 50%, and frequently >70%, of the variance in yearling abundance is explained by spat abundance in the preceding year (model II regressions were used because the independent variable, spat abundance, is as subject to measurement error as the dependent variable, yearling abundance). Similarly, regardless of spatial level, model II regressions of oyster abundances onto the preceding year's yearling abundances are significant although the amount of adult oyster variation in abundance explained is generally lower and more variable (20 to 60%) than occurred in the regressions relating yearling abundances to the preceding year's spat abundances.

The regression parameters (intercept and slope) can be used to estimate mean survivorship of the different life-history stages occurring in each of the beds. The slope of the yearling onto spat regressions estimates the proportion of spat surviving to the yearling stage. A slight decrease in spat survivorship and between-bed variation in survivorship occurs the farther a bed is from the mouth of the bay (Fig. 38). Yearling survival (estimated by the slope coefficients of the oyster onto yearling regressions) follows a similar upbay pattern to spat survival (Fig. 38). Oyster survival (estimated by the intercepts of the oyster onto yearling regressions, measured in this case as the mean number of oysters $20L^{-1}$ that is not related to yearling survival) increases slightly with increasing distance from the mouth of the bay. The intercepts of the yearling onto spat regressions are generally near or less than 0, as they should be, because all yearlings will grow into two-year olds or die. However, the intercepts for the beds in the Upper region are significantly greater than 0 (Table 10, Fig. 38). Oysters grow very slowly in the uppermost beds. The error rate in identifying yearlings (based on observations of overall size and physical appearance of the individual oyster) is probably highest in samples collected from these three beds (and apparently affects the data.)

Seed bed condition - Discussion.

Yearling abundance strongly depends on spat abundance from the preceding year in all years on all seed beds. This implies the absence of consistent region-specific differences in the mortality rate of oysters aged from approximately 5 to 14 months. The sources of mortality may differ in the different regions. Oyster drills (*Urosalpinx cinerea*, Say and *Eupleura caudata*, Say) cannot survive long in salinities below 15 ppt (Engle, 1953) and the distribution of drilled spat on the seed beds is consistent with distribution of higher salinities over the seed beds. In the Upper and Upper Middle regions salinities below 10 ppt may decrease juvenile oyster survival. Loosanoff (1953) demonstrated lower survival of oysters exposed to low salinities in the laboratory. Indirect evidence from the distribution of abundances in the field (Abbe, 1988) and temporal patterns of harvests (Ulanowicz *et al*. 1980) also indicate that areas (or years) that experience low salinities show decreased survival of oysters. The highest mean abundances of adult oysters found in Delaware Bay occur on the Upper beds, which have the lowest salinities and the greatest estimated survival of adult oysters (based on the intercepts of the regressions). Both spat and yearling survival (estimated by the slopes of the regressions) drop slightly on these beds compared to beds lower in the bay. This region of Delaware Bay is subject to highly variable salinities (Daiber 1988) and our data suggest that it may experience short term depressions in salinity, or some other factor, that larger oysters can resist, but that younger and smaller oysters cannot.

The relationship of adult oyster abundances to yearling abundances is also significant throughout all of the seed beds, but the exact nature of the relationship is not clear. The counts of oysters, unlike yearlings, include individuals of many different year-classes. The abundance of oysters in any one year results from recruitment of yearlings from the preceding year as well as yearling recruitment from several preceding years and subsequent age-specific mortalities of the adult oysters. Given this, the high frequency of significant regressions that explain 25 - 50% of the variation in adult abundance implies that the recruitment of the most recent yearling class is generally the most important. However, adult oysters will need to be aged in future samplings to uncover the true relationship of yearling survival in most years. Taken together, the results of the regression analyses reveal that a large determinant of adult oyster abundance on all of the seed beds examined is the recruitment and survival of oyster spat.

The 1972 year-class and succeeding sets produced a large number of oysters that increased mean abundances of adult oysters on most beds until the mid 1980s, but the factors affecting oyster survival had changed before that year. The results of the trend analysis show that adult oyster abundances increased several years in a row prior to 1972 in most regions. This occurred without any detectable change in the patterns of spat and yearling abundance, except in the Lower region. Both RSM and ROM decreased in the late 1960s. As shown below, this corresponds to an interval when the prevalence of MSX disease fell and when the relative amount of drill predation decreased as well. Consequently, much of the success of the 1972 year-class was likely a function of not only the size of the spat set but of the relatively benign conditions that these oysters experienced in the first few years.

Many large changes in temporal abundance and mortality patterns correspond among the different regions, but some consistent regional differences do exist. Mean abundances of spat, yearlings, and oysters were highest in the Upper region beds and decreased towards the Lower region. The RSM and ROM values were lowest in the Upper region and increased towards the Lower region. The apparent increased RSM on the lower beds may not be real. The results of the regression analyses discussed above suggested that spat survival was more variable in the Lower Middle and Lower beds but that it was somewhat higher or at least just as high as spat survival on the upper beds. The two measures of spat survival arise from different sources. The regression estimate results from the mean ratio of the number of yearlings found to the number of spat found there the year before. The other estimate of spat survival is the ratio of the number of dead spat to the total number of spat, live or dead, that are found in the same sample. The problem with the latter estimate is that in many samples in the lower half of the bay the number of spat found were frequently small. Conversion of numbers of small magnitude to proportions and comparison of these to proportions derived from large magnitude numbers can be misleading (e.g., if two spat are found, one live and the other dead the proportional mortality is 0.50, in a region where 300 spat are found 150 of them must be dead to achieve the same proportion.) The actual factors that, first, allow that many spat to be found at the latter location and then kill so many are likely to be different than the factors occurring at the first location. More intensive sampling on the Lower beds will be necessary to determine what the actual relative rates of spat mortality are among the seed beds.

MORTALITY

Mortality - Introduction.

There are three principal ways of estimating mortality on planted or natural oyster beds. One involves a single sample from a particular location such as a seed bed grid, in which dead oysters (boxes and gapers as defined in the Seed Bed Condition section) are compared to live and dead oysters. We used this method in the analysis of Seed Bed Condition and similar data are collected in the annual Maryland oyster survey (e.g., Krantz, 1991). Interpreting these data can be difficult because the life span of a box is rarely known, and varies seasonally and spatially. This uncertainty makes it is difficult to project the time span over which the calculated mortality occurred and limits the method's usefulness for obtaining cumulative mortality estimates over period of a year or more. Mortality estimates from samples taken only once per year do not permit description of seasonal patterns. The method is good, however, for comparing synoptically collected samples among themselves and with samples collected at the same time in other years.

A second method, used extensively by J. D. Andrews at the Virginia Institute of Marine Sciences (e.g., Andrews, 1966) is to deploy trays, containing known numbers of native oysters, on the bed being monitored. If a tray is tended regularly, interval and cumulative mortalities can be accurately calculated. The tray method is less useful in Delaware Bay because trays can become quickly fouled or mudded, and may disappear during storms.

The third method, which relies on frequent and regular sampling of specific locations, provides mortality estimates over short intervals and shows seasonal mortality patterns not available using the single-sample per year method. It is limited by the number of locations that can be sampled regularly and by the fact that it often relies on extrapolated data. Conversely, because the oysters are not constrained by a tray, natural spatial relationships and more nearly natural losses due to a host of environmental factors are recorded. The existence of two sets of mortality estimates, however, made by different methods from the same oyster populations, provide an opportunity to compare the two methods for Delaware Bay oyster seed beds.

Mortality - Methods.

A mortality sampling program was begun in an attempt to discover the cause of the 1957 epizootic that killed up to 95% of the oysters in Delaware Bay and was subsequently ascribed to the protozoan parasite *Haplosporidium nelsoni* (MSX). The program was continued to 1) obtain oysters for disease monitoring and 2) to estimate the amount and probable causes of recent mortality in oysters collected throughout the New Jersey side of the bay. Mortality and disease results from this program (through 1980) have been presented and discussed by Ford and Haskin (1982) and Haskin and Ford (1982). On the seed beds, dredge samples were taken ~6-10 times per year from a 4-grid plot (~40 hectares; 100 acres), referred to as the Test Area, on the most productive part of the bed. The beds monitored were selected early in the program, before cluster analysis grouped beds into regions according to salinity regimes; however, the chosen beds, in fact, represent each region: Arnolds Bed (Upper region), Cohansey Bed (Upper Middle region), Bennies or New Beds (Lower Middle region), and Egg Island Bed (Lower region). Bennies Bed was the principal bed sampled in the Lower Middle region, although sampling was switched to the adjacent New Beds (Fig. 1) for a 6-year period from 1970-1975. The data from both beds have been pooled to represent the Lower Middle region. Regular sampling from the Lower region did not begin until 1973, after the 1972 set had re-established a population of oysters on the bed. These same locations (and samples) provide the MSX-disease data.

Sampling Frequency. From about 1960 through 1970, sampling of each location was attempted on a monthly schedule, although weather and other interferences usually reduced this to 9-10 times per year. From 1971 through 1987, samples were collected about 7 times per year, at critical points in the annual infection cycle (Ford and Haskin, 1982). With few exceptions, collections were made at the same frequency and within a few days of each other on all beds. After 1987, sampling was too infrequent and irregular on the seed beds to permit calculation of annual mortalities. Approximately 950 dredge samples were collected on the New Jersey seed beds between 1958 and 1993 (Table 12). Samples of live and recently dead (gaping) oysters were preserved for histological determination of *H. nelsoni* infection prevalence and intensity (see MSX Disease section).

Sampling procedure. On each sampling date, the Test Area was dredged with a small oyster dredge (71.1-cm tooth bar with a bag capacity of about 80L), until 1-bushel (37 qt; 40.7L) of oysters, boxes, and gapers had been collected. In most cases this required more than one dredge haul, but in Upper region where oysters were most abundant, a single haul often sufficed. An important distinction between the mortality samples and the seed bed condition samples is that a 40.7L sample of the former contains only the elements used to calculate mortality (live oysters, boxes, and gapers) whereas the same volume of the latter may consist of mostly shell or other material, with only a small number of oysters, boxes, and gapers. Simply because of the larger numbers, the estimate of mortality from a single mortality sample is usually more robust than that from a single seed bed condition sample, although multiple seed bed condition samples are available for the estimate

All live oysters, gapers (G = dead oysters, flesh present), new boxes (NB = dead oysters, flesh gone, valves attached at hinge, inner valves unfouled) and old boxes (OB = dead oysters, flesh gone, valves attached at hinge, inner valves fouled) were counted. The most probable ("explained") cause of death (crabs, oyster drills, dredge damage) was determined for gapers and new boxes. If no cause could be assigned, mortality was listed as "unexplained". Gapers and new boxes were considered "recently dead":

Dead Oyster-Recent (DOR) = NB +G

Other information included the volume of oysters and boxes and an estimate of the "Recent Mortality Interval":

Mortality Interval-Recent (MIR) = estimated period during which "recently dead" oysters died.

Because "recently dead" oysters are defined on the basis of fouling and scavenging rates, the MIR varies with the time of year and local conditions. Estimates of MIR were corroborated during warm months by field placement clean shells that were checked for fouling and replaced at regular intervals. Where no corroborative or experiential information was available to estimate MIRs, a standard interval was applied based on long-term observations throughout the bay (Table 13).

Data Computations. One of the objectives of the mortality sampling program was to estimate the proportion of oysters that died each year at each sampled location:

Annual Percent Mortality (APM) = Percent of population that died in a defined 12-month period.

This was achieved by cumulating mortalities in short intervals rather than from total counts of live and dead oysters in the sample. The information obtained from each dredge sample was used to calculate a relative mortality for the MIR preceding that sample date, assuming that gapers and new boxes were alive at the beginning of the MIR:

$$\textbf{Relative Oyster Mortality-Recent } (\mathbf{ROM_R}) = \frac{G + NB}{G + NB + O}$$

The relative mortality during the MIR was then used to estimate relative mortality during the interval (Sampling Interval - SI) since the previous sampling:

$$\textbf{Relative Oyster Mortality-Sampling Interval } (\mathbf{ROM_{SI}}) = \frac{ROM_R}{MIR} \times SI$$

For instance if the sum of new boxes and gapers was 50 and there were 350 live oysters in the sample, the relative mortality during the MIR would be 50/400 = 0.125 (12.5%). If the MIR were 4 weeks and the SI were 5 weeks, the relative mortality during the SI was estimated to be 0.125/4*5 = 0.156 (15.6%).

This method works well when the two intervals are similar. The SI was rarely less than the MIR; however, as the SI increases relative to the MIR, the approximations and extrapolations become increasingly suspect. This potential problem is somewhat offset by the fact that sampling was more frequent during the summer months, when the MIR is approximately 4 weeks. Winter sampling could be less frequent, as the MIR is 10-12 weeks.

The ROM_{SI} is based on the number of oysters alive at the start of the sampling interval, not the start of the study period; thus, successive ROM_{SI} values cannot be summed to calculate cumulative mortality because they will eventually total more than 1.0 (100%). It is necessary to correct ROM_{SI} values to the proportion of oysters alive at the start of the study period, which is considered to be 1.0 (100%). For the first interval, the relative mortality, corrected mortality, and cumulative mortality are all equal:

$$\textbf{Corrected Relative Oyster Mortality-Sampling Interval 1 } (\mathbf{CorM_1}) = ROM_{SI1}$$

$$\textbf{Cumulative Relative Oyster Mortality-end of Sampling Interval 1 } (\mathbf{CumM_1}) = (CorM_1)$$

In the second and subsequent intervals, cumulative mortality to the start of that interval must first be subtracted from the proportion of oysters alive at the start of the study (i.e., 1.0):

$$\mathbf{CorM_2} = (1.0 - CumM_1) * ROM_{SI2}$$

$$\mathbf{CorM_3} = (1.0 - CumM_2) * ROM_{SI3}$$

$$\mathbf{CorM_j} = (1.0 - CumM_{(j-1)}) * ROM_{SIj}, \text{ etc.}$$

Cumulative mortalities to the end of each sampling interval can then be computed as the sum of corrected interval mortalities to date:

$$\mathbf{CumM}_{\mathbf{(2\ to\ j)}} = (\mathrm{CorM}_1 + \mathrm{CorM}_2 \ldots\ldots + \mathrm{CorM}_{(j-1)} + \mathrm{CorM}_j)$$

Proportional values can be converted to percent mortality by multiplying by 100.

For this study, the Annual Percent Mortality (APM) is calculated for a year beginning on July 1 (= survival 1.0 or 100%) and extending through June 30 of the following year (=MSX Year) to fit into the annual MSX disease cycle (Ford and Haskin, 1982; Haskin and Ford, 1982). Only yearlings and older oysters were included in the counts. Mortality is cumulated separately for that which is from known causes (explained), and that which is from unknown causes (unexplained). Known causes include predation by crabs and oyster drills. Unknown causes include diseases, fresh water, and other factors that leave no obvious external sign. In some cases, the sampling frequency was inadequate to estimate a percent mortality for the entire year. Usually this was because the period of time between samples was too great to allow reliable extrapolation. In these cases, APMs were not estimated.

The mortality sampling program was not designed to include extensive replication of sample collection at a particular site on the same day; however, on several dates, multiple mortality samples were collected from the same beds. These samples were used to obtain an indication of the variability associated with this type of mortality estimator.

Mortality - Results

Baywide Patterns of Mortality. Because of data gaps, primarily the complete lack of samples from the Lower region before 1973, we have not derived baywide APM means. Nevertheless, an inspection of patterns in the individual regions shows that APMs have roughly the same overall pattern as do the percent mortalities based on one-per-year seed bed samples (compare Fig. 17c with Fig. 39). Although APMs on the seed beds were temporally quite variable, they were usually less than 20%, compared to an APM mean of about 45% for the lower bay planted grounds (Ford and Haskin, 1982). In general, most of the mortality occurred in the winter and spring, except in some years when MSX-disease was prevalent or when predation was high (Fig. 40).

Certain patterns were common to all four regions (Fig. 39). For instance, mortality rates were high in the early 1960s, the mid 1960s, the mid 1970s, the early 1980s, and the mid 1980s. Mortalities in 3 of these 5 periods (1965-66, 1980-81, and 1985-87) were strongly associated with MSX disease (see MSX Disease section).

Mortalities in the Upper region. Explained mortality occurred in 10 of 27 years of record, but was <1% annually except in 1980 and 1981, when it was 2-3% (Fig. 39a). Crab damage was the most frequent cause of explained mortality. Unexplained mortality was highly variable, ranging from a yearly low of 3% in 1978 to a high of 62% in 1971. Of the 27 recorded years, 10 (37%) had APMs ≥20%, 9 (33%) were ≥10% and <20%, and 8 (30%) were ≤10%. In some years, high mortalities were recorded in this region, but not in the more downbay regions. For instance, mortalities were high from 1959 through 1962, and again in 1971-72. In the first period, they occurred mostly in the spring, but in 1971-72, autumn mortalities predominated (40a).

Mortalities in the Upper Middle region. Explained mortalities occurred in 15 of 28 recorded years, but was <1% in all but 5 of them (1965, 1974, and 1985-87). Oyster drill-caused mortality was recorded only from 1965 through 1967; crabs were the primary associate of explained deaths in the other years. Unexplained mortality was less variable than in the upper region, ranging, yearly, from 2% in 1982 to 42% in 1987 (Fig. 39b). Of the 28 recorded years, 8 (29%) had APMs ≥20%, 12 (42%) were ≥10% and <20%, and 8 (29%) were ≤10%. No unusually high mortality occurred here that was not also reflected in the other regions. In most years, mortality occurred primarily in the spring (Fig. 40b).

Mortalities in the Lower Middle region. Explained mortalities occurred in 18 of 26 years of record, were <1% in 13 years, and were nearly always associated with oyster drills. In three years (1963, 1964, and 1986) explained mortalities approached 10% per year (Fig. 39c). Unexplained mortalities ranged from 4% in 1982 to 51% in 1987. Of the 26 recorded years, 10 (38%) had APMs ≥20%, 9 (35%) were ≥10% and <20%, and 7 (27%) were ≤10%. The APM pattern over this period was generally similar to that of other regions. Autumn mortalities predominated in some years, spring mortalities in others (Fig. 40c).

Mortalities in the Lower region. Explained mortalities, usually caused by oyster drills, were recorded in 13 of 15 years when samples were taken (Fig. 39d). They were always >1% each year and exceeded 10% in 4 years (1973, 1977, 1985, and 1986). Unexplained mortalities ranged from 4% in 1973 to 45% in 1985 (note that although sampling in this region did not begin until 1973, the span of sampling did encompass the years of high and low mortalities in the other regions, except for the 1971 peak in the upper region.) Within the abbreviated sampling period, the proportions of years with APMs <10%, ≥10% <20%, and ≥20% were about equal. Autumn mortalities equalled or exceeded those recorded in the spring (Fig. 40d).

Differences in seasonal mortality patterns are illustrated by comparing cumulative mortalities over a year with high APM, but *without* MSX disease (1962); and one with high APM and with high MSX disease (1985). In all sampled regions, mortalities in 1962 occurred in the spring and were highest in the Upper region (Fig. 41). Conversely, in 1985, mortality rates were fairly constant throughout the year, except in the Lower region, where they occurred primarily in the autumn and where they were also the highest (Fig. 42).

Sampling variability. On three occasions in May 1981, more than one part of a seed bed was sampled the same day (Table 14). These revealed a great deal of variability among samples. For instance, samples from 6 different grids on Egg Island Bed gave recent mortality estimates ranging from 6.4% to 45.4%, mostly from unexplained causes. These data reflect the uncertainty of using one sample to represent the mean mortality. Whether this variability is due to spatial, temporal, or other factors cannot be determined from these samples.

Mortality - Discussion.

The mortality samples showed the same general patterns and lead to the same overall conclusions as did the mortality estimates from the seed bed condition samples. High mortalities occurred in some years in all regions. These were associated with MSX disease and with periods of low Delaware River flow that elevated salinities over the seed beds (see Hydrography and MSX Disease sections). Year-to-year fluctuation in mortality was strongly associated with

MSX disease in the Lower and Lower Middle regions. To a lesser extent, MSX disease was associated with elevated mortality in the Upper Middle region, but the greatest mortalities in the Upper region were not associated with the disease. The mortality samples provided addition information not available from the seed bed condition samples. For instance, it was evident that explained (predation-caused) mortality, primarily by oyster drills, increased in a downbay direction on older oysters as well as on spat (see Seed Bed Condition section). Mortalities in the summer and autumn were typically greater than winter spring losses in the two lower regions where MSX disease and predation were the principal causes. Conversely, the greatest mortalities on the Upper and Upper Middle regions occurred in winter and spring, and were probably associated with high spring freshwater runoff.

Interestingly, despite the presumption that mortality estimates from the seed bed condition samples would underestimate annual mortality because of the disintegration of the hinge holding valves together, these estimates were higher than those obtained by the cumulative mortality method (compare Fig. 17c with Fig. 39). There are a number of possible reasons for this unexpected results: 1) we have underestimated true mortality rates by the cumulative mortality method because of different sampling and computation procedures; 2) old boxes last longer than one year so that counts in the seed bed condition samples represent the accumulation of boxes over more than one year; 3) apparent mortalities in the seed bed condition samples were elevated by storage before workover; or 4) some combination of these or other factors.

MSX DISEASE

MSX Prevalence and Intensity - Introduction.

Between 1957 and 1959, an estimated 90-95% of the oysters on the planted grounds in the lower Delaware Bay were killed by *Haplosporidium nelsoni*, the cause of MSX disease (Haskin et al. 1966). The epizootic moved upbay in 1958 and 1959, killing at least half of the oysters on the seed beds (Haskin and Ford 1982; Fig. 17c). The disease has remained in Delaware Bay since 1957. Annual infection cycles, associated mortality rates, and year-to-year fluctuations in disease activity on the planted grounds, where high salinity favors the parasite, have been described by Ford and Haskin (1982). Lower salinities over the seed beds, especially on the Upper and Upper Middle regions, generally prevents high disease pressure, but periods of low river flow allow the parasite to move upbay. Resulting infections may cause oyster mortalities, although the relationship between disease and mortality is not as strong as on the lower bay planting grounds (Haskin and Ford 1982). Here we report MSX disease prevalences and intensities on the seed beds from 1958 through 1992, extending the data base for an additional 12 years beyond the study of Haskin and Ford (1982). Statistical analyses of the data, which were not provided by the earlier study, are also presented.

MSX Prevalence and Intensity - Methods.

In late autumn/early winter and in the following late spring (usually in May) of each MSX year (July 1 to June 30 of the following year) from 1959 to 1992 samples of oysters (n = 20 except for a few beds in 1959 - 1962 where n = 10) were selected from dredge samples collected as part of the oyster mortality study (seed Mortality section). Spring and autumn correspond to annual infection peaks (Ford and Haskin, 1982). Gapers (see Mortality Section) were collected from all samples. All gapers were processed; results from June 1 to December 31 collections were pooled to represent late summer/autumn and from January 1 to June 30 collections, to represent the late winter/spring period (Table 15). In most years, the spatial scope of the samples included the Upper region (Arnolds Bed), Upper Middle region (Cohansey Bed), Lower Middle region (Bennies Bed and New Beds), and Lower region (Egg Island Bed).

The oysters and gapers were returned to the laboratory where they were prepared for histological analysis of prevalence and intensity of MSX infection (Ford and Haskin 1982). Only gapers without evidence of predation or other explained cause of death are included in the analysis. Microscopic examination of stained tissue sections were used to determine whether individual oysters were free of detectable infection, contained parasites localized in the gill, usually in the epithelium (local infection), or contained parasites throughout all tissues (systemic infection). About 90% of oysters dying with MSX disease have systemic infections, suggesting that local infections are not lethal. Thus, at the time they are diagnosed, local infection can be considered benign whereas systemic infections are likely to kill. Of course, local infections are likely to develop into systemic infections at some late time. The rate at which this happens is slower, and the likelihood that systemic infections will be lethal, is lessened in oysters that have developed some degree of resistance to MSX disease (Ford and Haskin 1987).

Infection data have been converted into proportions (= prevalence) of MSX infected oysters in each sample:

$$\textbf{Total Prevalence (TP)} = \frac{\text{Number of individuals with detectable infections}}{\text{Total number of individuals examined}}$$

The same calculation was made to determine gaper prevalence from the total number of gapers examined (separately pooled within the two periods described above).

The proportion of systemically infected oysters was used as an index to the severity of infections and was calculated in two ways: 1) as the proportion of all oysters examined and 2) as the proportion of infected oysters only:

$$1)\ \textbf{Systemic Prevalence-Total } (\mathbf{SP_t}) = \frac{\text{Number of individuals with detectable systemic infections}}{\text{Total number of individuals examined}}$$

$$2)\ \textbf{Systemic Prevalence-Infected } (\mathbf{SP_i}) = \frac{\text{Number of individuals with detectable systemic infections}}{\text{Total number of individuals with detectable infections}}$$

Identical calculations were made for gapers. The value SP_t was used primarily for graphic presentation, because it can be easily done in conjunction with total prevalence while still permitting visual determination of the proportion of systemic infections among all infections (Figs. 43 and 44). The value SP_i was used for statistical analyses.

Samples from Upper, Upper Middle, and Lower Middle regions were collected in most years. The Lower region has been sampled since 1973 (Table 12). Data from Bennies and New Beds have been pooled to represent the Lower Middle region graphically (Figs. 43c and 44c; see Mortality section also), but have been analyzed separately. All proportional data were angular transformed prior to use in any analysis.

MSX Prevalence and Intensity - Results.

In most years, TP was less than 0.20 in the Upper and Upper Middle regions (Fig. 43a and b). In the Lower Middle and Lower regions, TP exceeded 0.20 in most years and 0.50 in some years (Fig. 43c and d).

When infected oysters were found in the Upper and Upper Middle region samples, they usually occurred in the autumn. An obvious seasonal difference in disease prevalence did not exist for the Lower Middle and Lower regions. On all beds, the late 1960s and most of the 1970s were intervals characterized by low MSX prevalences. The mid 1960s, and the 1980s, especially 1985 and 1986, were years when MSX infections were prevalent on all beds. High prevalences again occurred in the early 1990s, but were more pronounced on the Upper and Upper Middle regions. High mortalities due to *Perkinsus marinus* (Dermo disease) were occurring in the Lower Middle and Lower regions at that time (Ford, unpublished), complicating interpretation of MSX disease levels in these regions. In most regions, in most years, more than half of the infections were systemic (Fig. 43a-d). With the exception of the Lower region, MSX disease prevalence and intensity on the seed beds was never as great as on the planted grounds (Table 17).

Gapers occurred more frequently in spring dredge samples from all regions; gapers were uncommon in autumn samples (Table 15). When gapers were found in samples from the Lower and Lower Middle regions, TP generally exceeded 0.50 and most infections were systemic (Fig. 44c and d). The same was true for the few gapers collected in autumn dredge samples from the Upper Middle and Upper regions. The TP was generally less than 0.50 in gapers collected in the spring from these regions, although most infections were systemic (Fig. 44a and b).

The TP of oysters in the spring was not well correlated with the TP of oysters in the autumn of the same calendar year (different MSX years) for any of the beds (Table 18). Likewise, no significant correlations occurred between SP_i in the spring and SP_i autumn for any bed (Table 18). Neither index, measured in the autumn, was well correlated with the same measure the following spring (same MSX year) (Table 18). On the other hand, high (> 0.75) and significant Pearson correlations occurred between TP and SP_i in both the spring and autumn for all beds (Table 18).

MSX Prevalence and Intensity - Discussion.

Inspection of all four regions shows that MSX disease infections have waxed and waned over fairly long intervals (Fig. 43). Two very high peaks of infection occurred in the mid 1960s and mid 1980s. The former occurred during a period of prolonged drought in the Delaware watershed (Fig. 10); the second was also associated with a period of low runoff, but this was of shorter duration and occurred mostly in the spring (O'Connor et al. 1986). Infections were relatively low immediately before the first peak, in between the two peaks, and immediately after the second peak. The temporal correspondence of these trends to the changes in adult abundance and to mortalities on the seed beds described above is strong. Adult abundances were generally low in the mid 1960s, increased in the very late 1960s and remained relatively high until the mid 1980s (Fig. 16c). In both the mid 1960s and mid 1980s, baywide mortalities were elevated (Figs. 17c and 39).

Haplosporidium nelsoni infects oysters during the warm months from June through October in high salinity, lower portions of Delaware Bay (Haskin et al. 1965). The onset of new infections in seed bed oysters has not been similarly documented by the timed deployment of uninfected oysters, but it is likely that they are acquired during the same general period, although perhaps somewhat delayed compared to the lower bay (Andrews 1964, Haskin and Ford 1982). The subsequent development of infections these infections occurs over the following year. Late autumn/early winter prevalence represents the first peak in the development of that summer's infections and the following spring prevalence represents a second peak, at the end of the annual infection cycle (Ford and Haskin 1982). The absence of strong and significant correlations between the two peaks implies that they are influenced by different factors, even when they are part of the same infection cycle. Within a disease cycle, the typical progression is for an infection to become established in the gill (local) and to eventually become systemic (Ford and Haskin, 1982). Some infections, however, may never become systemic, particularly in MSX-disease resistant oysters. The high correlations between total infections and systemic infections suggest that conditions that keep the numbers of infected oysters relatively low on the seed beds do not restrict the development of infections once they are established in oysters.

The principal factor influencing MSX disease on the seed beds, particularly in the Upper and Upper Middle regions, is salinity. Low salinity kills *H. nelsoni* both *in vivo* and *in vitro* (Ford 1985, Ford and Haskin 1988). The very low prevalences in the spring samples from the two uppermost regions, indicates that spring runoff plays a strong role in mediating MSX disease. Resulting low salinities are particularly important in destroying or reducing infections that were acquired and proliferated the previous summer and autumn; consequent mortalities are low. When spring runoff is depressed, as was the case in the mid 1980s, this does not occur and mortalities rise. The importance of salinity to MSX disease levels on the seed beds can further be seen by the upbay-downbay gradient: the disease was much more frequent and of higher intensity on the Lower Middle and Lower regions than in the two upper regions. The high proportion of systemic infections in gapers in all seasons indicates that most oysters deaths in the Lower Middle and Lower regions, not caused by predators, were caused by MSX disease. On the Upper and Upper Middle beds, some other factor, such as exposure to freshwater or starvation, is apparently responsible for nonpredation mortality in most years.

SEED BED HARVESTS

Seed bed Harvests - Introduction.

Studies on the harvest of oysters from Delaware Bay seed beds began in 1956. Prior to that time, estimates were made from information collected from boat captains, planters, and oyster resource agents. Records from the Haskin Shellfish Research Laboratory (then called the New Jersey Oyster Research Laboratory) personnel at the time the seed bed harvest studies were initiated indicated that these records were generally considered to be unreliable. The lack of appropriate data resulted in the development of a program to measure which boats were working, where they were working, and how much they harvested. These data are the basis for this section.

Statistics based on catch per unit effort (CPUE) have been one of the most common means to manage fish populations, and have often been used as a basis for measurement of abundance. Statistical models deriving variance estimates for CPUE have recently been developed (Richards and Schnute, 1992), but many uncontrolled variables affect these data. The size of the vessel (tonnage), gear, and the behavior of individuals can interact with changes in the abundance of the organism being harvested. Such measures are of concern to fisheries biologists, but economists have also been interested in the efficiency of harvests. The economic terms such as fleet capacity, capacity utilization and the ratio of catch to capacity (Smith and Hanna, 1990) are derived data similar to CPUE, but economists measure additional parameters that affect the fleet such as whether a boat is working or not. The economic measures estimate factors that often go undetected, but are important for fishery management, such as an overall increase in fleet efficiency. These terms can be particularly important in limited entry fisheries.

While CPUE calculations are common for fish, the literature on the use of such statistics for managing molluscan populations is less voluminous. Berg and Olsen (1989) and Murawski and Serchuk (1989) examined CPUE for queen conchs and surf clams, respectively. Berg and Olsen (1989) utilized these data to make estimates of optimal fishing effort for queen conchs, but this was not done by Murawski and Serchuk (1989) for surf clams in the same volume. The extensive report on the oyster industry in Virginia (Haven *et al.* 1978) does not utilize catch and effort data in deriving recommendations for the industry. The reason that catch and effort data have not been not used in analysis of oyster data is not apparent. Our data includes an extensive catch and effort compilation for harvests from the New Jersey Delaware Bay seed beds and we have attempted to utilize CPUE analysis at various spatial scales.

Seed bed Harvests - Methods.

Beginning in 1956, Haskin Shellfish Research Laboratory personnel were on the bay during the seed bed harvest season as often as conditions would allow safe vessel use. Prior to a season, a list of all licensed boats and their tonnage was obtained from the state shellfish office. After the first few years a data sheet was prepared. The data sheet listed the boat name, gross tonnage, license number, captain, crew numbers, seed bed worked and bushels of oysters on deck (we continue to use the term bushel when referring to the data sets, but convert to liters (L) (1bu = 40.7L) for analysis. Later data sheets dropped the tonnage, captain's name, and crew size. One data sheet was prepared for each day of the seed bed harvest season. Typically, the laboratory crew consisted of the boat operator and a senior biologist. D. Kunkle was responsible for the vast majority of the observations from 1956 through 1988. From 1956 to 1977 Mr. Kunkle was assisted by W. Richards as boat captain; in 1978 C. Phillips took over as captain. Observations in 1990 and 1991 were conducted by the New Jersey Department of Environmental Protection (DEP) by Mr. J. Dobarro and Mr. R. Reed.

The standard method for obtaining seed harvest data was to patrol the seed beds in the morning to determine which boats were on which beds. During the afternoon, the laboratory boat moved down bay and continued to check on the harvest boats with binoculars. As the oyster boats passed down bay to the planting grounds the laboratory boat would approach, record the vessel name, and estimate the deck load of oysters. Periodically, these estimates were checked against the captain's estimates, or against measured deck loads. According to notes and unpublished data, these checks indicated that observer estimates usually were within 10% of captain or deck load measurements. On days when it was too rough for the laboratory boat, shellfish enforcement officers were contacted and a telescope used to survey boats from the nearest shore point, to make estimates. Ancillary information was often recorded on the data sheets. These data include weather conditions (usually only extremes), % shell determined by enforcement officers checking deck loads for compliance with the Rough Cull Law (a volume of no more than 15% shell could be taken with the seed oysters to be planted), whether or not a boat worked a full day, whether a boat had not planted seed caught the previous day, when a boat worked more than one bed, when a boat broke down, and when a boat was on the bay, but not working. This last information may have indicated a vessel was not dredging, but buying oysters.

At the end of each week during the seed harvest season, samples of at least 40L were taken directly from deck loads of boats on various beds. The beds sampled were those that had been worked particularly hard, had started the week with relatively low percent oyster, or both. Typically, samples were collected from two or three boats per bed. On shore, the samples were sorted, by a committee composed of industry, DEP, and laboratory personnel, into oysters (=adults, yearlings, and spat) and shell (anything without an oyster attached). The volumes of oyster and shell were recorded for each sample and averaged for the bed. Results were used to determine when a bed or series of beds should be closed to further harvest. The rule of thumb was when the samples averaged less than 40% oyster, the bed should be closed.

The seed bed harvest data have been analyzed in stepwise fashion starting with simple graphing techniques to show numbers of boats registered and working during a season, and numbers of days in the season. Following these preliminary analyses, data are presented for baywide trends, trends within the four region of the bay, and lastly by individual beds. Within each of these presentations, boat information is discussed first then harvest information is provided, and finally these are combined as catch and effort.

The potential harvest for each boat is based the maximum observed seed harvest for that boat in a given year. Using this figure as 100% effort normalizes year-to-year changes that may have taken place in the boat. Such changes, due to a new captain, a change in deck gear, or the amount of effort that was put into preparing for the season, have more to do with a boat's performance in this fishery, than does oyster abundance.

There are substantial differences in the size of the boats registered for oyster harvest in New Jersey's Delaware Bay fleet. In addition to normalizing for changes in the boat, the use of the maximum load for a boat in a given year normalized for boat size. Multiplying boat size (= deck-load capacity) times the number of days it operated in a particular year provides an estimate of the Potential Harvest capacity for that boat in that year:

Potential Harvest-boat (PH_b) = maximum load that year x number of days operating

Summing these data for all boats provides a basis for estimating total possible harvest (Potential Harvest) in the same year:

Potential Harvest (PH) = $\sum PH_b$

Likewise, multiplying the boat's capacity by the number of days it spent in various regions or on various beds and summing these data for all boats on the same region or bed provides a basis for estimating the regional or individual bed potential harvest for a given year.

Seed bed Harvests - Results.

Seed harvest data exist from 1956 to 1991 (Table 19). The first year of the effort (1956) to evaluate seed bed catch and effort are not included in the data sets because of the difficulty interpreting the records. There are a number of inconsistencies in the data - such as missing days - that have lead us to exclude the information in the detailed analysis, but total production figures are included.

Baywide vessels registered and working. The season length, number of boats registered in the fishery, the number of boats working, and the harvest potential for these boats varied considerably over the years (Fig. 45, Table 20). The large number of boats registered in 1981 was caused by initiation of limited entry. The number of boats registered in the fishery has remained relatively constant since that date, but the numbers of boats working in any year has often been substantially less than those available. The number of boats working ranged from 128 in 1958 to 35 in 1990 (mean = 60, S.E. = 4.6, n = 27) while those registered ranged from a high of 152 in 1958 to 21 in 1960 (mean = 77, S.E. = 5.47, n = 34). The drop in registered boats in 1949, 1960, 1963, and 1964 reflect conditions before limited entry. At that time, many boat owners would not register their boats if the seed beds were to be closed.

Baywide seed bed harvest. The greatest volume of oysters removed from the seed beds was 18.7×10^6 L (1979) while the least was 2.9×10^6 L in 1986 (Fig. 46, Table 21) Seed beds were closed in 1959, 1960, 1963, 1965; from 1987 through 1989; and again in 1992 and 1993. Closures of portions of the beds occurred 1958, 1961, 1964, 1967, 1970 through 1974, and in 1979 and 1980 (Table 19). For the 27 year period in which the beds were open, harvests averaged 10.6×10^6 L (S.E. = 9.27×10^5, n = 27). If the years in which no harvest was permitted are included, average harvest for the period drops to 8.4×10^6 L (S.E. = 1.05×10^6, n = 34). The Delaware Bay Shellfish Council voted in January to open the seed beds in 1957, but subsequent action by the State after the epizootic mortalities due to MSX disease that spring, canceled seed bed harvests that year**.** Because of this action, and the lack of a complete data set in 1956, data other than total harvest start in 1958.

The New Jersey side of Delaware Bay has 5474 hectares of seed beds (Table 1), but not all of this is productive. If the entire area is considered, 45.1L $ha.^{-1}$ of oyster seed was produced each year for the 34 years covered by this study. The amount increased to 71.7L $ha.^{-1}$ $yr.^{-1}$ if only the 27 years the beds were opened is considered. This low production reflects the large acreage that is not harvested each year (Table 19) and the large acreage that is peripheral to the best areas of the beds.

<u>Baywide potential harvest and catch effort</u>. The average Potential Harvest (PH) for the 27 years in which seed were moved down bay was 17.2×10^6L (S.E. = 1.32×10^6, n =27). Harvest Potential peaked in 1981 at 29.9×10^6L and was least in 1986 when only 4.6×10^6L could have been moved (Fig. 47, Table 20). If the yearly baywide seed bed harvest is compared to the baywide oyster abundance as measured by concentrations in the seed bed condition samples, there was no indication that oyster abundance affects the quantity of seed harvested (Figs. 48 and 49).

The maximum load of each boat operating in a given year (potential harvest for that year) was used to provide a base for catch per unit effort (CPUE) calculations which were derived for the entire bay by year (Figs. 50 and 51).

$$\textbf{Catch Per Unit Effort (CPUE)} = \frac{\text{Actual Harvest}}{\text{Potential Harvest}}$$

The data indicate no depletion of the resource through this entire period (Fig. 50) and suggests that there was no overfishing on the resource. It is important to note that the peak landings occur in the middle of the data set (Table 19). The central occurrence of this peak drives the data interpretations. If, as with most fishery data the peak were at the earliest portion of the study (three years after the 1972 set) one could easily suggest that overharvesting was beginning to occur in the middle 1980s and that the lack of harvest in 1987-89 was responsible for the rebound in efficiency in 1990 (Fig. 51).

The ratio of the actual seed harvested to the Potential Harvest indicates that for the 27 years when beds were open, the boats were operating around a 60% efficiency (Fig. 51, Table 20). Lower operating efficiencies are clustered primarily in the years prior to 1970. The operating efficiency since 1974 (two years after the large set) has never been lower than 0.6 (mean 0.66) while in the early years efficiencies were below 0.5 for 4 of the 12 years (mean 0.54). There does not appear to be any relationship between the numbers of boats in operation or season length and the efficiency of the seed harvest. The lowest efficiency was in 1968 (0.39) when only 42 boats were harvesting during the 15 day season, while the greatest efficiency was during 1990 (0.74) when 35 boats harvested seed for a 10 day season. The greatest numbers of boats were operating in 1958 when 128 boats worked for 15 days at an efficiency of 0.59. One major change in the fishery was the installation of mechanical culling machines that replaced crew members. This process began in 1975 and within two years most boats had these systems and during that time deck hands were reduced from 10-14 to 1-2 individuals. Because we used the maximum load of a boat in a given year as the greatest potential harvest the boat was capable of during that year, any bias caused by the advent of the mechanical devices should have been removed from the data. It is most likely that the increase in efficiency is due to the greater number of oysters available to the fishery.

Vessel data by region. Of the 27 years in which seed beds were open, boats worked the Upper region in only 17 years (Fig. 52, Table 21). This is similar to the numbers of years (16) boats worked on the Lower beds (Fig. 52, Table 22). Similar numbers of boats worked on the Upper beds and Lower beds in years when they were open (Upper beds - range 1-43, mean = 14.2, S.E. = 3.2, n = 17) (Lower beds - range 1-54, mean = 19.8, S.E. = 3.49, n = 16). Beds in the Upper Middle region were harvested every year they were open (Fig. 52). Numbers of vessels in this region ranged from 118 in 1958 to 18 in 1976 (mean = 48.6, S.E. = 5.21, n = 27; Table 23). Boats fished the Lower Middle region in 25 of 27 years, but were sparse until 1971 (range 1-29, mean = 11.4, S.E. = 3.89, n = 7) when numbers increased dramatically (Fig. 52, Table 24). Beginning in 1971, the number of boats harvesting these beds ranged from 35 to 73 (mean = 49.4, S.E. = 2.71, n = 18). Because of the lack of activity in the early years, the average number of boats (mean = 38.76, S.E. = 4.11, n = 25) harvesting oysters for the 27 years appears to be lower than for the Upper Middle portion of the seed beds, but because of the high variances, the means are not significantly different.

Seed bed harvests by region. Average annual harvests in the Upper and Lower regions (Upper mean = 4.8 x 10^5 L, S.E. = 1.67 x 10^5, n = 25; Lower mean = 5.5 x 10^5L, S.E. =1.67 x 10^5 , n = 21) were similar during the periods they were open (Fig. 53). Over the time of this study only 8.9% of the seed oysters came from the combined Upper and Lower regions. Lower beds were not harvested until 1971 and have not been heavily utilized since the middle 1980s. From 1971 to 1991 Lower region beds were harvested for 16 of the 18 years they were open (Fig. 53) for an average annual harvest of 7.8 x 10^5L, S.E.= 2.09 x 10^5, n = 16. The Upper region followed the reverse pattern with greatest production from 1958 to 1971 (mean = 1.1 x 10^6L, S.E. = 3.77 x 10^5, n = 9). Moderate levels of seed were removed from the Upper region in 1982 and 1986. The use of the Upper seed has been restricted because they typically take longer than one season to reach market size on the planting grounds, which often results in unacceptably high mortalities due to disease. Both the Upper and Lower regions have been harvested about one half the time.

Total harvest for the 1958 to 1991 period was equally distributed between the Upper Middle and Lower Middle regions (Table 19). Harvests were more consistent in the Upper Middle region than in any other area of the bay (Figs. 53 and 54). These beds were open in 26.5 of the 34 years of record (closures of a portion of the region for part or all of a year were scored as a one half year opening) while the Lower Middle region was open in only 22.5 years. Amounts of seed removed from the Upper Middle region were less variable from year to year (mean = 4.6 x 10^6L, S.E.= 4.46 x 10^5, n = 26.5) than amounts taken from the Lower Middle Region (mean = 5.7 x 10^6L, S.E.= 9.40 x 10^5, n = 22.5) during the open years, but average annual harvest volumes based on the total 34-year study period (3.9 x 10^6L and 4.1 x 10^6L respectively) were not significantly different. Prior to 1971, only 5.6 x 10^5L were harvested from the Lower Middle beds, but a large harvest in 1972 followed by excellent survival and production from the large 1972 set shifted seed production from the Upper Middle beds to the Lower Middle beds for the next decade (Fig. 53, Tables 23 and 24).

If seed harvest by region is examined relative to the size of the beds within the region, the two middle regions averaged the greatest amount of seed per hectare (Upper Middle = 96.6L ha.$^{-1}$ yr.$^{-1}$, Lower Middle = 99.5L ha.$^{-1}$ yr.$^{-1}$) for those years the beds were open. In contrast, the Upper and Lower regions were only about one half as productive (37.3 and 42.5L ha.$^{-1}$ yr.$^{-1}$ respectively).

<u>Potential Harvest and catch effort by region</u>. Average efficiencies (=CPUE) for the entire study period by sector are higher where there are more oysters (Fig. 55). The boats were more efficient in the Upper region (mean = 0.686) and least efficient in the Lower region (mean = 0.519). Harvest efficiencies for two middle bay regions were intermediate between the Upper and Lower regions and not significantly different (Upper Middle mean = 0.602, Lower Middle mean = 0.605).

Comparison of oyster harvest with oyster abundance by region, as indexed by the seed bed condition samples (Fig. 54), shows the shift from the dominance of the Upper and Upper Middle regions before 1971 to the Lower Middle and Lower regions after that date. As with the baywide dates, there is no indication that the abundance of oysters has any effect on the total harvest (Fig. 56).

<u>Potential Harvest and catch effort by bed</u>. The total volume of oysters harvested from individual beds for the entire period clearly shows the dominance of four beds (Fig. 57). Two of the beds, New Beds and Bennies, are the largest beds (Table 1) and lie in the Lower Middle region. The other two, Shell Rock and Cohansey, are in the Upper Middle region. Examining potential harvest for each bed throughout the period (Fig. 58) again reflects the dominance of the same four beds. Production of seed on these four beds relative to the size of the bed reveals that they were highly productive. During the years they were open, yields averaged 2918, 4412, 2294, and 4164L ha.$^{-1}$ yr.$^{-1}$ for Cohansey, Shell Rock, Bennies, and New Beds, respectively.

By examining the slope of the daily CPUE line against the cumulated harvest for a given bed it is possible to calculate the initial population size in terms of liters of oysters. These calculations provided highly significant r^2s on some beds in some years, but comparison of final population estimates from one year's calculations with starting population estimates based on the following years calculation (also with significant r^2s) yielded inconsistent results. Because of these inconsistencies we have chosen not to further analyze the data.

Seed Bed Harvest - Discussion.

The detailed information available (boat harvest by bed by day) provides the basis for examining a number of parameters that are not available in other studies. Several important management factors are reflected in the harvest data.

By law, the seed beds could be harvested over two months, but during the 34 years of this study the beds were open a maximum of only 20 days. Beds were opened or closed based on decisions by the Delaware Bay Shellfish Council. This council relied on information provided by an independent third party (Haskin Shellfish Research Laboratory). The basis for the decision on which beds to open or close was the 40% rule, which had been initiated early in our study period by H. H. Haskin. It derived from his feeling that once the proportion of oysters on a bed was less than the proportion of shell (i.e., 40% vs. 60%), that bed should be closed. This informal rule was gradually accepted by the industry, which makes up the Shellfish Council; the state of New Jersey generally follows the decisions of the Council. In practice, several beds in a region, rather than individual beds, were closed.

When this study was initiated, the seed oysters were culled from the cultch and other materials by hand. Many boats had deck crews of 10-14 individuals. The transition to mechanical culling devices began in 1975 and was nearly complete within two years. Today there is only one active boat without these devices. How this transition affected overall efficiency of the fleet is difficult to assess because the transition took place during the period of high oyster abundance. What is obvious from the data is that all of the low efficiencies are in the first part of the data set and that they stabilized at over 60% after 1970. This stabilization took place in spite of fluctuating abundance thereafter (Fig. 16c).

Limited entry was established in 1981 and the numbers of boats registered has remained relatively static since that time. Prior to limited entry, the numbers of boats registered was reflected in the number of boats working. Because a number of companies have fleets of boats, they often would not register all boats in years when the seed beds were closed. Following limited entry, the major change as been the decoupling of the numbers of boats working from the number of boats registered. The advent of limited entry did not change the number of boats working but provided a larger number of registered boats to provide revenue to the state.

There is no provision for boats to harvest directly from the seed beds and market the oysters. This means the boats have to plant on leased grounds in the lower bay. Decisions on whether to open the seed beds, and which beds are the preferred ones to harvest, also reflect this regulation. The Delaware Bay Shellfish council considers not only the condition of the seed beds, but whether or not the oysters will live once they have been moved. The increase of Dermo disease in the bay has had more effect on recent decisions to close the seed beds than has the numbers of oysters on the beds.

What is apparent from these data is that , during the study period, the oyster fleet on the New Jersey side of Delaware Bay has not overharvested the resource. Individual beds may have been harvested more heavily (the low efficiency on the Lower region) or less intensely (Upper region), but this reflects the oystermen's decisions on the potential for the oysters to reach market size, and not the density of oysters on the beds. It is also apparent that environmental and biological conditions that control recruitment can act over periods of many years. This variability requires a mechanism by which the industry has the flexibility to manage the resource by altering harvest locations with the changing conditions. Through the past 34 years the tripartite system of state regulation, strong industry leadership on the Council, and a consistent independently collected (by the laboratory) data base that both the state and the industry trust has allowed continuation of a resource despite variable recruitment, changes in harvesting techniques, and the incursion of epizootic disease.

RELATIONSHIPS

MSX disease infections versus oyster abundance and oyster mortality - Analysis.

The measures of MSX infection, oyster abundance, and oyster mortality all contain substantial amounts of sampling error. Because the degree of sample variation is unknown and unpredictable in the respective data sets we have chosen a conservative analysis procedure for the initial inspection of the data. We used Pearson correlation analyses as the primary tool to examine the data for linear relationships among the various measures of disease infection and changes in oyster abundance. The significance of the correlations were determined using Bonferroni-adjusted probabilities that adjust the type I errors for multiple contrasts (Wilkinson *et al*. 1992). We also calculated Spearman correlations for most comparisons. Spearman correlations derive from the ranks of the observations and not the absolute magnitude of those observations. Comparison of respective Pearson and Spearman correlations reveal whether specific pairings of data have an undue influence on Pearson correlations as a consequence of their large relative magnitudes. In all cases the Spearman correlations followed the same pattern of relationships among the variables as revealed by the Pearson correlations. Consequently, we will present only the latter.

All four measures of disease infection (TP and SP_i for both oysters and gapers as defined in the MSX Disease section) examined above were used. Correlation statistics were calculated between the disease measures and four measures of oyster abundance or mortality obtained from the seed bed condition samples (see Seed Bed Condition sections). Relative mortality values were angular transformed prior to their use in any correlation analyses. Analyses were performed on data from the individual beds that represent the four regions.

MSX disease infections versus oyster abundance and oyster mortality - Results.

From 1958 to 1988 the proportion of oysters infected in the spring or autumn rarely predicted changes in oyster abundance in the seed beds that were sampled (Table 25). Only four of the 80 Pearson correlations examined between MSX infection measures and various measures of oyster abundance or mortality on the representative beds were significant, exactly what would be expected at 5% error rate. More importantly, relatively few of the correlations were >0.50 and many were <0.25. Examination of Spearman correlations provided the same conclusion as the Pearson correlations: neither TP nor SP_i related positively or negatively to oyster abundance or oyster mortality across all years. The few comparisons with high and significant Pearson correlations produced substantially lower magnitude Spearman correlations suggesting that those Pearson correlations were strongly influenced by a few pairings that were large (positively or negatively) in magnitude.

When data were pooled across all beds, both measured of disease were negatively and significantly correlated with oyster abundance, and positively and significantly correlated with relative mortality (Table 25). This was true for spring and autumn disease measurements, but correlations were only ~0.40. Correlations with oyster change and oyster mortality were not significant.

MSX disease versus oyster abundance and oyster mortality - Discussion.

The absence of strong correlations between MSX disease and oyster abundance could be influenced by the fact that the latter combines between-year differences in 1) oyster recruitment from the yearling stage and 2) survival of older oysters. Infections by *H. nelsoni,* the agent of MSX disease, are typically much lower in small oysters, compared to large oysters, probably because small individuals filter much smaller volumes of water and their chances of encountering water-borne infective particles is relatively low (Ford and Tripp, in press). Consequently, the effect of MSX infections on oyster survival could be obscured by the entry of the yearlings into the older oyster population. The oyster change measure (the difference in mean oyster abundance between the preceding and current year) also combines both recruitment from the yearling class and adult survival and likewise does not correlate well with the proportion of infected oysters.

Measures of disease infection correlate better with both absolute and relative measures of oyster mortality than they do with measures of oyster abundance or change. However, no consistent pattern relating them across all beds in all years is apparent. Measures of oyster mortality, in this analysis, do not distinguish between predation and nonpredation mortality. Evidently, other mortality sources contribute enough boxes and gapers to obscure the effect of disease alone. In addition, the utility of boxes as a measure of oyster mortality depends on the rate of decomposition of the hinge ligament of old boxes. This rate almost certainly varies between regions and between years, increasing the amount of variation occurring within the mortality measures used here; however, large variability was found in mortality calculated by the cumulative mortality method, which does not rely on old boxes.

The lack of significant correlations of disease infections with 1) oyster abundance and 2) mortality seems incongruous with the conclusions of the MSX Disease section. Only the Cohansey Bed (Upper Middle region) data had any significant correlations between infections (in spring only) and the relative mortality of adult oysters. The fact that pooling data from all beds produces highly significant relationships with oyster abundance (negative) and relative mortality (positive) suggests that too few observations (n) on each of the beds have been taken to reveal the variable relationship between disease infection and mean oyster abundance. Although it is clear that MSX disease frequently kills oysters, the final outcome of an infection can be modified by ambient temperature and salinity (Douglass, 1972; Ford and Haskin, 1982; Haskin and Ford, 1982; Ford, 1985). In addition, oyster abundance varies in response to several other factors as well, such as yearling survival rates, predation intensity, and variation in environmental conditions other than those that affect MSX disease. The variation in all of these factors is sufficiently great that fairly large sample sizes are required to uncover the underlying relationships. The sample sizes for the individual beds here are not great enough to allow the formation of unambiguous conclusions.

Seed bed harvest versus oyster abundance and oyster mortality - Analysis.

We also used correlation analyses to compare harvest with oyster abundance data because the harvest estimates are subject to measurement error (see). The harvest estimates were compared to the same oyster abundance and mortality measures that were used in correlations with the disease measures (see Seed Bed Condition and MSX Disease Methods sections for formulae). In addition harvest estimates were correlated to mean yearling and mean spat abundances (numbers $20L^{-1}$) as well as several estimates of spat mortality. We did this because it is conceivable that harvest activity could directly affect yearling survivorship and indirectly, via alteration of the seed bed bottom, affect spat recruitment and survival. All relative measures were angular transformed prior to use in any correlation analysis. The correlations are based on oyster abundances occurring in the winter after the respective seed bed harvest occurred.

Seed bed harvest versus oyster abundance and oyster mortality - Results.

As with disease measures, few correlations between seed bed harvest intensity and the various of indices of oyster abundance and mortality were large (> 0.50) and very few were significant (Table 26). For the three lowermost beds (Lower Middle and Lower regions) high and generally significant correlations existed between the abundance of oysters and the magnitude of the harvest. The absence of any large and significant correlations (positive or negative) between harvest intensity and yearling or spat abundances suggests that harvests at the intensities occurring on these seed beds did not affect survivorship of young oysters. Consequently, the positive correlations between the numbers of adult oysters and seed bed harvest size simply reflects that fact that more seed oysters are taken when oysters are more abundant. In addition, even after relatively large harvests, high numbers of oysters remained on the beds.

There is some indication that large harvests account for a large portion of the oyster change variable, at least on Bennies and New Beds (Lower Middle region; Table 26). The absence of any strong relationship between absolute or relative oyster mortality implies that the change in oyster numbers is via removal of oysters alone; there is no indication that survivorship of the remaining oysters is altered in any consistent way by the size of the seed bed harvest.

Between-year patterns of both total spat mortality and non-drill spat mortality were unrelated to harvest activity on all of the beds (Table 26).

Seed bed harvest versus oyster abundance and oyster mortality - Discussion.

Seed bed harvest had few detectable relationships with oyster abundance or mortality. In almost all cases not only are the correlations non-significant, but the magnitude of the r values are small (-0.20 to 0.20). Only the data from Bennies and New Beds display several significant correlations. These two beds contributed the largest volumes of seed during the 1970s (see Seed Bed Harvest section). However, the signs of the correlations from these beds are contrary to predicted directions if harvests were having a negative effect on oyster abundances. The significant (all are probabilities of 0.01 or less) correlations associated with oyster abundance and oyster change are positive, those with relative oyster mortality are negative. Considered together, all of these point to large or increasing oyster abundance when oyster seed bed harvests are high. This paradoxical conclusion arises from two factors. First, seed bed harvest was monitored and limited during the years included in this study (see Seed Bed Harvest section). Seed beds were closed to harvest before the majority of adult oysters were removed. Indeed the decision to close a seed bed was based on a relative endpoint (~40% oyster by volume) that was held constant across years (see above). Second, the best harvests occurred in years when oysters were abundant and when, apparently, disease, predation, and other oyster mortality sources were low. Consequently, these correlations simply indicate that seed bed harvests were larger when oysters were more abundant and that harvests were small or absent when oyster abundances were low. Harvest pressure was not allowed to increase to levels that significantly reduced the resource.

No indirect effects of seed bed harvest occurred either. That is, the correlations provide no evidence that harvest disturbance on the beds increased or decreased spat and yearling survival or altered oyster drill activity on any bed. However, low harvest pressure would also likely have minimal disturbance effects on the beds. The absence of any indirect effects here indicates nothing about the effects of more intense harvest activity on seed beds.

GENERAL MODEL - Analysis.

To provide the best model for the combined data sets we used a multivariate regression analysis (Chatfield and Collins 1980). Adult abundance, yearling abundance in the preceding year, and mean annual Delaware River flow at Trenton, NJ were ln-transformed prior to use to increase the normality of the data. Proportion of oysters infected in the spring and proportion of oysters infected in the autumn were angular transformed prior to use for the same reason. Harvest was not transformed because inspection of probability plots revealed that this variable was most normal without transformation. The dependent variable was adult abundance, all other variables were entered into the model as independent variables. Once the standard coefficients and tolerances were obtained for all of the independent variables a stepwise (upward) regression procedure was used select only those variables that explain significant amounts of variation in adult oyster abundance (Kleinbaum and Kupper 1978). This procedure was conducted on the data for each of the five beds (Arnolds, Cohansey, Bennies, New Beds, and Egg Island) where synoptic data were available for all variables and on the pooled data for all five beds. As has been noted before, these beds represent the four regions previously described (Fig. 7): Upper (Arnolds); Upper Middle (Cohansey); Lower Middle (Bennies and New Beds); and Lower (Egg Island).

General model - Results.

For all five beds combined, the regression including all independent variables is highly significant ($P < 0.001$) and explains two-thirds of the variance of the dependent variable, oyster abundance (Table 27). Inspection of the tolerances for each independent variable reveals that multicollinearity was not a problem; that is, the independent variables act independently within the model. (Note: Tolerances provide no information as to how the independent variables relate to each other in the environment, just how they interact within the framework of the statisticasl model.) The standard coefficients show that yearling abundance in the preceding year was the independent variable with the greatest influence on adult abundance. Annual Delaware River flow and the proportion of spring infections were the next two most important independent variables with flow having a positive effect and spring disease infections having a negative effect on adult abundance. The coefficients of the other independent variables were not significant.

The regression results for the separate beds differ from the overall model as well as from each other (Table 27). The overall regression for New Beds (Lower Middle region) was not significant. The number of observations used in that model was very low (n = 8). The regressions for Bennies (Lower Middle region) and Egg Island (Lower region) beds were significant but the only independent variable that was significant within the model was yearling abundance in the preceding year. The regression results for Arnolds bed was most similar to those of the general model except disease infection was not a significant independent variable. The significant regression for Cohansey bed (Upper Middle region) showed that yearling abundance in the preceding year, annual flow, and the proportion of autumn disease infection were significant independent variables. The standardized coefficients for the Cohansey model indicate that annual flow contributes more to adult abundance changes than yearling abundance in the preceding year does. In addition, the significant effect with autumn disease infections is positive.

General model - Discussion.

The results of the multivariate regressions are consistent with the earlier correlation analyses. The only bed in which the overall regression was non-significant was New Beds. The few observations from this bed have made detecting any relationships among variables difficult. The other beds all have highly significant regressions in which yearling abundance in the preceding year is a large and significant determinant of adult oyster abundance. Disease is significant only in the model for all beds combined and for Cohansey Bed (Upper Middle region) alone as was seen in the correlation results above. Oddly, the significant coefficient relating autumn infections on Cohansey Bed to adult oyster abundance is positive. Given the moderately small number of observations in the model, the occurrence of this result in this data set only, and the inconsistency of this result with the known biological relationship between oysters and MSX, this result should be cautiously regarded as anomalous unless further evidence is produced to support this statistical relationship. Annual flow is significant in all models except New Beds and Egg Island (Lower Middle and Lower regions). One mechanism by which annual flow could positively affect oyster abundances is indirect. Increased river flow will lower salinities over the seed beds and, as discussed above, lead to decreased prevalences and intensities of MSX disease infections. Seed bed harvest is a non-significant component of all the models.

The final model, derived via a stepwise procedure of the regression that pools all five beds, is highly significant, explains almost two-thirds of the variance in adult oyster abundance, and includes only three variables (Table 28):

$$\mathbf{OYS = -3.55 + 0.44(YRL) + 0.74(FLO) - 0.64(MSX)}$$

where OYS = mean adult abundance$_{(\text{year } t)}$, YRL = mean yearling abundance$_{(\text{year } t\text{-}1)}$, FLO = mean annual Delaware River flow$_{(\text{year } t)}$, and MSX = mean proportion of oysters infected with MSX disease in the spring$_{(\text{year } t)}$. Some similarities exist between this model and a multivariate model that Ulanowicz *et al*. (1980) developed for spat production in the central Chesapeake Bay. In their model, seed bed harvests were found to be a function of several factors relating to salinity changes over the seed beds (e.g., droughts and maximum rainfall). Our model also highlights the importance of factors influencing salinity and the abundance of recruits. In contrast, the Ulanowicz *et al.* (1980) model includes harvest as an important variable, a variable that was not important within our system. Indeed the absence of this variable from our model has management implications. Successful seed bed harvests that enabled many boats and oystermen to stay in the fishery for many years (see Seed Bed Harvest section) were possible without adversely affecting the resource. The only factor that decreased oyster abundance that has proved significant within our data sets is MSX disease. In a second model Ulanowicz *et al.* (1980) used their model results of spat production to estimate future oyster harvests, with considerable success. Their ability to do so demonstrates the importance of spat numbers to producing adult oysters in their system, a relationship that is equally important within the Delaware Bay oyster seed beds and our model as well.

Management has few opportunities to control or affect river flow and oyster disease, two factors that are important in our model (although attempts to reduce the flow of freshwater by construction of dams or withdrawals would clearly have a negative effect on oyster abundance in Delaware Bay). However, efforts to increase yearling abundance, by increasing spat abundance, should be productive management activities. Practices that increase settlement substrate (e.g., returning cultch overboard, decreasing silt cover on seed beds prior to set) and decrease predator abundance (e.g., trapping or sweeping), some of which have been used for decades (Perkins 1931), may be management's and the fishery's most effective means of increasing the number of oysters on seed beds. Alternatively, but more costly, would be to produce seed oysters in a hatchery, but use the seed beds as a first-year nursery before moving the yearling to the planted grounds. If nothing else, the current management scheme, including the 40% rule, should be retained as an appropriate mechanism for preserving sets and maintaining adult populations on the beds.

CONCLUSIONS

- Oyster abundance on the natural beds in the upper Delaware Bay is best described by a multivariate regression model that explains almost two-thirds of the variance in adult oyster abundance and includes only three variables. Yearling abundance in the preceding year has the greatest influence. Delaware River flow and spring MSX infections are next in importance, and equal to each other, with flow having a positive effect and disease, a negative effect.

- The harvesting of seed had an insignificant impact on oyster population abundances and there is no evidence that the seed beds have been overharvested during the period of the study (1958-1992).

- The significant, positive correlation of seed oyster abundance with Delaware River flow emphasizes the importance of fresh water in maintaining the proper balance between fresh and salt water over the seed area. Projects that alter the flow of fresh water (e.g., dams or withdrawals) or salt water (e.g., channel dredging) could negatively affect oyster abundance on the beds.

- The development of a management scheme, based on long-term data collection and its timely presentation to the industry, has had profound effects on the maintenance of the resource in spite of significant fluctuations in both biological and physical variables.

- Despite the large quantity of samples collected in our study, there were often insufficient numbers to provide statistically significant relationships except when data were pooled for seed bed regions or for the entire seed bed area. This emphasizes the need for large numbers of replicates through long periods of time to be able to detect change.

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Table 1. Spatial characteristics of the larger oyster seed beds located in the eastern (NJ) half of the the upper estuary of Delaware Bay. All measurements relate to the sampling grid system of each bed used in the random sampling study (see text for details). Area estimates the total amount of bottom within the seed beds respective grid system that produces oysters. The nearest and farthest upbay distances estimate the distances of the grids that are closest to and farthest from the mouth of Delaware Bay. The nearest and farthest offshore distances estimate the distances of the grids that are the closest to and farthest from emergent land. The last column displays abbreviations for the grids that are used in other places in the paper.

Seed bed	Area (hectare)	Nearest upbay distance (Km)	Farthest upbay distance (Km)	Nearest offshore distance (Km)	Farthest offshore distance (Km)	Abbrev.
ROUND ISLAND	162	67.7	70.1	1.0	2.6	RIS
UPPER ARNOLDS	121	66.8	68.2	1.2	2.8	UAR
ARNOLDS	232	64.1	67.0	0.1	2.9	ARN
UPPER MIDDLE	20	60.3	62.1	1.1	2.6	UMD
MIDDLE	374	57.5	60.2	1.2	3.6	MID
COHANSEY	545	54.4	58.5	0.1	3.4	COH
SHIP JOHN	454	54.3	57.6	3.4	5.1	SHJ
SHELL ROCK	404	50.5	53.4	1.4	3.6	SHR
BENNIES SAND	101	49.1	50.8	1.4	3.6	BNS
BENNIES	636	45.4	49.7	1.7	5.4	BEN
NANTUXENT PT.	212	44.7	47.0	0.0	1.8	NPT
HOG SHOAL	111	44.6	45.8	1.3	2.3	HGS
NEW	667	41.0	45.2	2.4	5.0	NWB
STRAWBERRY	162	42.0	44.2	0.9	2.4	STR
HAWK'S NEST	202	41.0	43.0	0.8	2.7	HKN
BEADONS	293	39.5	41.7	0.0	1.8	BDN
VEXTON	162	39.6	41.2	2.0	3.2	VEX
EGG ISLAND	394	36.2	40.1	1.0	4.6	EIS
LEDGE	222	38.5	41.5	6.4	9.0	LDG

Table 2. Bottom temperature and salinity sampling effort by the research vessel *Julius Nelson* on Delaware Bay New Jersey oyster seed beds.

YEAR	RIS	UAR	ARN	UMD	MID	COH	SHJ	SHR	BNS	BEN	NPT	HGS	NWB	HKN	BDN	VEX	EIS	LDG	TOTAL
1953	0	4	4	2	10	45	6	49	1	55	3	11	10	0	7	0	14	8	229
1954	0	9	10	0	8	18	4	26	0	23	2	2	11	0	25	0	13	13	164
1955	0	9	15	3	19	33	17	48	0	39	0	32	21	0	25	0	17	13	291
1956	0	12	3	13	25	29	4	41	0	25	2	14	13	0	14	0	13	11	219
1957	0	3	13	4	12	17	13	17	0	19	0	15	10	0	10	0	10	10	153
1958	0	2	20	11	17	16	13	22	0	19	1	14	12	3	10	0	19	10	189
1959	0	2	27	10	21	24	21	29	0	32	1	13	14	0	21	0	9	12	236
1960	0	0	13	10	12	35	13	18	0	36	0	18	18	0	7	0	12	14	206
1961	0	1	12	1	20	31	13	20	0	37	0	10	11	0	13	0	4	11	184
1962	0	1	15	9	13	21	12	20	0	32	1	13	19	0	8	0	8	9	181
1963	0	2	14	4	10	14	10	13	0	22	1	9	116	8	12	0	3	7	245
1964	0	0	15	4	8	22	7	13	0	20	3	6	46	4	15	0	2	7	172
1965	3	1	16	1	3	23	4	6	0	22	6	8	21	0	14	0	1	3	132
1966	0	0	14	3	10	19	9	10	0	24	14	2	7	4	4	0	2	6	128
1967	4	1	15	2	9	18	4	10	0	16	8	5	11	0	6	0	0	2	111
1968	6	0	13	1	10	20	4	8	1	24	7	5	8	0	6	0	2	2	117
1969	4	0	14	0	8	19	3	15	1	24	9	3	12	2	7	0	0	3	124
1970	8	0	14	1	9	31	6	19	0	14	11	5	22	1	6	0	4	2	153
1971	5	0	9	2	7	38	2	14	0	8	7	4	46	0	2	0	2	1	147
1972	9	1	9	1	13	31	5	27	0	17	10	7	31	0	5	0	4	2	172
1973	4	0	9	0	9	21	5	17	0	12	6	2	20	0	4	0	4	4	117
1974	3	1	12	1	8	19	3	20	0	23	8	4	21	0	5	0	13	6	147
1975	2	0	11	0	10	18	2	20	0	25	5	4	27	2	7	0	8	4	145
1976	1	0	11	0	9	15	5	17	0	22	7	2	21	0	4	1	16	1	132
1977	2	1	12	0	7	16	1	13	0	9	1	1	14	0	0	0	10	6	93
1978	3	0	11	1	8	15	2	18	0	19	5	0	17	0	4	0	10	7	120
1979	1	0	10	1	5	15	2	19	1	22	3	1	19	1	1	1	13	7	122
1980	0	0	8	1	3	13	2	14	0	11	1	1	13	1	3	0	10	2	83
1981	1	0	13	0	1	18	0	12	0	15	3	0	17	0	4	0	10	6	100
1982	1	0	14	0	4	16	3	19	1	19	1	1	10	0	4	2	13	3	111
1983	2	1	16	1	9	17	3	20	0	24	0	1	21	0	3	2	17	14	151
1984	1	0	15	1	6	20	2	19	0	26	4	1	21	1	4	0	27	9	157
1985	0	0	12	0	5	17	1	16	3	28	1	0	17	1	7	6	18	12	144
1986	2	0	12	1	3	15	0	20	3	18	0	1	11	1	4	1	8	4	104
1987	2	1	13	1	3	18	1	17	3	19	1	1	10	2	3	1	11	2	109
1988	3	0	10	0	0	8	1	6	0	15	6	0	3	0	7	1	9	8	77
1989	0	0	3	0	0	3	1	2	1	2	1	0	0	0	2	0	3	0	18
1990	0	0	2	0	1	2	0	1	0	2	0	0	1	0	0	0	1	0	10
TOT	67	52	459	90	335	770	204	695	15	819	139	216	722	31	283	15	340	241	5493

Table 3. Bottom temperature and salinity effort by the research vessel Julius Nelson on Delaware Bay New Jersey oyster seed beds, 1953 – 1990.

YEAR	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	TOTAL
1953	0	0	0	8	12	38	56	16	24	0	38	37	229
1954	0	3	0	12	20	18	46	33	8	7	15	2	164
1955	14	1	5	0	0	27	106	57	30	10	26	15	291
1956	3	6	3	9	40	20	45	42	16	15	13	7	219
1957	4	10	2	0	10	9	47	26	22	8	10	5	153
1958	0	0	11	3	28	16	36	44	29	8	13	1	189
1959	0	6	11	0	6	10	47	64	27	4	3	58	236
1960	11	10	4	5	5	18	47	51	40	1	11	3	206
1961	3	2	4	5	30	10	33	56	14	1	11	15	184
1962	4	0	5	3	18	19	48	46	11	12	11	4	181
1963	0	0	6	7	6	39	59	83	13	9	13	10	245
1964	3	3	1	7	11	14	53	28	16	22	4	10	172
1965	8	0	4	3	11	10	25	23	24	7	6	11	132
1966	0	0	11	2	6	2	46	35	9	9	5	3	128
1967	11	5	3	4	3	6	21	29	13	6	4	6	111
1968	3	8	7	2	3	5	30	35	8	9	3	4	117
1969	0	3	5	6	8	8	36	27	19	8	4	0	124
1970	1	1	7	9	17	8	29	29	20	13	10	9	153
1971	1	3	9	10	18	6	22	28	28	13	4	5	147
1972	8	5	8	11	17	11	29	35	26	9	10	3	172
1973	10	5	4	2	4	6	5	38	17	13	3	10	117
1974	6	5	12	8	8	21	35	25	16	0	3	8	147
1975	8	7	2	12	14	10	21	38	17	1	7	8	145
1976	0	3	8	1	14	16	29	26	12	9	4	10	132
1977	0	2	4	8	12	7	21	25	9	5	0	0	93
1978	0	2	17	1	13	6	19	35	10	9	1	7	120
1979	3	0	19	0	11	7	34	19	10	0	11	8	122
1980	7	0	10	0	12	8	15	20	9	2	0	0	83
1981	0	0	14	8	12	22	15	10	14	0	1	4	100
1982	0	4	14	3	21	5	27	13	11	7	4	2	111
1983	6	3	0	10	15	18	33	34	15	2	7	8	151
1984	4	6	6	15	9	33	30	24	11	9	2	8	157
1985	1	3	11	5	14	5	32	36	12	13	0	12	144
1986	0	5	13	10	17	12	10	15	16	0	0	6	104
1987	9	2	11	4	10	7	34	13	9	4	0	6	109
1988	0	2	4	3	6	9	17	23	8	2	3	0	77
1989	0	2	2	5	2	3	0	0	0	4	0	0	18
1990	0	0	5	3	0	0	0	2	0	0	0	0	10
TOTAL	128	117	262	204	463	489	1238	1183	593	251	260	305	5493

Table 4. Average bottom salinites and temperatures on Delaware Bay New Jersey oyster seed beds as measured the *R/V Julius Nelson*.

	Average Bottom Salinity					Average Bottom Temperature				
YEAR	ALL BEDS	UPPER	UPPER MIDDLE	LOWER MIDDLE	LOWER	ALL BEDS	UPPER	UPPER MIDDLE	LOWER MIDDLE	LOWER
1953	16.6	7.4	14.8	15.7	19.0	19.9	26.6	16.9	18.0	22.1
1954	20.7	12.5	17.5	18.3	21.7	20.4	21.3	18.1	20.5	23.6
1955	17.5	12.8	14.2	17.5	19.7	21.4	23.9	20.5	22.1	22.1
1956	16.8	9.1	11.7	16.3	18.4	18.8	20.6	17.9	19.2	21.9
1957	21.0	15.3	16.8	20.3	22.0	20.2	19.7	18.8	20.5	20.6
1958	18.4	9.2	12.8	17.0	19.5	20.8	18.8	20.1	20.4	20.6
1959	18.6	10.7	14.2	15.2	20.7	20.7	17.4	18.0	16.2	21.8
1960	16.7	9.7	12.1	15.5	19.8	20.2	20.8	19.4	20.3	19.8
1961	18.3	9.7	13.9	17.2	20.7	20.6	18.8	18.1	19.6	19.4
1962	20.0	12.1	15.6	19.2	21.7	20.6	20.1	20.3	19.7	20.2
1963	20.2	13.4	17.0	20.1	23.0	19.6	17.8	19.8	21.8	18.4
1964	19.9	13.5	16.8	19.4	21.8	18.4	20.5	19.4	18.9	17.0
1965	20.3	14.5	18.1	20.2	19.9	18.3	18.5	18.7	18.7	11.0
1966	20.8	13.4	17.6	19.7	23.6	19.8	18.3	20.7	19.5	20.2
1967	18.1	10.1	13.9	17.0	20.8	17.6	15.9	17.3	16.2	15.9
1968	18.3	11.2	14.0	17.5	21.4	19.5	16.3	18.3	19.5	12.4
1969	18.1	10.3	13.9	16.8	19.7	19.9	18.9	21.2	19.6	18.3
1970	17.5	10.0	14.0	16.7	19.0	19.7	19.9	18.0	18.6	14.8
1971	16.9	9.3	12.7	15.5	17.6	19.7	19.1	18.6	18.6	12.0
1972	14.9	9.0	11.8	14.2	15.9	18.8	19.6	17.8	18.5	10.1
1973	17.2	9.9	14.6	16.0	17.1	18.7	20.9	16.2	17.0	17.6
1974	18.5	10.9	14.0	16.5	20.2	19.1	19.2	18.8	17.0	18.7
1975	17.3	9.1	12.1	15.4	16.9	19.1	19.8	18.0	17.5	17.0
1976	17.1	9.5	13.5	17.0	19.3	18.4	16.9	17.9	18.7	17.0
1977	19.6	12.6	15.9	18.4	20.1	20.4	19.9	20.5	19.1	20.5
1978	17.8	9.3	13.0	16.3	19.2	19.8	18.2	17.0	18.3	17.1
1979	17.2	9.2	11.5	14.9	17.4	19.0	19.8	17.0	17.7	16.6
1980	20.3	12.5	15.4	18.4	21.5	19.3	22.7	18.7	18.2	13.7
1981	21.4	13.6	15.6	19.3	21.7	17.9	18.9	19.2	18.7	14.2
1982	19.5	11.6	13.6	17.2	19.5	17.9	21.5	19.6	16.1	14.0
1983	17.7	9.4	12.5	15.8	19.4	19.9	20.2	19.7	18.6	19.4
1984	17.1	10.3	11.1	14.8	17.5	17.6	20.2	18.5	17.5	16.2
1985	20.4	13.7	16.9	19.2	21.7	18.9	21.1	19.6	18.6	20.1
1986	17.8	12.2	14.8	17.6	19.6	17.4	18.7	17.1	15.4	17.9
1987	18.2	12.5	16.2	17.6	18.8	20.0	20.4	18.3	16.2	16.9
1988	18.0	11.6	15.0	17.2	19.3	22.8	20.3	20.5	19.7	21.7
1989	15.4	11.8	14.7	17.3	17.6	14.4	15.7	12.8	13.0	20.6
1990	15.2	9.0	13.0	16.5	16.0	8.2	8.9	8.7	8.0	7.1

Table 5. Results of cluster (K-means) analyses associating seed beds using estimates of bottom salinities collected over a 40 year interval (1953 - 1990). The total number of bottom salinities used, the grand mean bottom salinity, and the minimum and maximum bottom salinities for each region are presented. All salinity values are presented as parts per thousand. The designation of the regions is based on their geographic position in Delaware Bay relative to the mouth of the bay.

	REGION			
	Upper	Upper Middle	Lower Middle	Lower
n	560	2,020	1,832	833
Mean salinity ppt (1 S.E.)	10.8 (0.33)	13.9 (0.38)	17.2 (0.29)	19.9 (0.77)
Mininum salinity ppt	10.3	12.8	16.1	19.1
Maximum salinity ppt	11.4	15.2	18.3	20.6
Beds included	Round IslandUpper ArnoldsArnolds	Upper Middle Middle Cohansey Ship John Shell Rock	Bennies Sand Bennies Nantuxent Point Hog Shoal New Strawberry Hawk's Nest Beadons Vexton	Egg Island Ledge

Table 6. Relationship between measured bottom salinities on Delaware Bay New Jersey oyster seed beds and the flow of the Delaware River at Trenton, NJ. Pearson correlation coefficients were calculated for a) individual salinity measurements with river flow for the day of the sample and b) monthly salinity averages with monthly average flow rates over the same period.

Correlation Between:

Bottom Salinity and Daily Flow Rate	Correlation Coefficient	Sample Size (n)
Upper	-0.64	560
Upper Middle	-0.59	2018
Lower Middle	-0.57	1831
Lower	-0.48	833
Baywide	-0.48	5242

Average Monthly Bottom Salinity and Average Monthly Flow Rate	Correlation Coefficient	Sample Size (n)
Upper	-0.68	277
Upper Middle	-0.66	348
Lower Middle	-0.66	351
Lower	-0.57	300
Baywide	-0.48	1276

Table 7. Seed bed sampling proficiency. The first column lists the number of grids designated for each bed. The next three columns indicate how many of those grids have been sampled in at least one year, in more than five years, and in more than ten years, respectively. The last column shows how many years (out of 40 total) at least one grid from the bed was sampled. The values for the regions represent the sum of the respective parameters for the beds included within each region.

BED	TOTAL # GRIDS	GRIDS SAMPLED	GRIDS SAMPLED >5 TIMES	GRIDS SAMPLED >10 TIMES	# YEARS SAMPLED
Round Island	28	24	7	4	27
Upper Arnolds	18	15	4	2	33
Arnolds	55	43	13	8	40
Upper Region	101	82	24	14	40
Upper Middle	20	7	2	0	18
Middle	45	43	23	10	39
Cohansey	74	71	34	13	40
Ship John	42	42	21	9	40
Shell Rock	54	51	26	15	40
Upper Middle Region	235	214	106	47	40
Bennies Sand	24	15	5	0	18
Bennies	140	117	29	8	39
Nantuxent Point	30	27	8	2	32
Hog Shoal	25	17	9	5	34
New	112	79	22	6	38
Strawberry	19	17	3	0	17
Hawk's Nest	24	22	3	1	27
Beadons	32	30	15	7	38
Vexton	21	19	2	0	16
Lower Middle Region	427	343	97	29	40
Egg Island	125	60	12	3	35
Ledge	53	30	12	1	32
Lower Region	178	90	24	4	37
All beds	941	729	251	94	40

Table 8. Temporal sampling of the seed beds within years. Under each sampling milestone is the Julian day of the nominal year (year in which sampling began) on which the indicated samples were taken. Reference dates: Nov 1 = 305, Jan 1(second year) = 366, Mar 1 (second year) = 426.

YEAR	**First Sample Taken**	**25% of samples done**	**50% of samples done**	**75% of samples done**	**Last sample taken**
1953	321	328	343	355	482
1954	300	316	326	342	389
1955	304	306	326	335	356
1956	297	310	320	355	402
1957	324	325	330	337	485
1958	321	329	413	441	447
1959	336	338	344	350	397
1960	312	316	333	378	491
1961	272	317	319	345	459
1962	307	311	316	323	463
1963	309	315	322	339	491
1964	307	310	345	379	498
1965	319	323	351	445	470
1966	318	335	375	396	476
1967	314	342	352	402	440
1968	326	353	403	453	491
1969	303	421	461	468	535
1970	313	343	352	436	482
1971	321	371	396	445	481
1972	333	369	398	423	434
1973	296	317	338	387	430
1974	311	347	372	393	429
1975	296	322	329	422	454
1976	314	341	434	478	503
1977	425	438	448	497	552
1978	333	363	433	495	570
1979	319	339	382	477	507
1980	436	448	451	472	494
1981	327	425	454	489	498
1982	322	379	477	484	503
1983	350	420	452	467	496
1984	333	425	447	492	501
1985	350	420	442	491	498
1986	350	370	386	429	464
1987	414	436	454	467	513
1988	313	323	453	480	504
1989	296	296	297	298	299
1990	288	288	289	289	290
1991	287	287	288	289	291
1992	293	295	296	297	297

Table 9. Linear regressions (Model II) of ln-transformed yearling abundances from year$_{(t)}$ onto ln-transformed spat abundances from year$_{(t-1)}$. Significance values (n s = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$ and *** = $P < 0.001$) are presented for the entire regression (REG.), intercept (a_V), and slope (v).

		REGRESSION COEFFICIENTS			SIGNIFICANCES		
AREA	**n**	**a_V**	**v**	**r^2**	**REG.**	**a_V**	**v**
BAY	39	1.03	0.84	0.733	* * *	* *	* * *
UPPER	39	1.00	0.68	0.785	* * *	* * *	* * *
UPPER MIDDLE	39	-0.04	0.86	0.661	* * *	n s	* * *
LOWER MIDDLE	39	-0.81	0.95	0.778	* * *	* *	* * *
LOWER	35	-0.53	0.80	0.740	* * *	*	* * *
ROUND ISLAND	24	1.08	0.63	0.71	* * *	* *	* * *
UPPER ARNOLDS	28	0.72	0.77	0.60	* * *	n s	* * *
ARNOLDS	39	0.93	0.71	0.73	* * *	* *	* * *
UPPER MIDDLE	6	-1.33	1.31	0.71	*	n s	*
MIDDLE	37	0.04	0.83	0.53	* * *	n s	* * *
COHANSEY	39	0.24	0.82	0.65	* * *	n s	* * *
SHIP JOHN	39	-0.49	0.96	0.56	* * *	n s	* * *
SHELL ROCK	39	-0.80	1.00	0.68	* * *	n s	* * *
BENNIES SAND	16	-1.57	1.15	0.35	*	n s	*
BENNIES	37	-0.63	0.92	0.70	* * *	n s	* * *
NANTUXENT PT.	27	-0.18	0.84	0.57	* * *	n s	* * *
HOG SHOAL	28	-0.87	1.04	0.72	* * *	*	* * *
NEW	35	-0.66	0.89	0.72	* * *	*	* * *
STRAWBERRY	11	-2.64	1.43	0.67	* *	*	* *
HAWK'S NEST	20	-2.35	1.19	0.15	n s	*	n s
BEADONS	35	-1.21	0.90	0.57	* * *	* *	* * *
VEXTON	13	-1.75	1.24	0.71	* * *	n s	* * *
EGG ISLAND	32	-0.68	0.84	0.76	* * *	*	* * *
LEDGE	25	-0.37	0.74	0.72	* * *	n s	* * *

Table 10. Linear regressions (Model II) of ln-transformed oyster abundances from year$_{(t)}$ onto ln-transformed yearling abundances from year$_{(t-1)}$. Significance values (n s = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$ and *** = $P < 0.001$) are presented for the entire regression (REG.), intercept (a_V) and slope (v).

		REGRESSION COEFFICIENTS			SIGNIFICANCES		
AREA	n	a_V	v	r^2	REG.	a_V	v
BAY	39	2.41	0.58	0.305	* * *	* * *	* * *
UPPER	39	3.12	0.56	0.253		* * *	* * *
UPPER MIDDLE	39	2.54	0.62	0.272	* * *	* * *	* * *
LOWER MIDDLE	39	2.39	0.60	0.499	* * *	* * *	* * *
LOWER	35	1.57	0.89	0.632	* * *	* * *	* * *
ROUND ISLAND	24	4.25	0.41	0.24	*	* * *	*
UPPER ARNOLDS	28	3.43	0.50	0.24	* *	* * *	* *
ARNOLDS	39	3.14	0.57	0.20	* *	* * *	* *
UPPER MIDDLE	6	3.34	0.52	0.16	n s	* * *	n s
MIDDLE	37	2.71	0.59	0.14	*	* * *	*
COHANSEY	39	2.49	0.62	0.24	* *	* * *	* *
SHIP JOHN	39	2.74	0.58	0.18	* *	* * *	* *
SHELL ROCK	39	2.55	0.62	0.61	* * *	* * *	* * *
BENNIES SAND	16	2.48	0.67	0.15	n s	* * *	n s
BENNIES	37	2.49	0.60	0.58	* * *	* * *	* * *
NANTUXENT PT.	27	3.06	0.53	0.32	* *	* * *	* *
HOG SHOAL	28	1.74	0.92	0.62	* * *	* * *	* * *
NEW	35	2.21	0.72	0.63	* * *	* * *	* * *
STRAWBERRY	11	3.98	0.32	0.29	n s	* * *	n s
HAWK'S NEST	20	3.16	0.55	0.55	* * *	* * *	* * *
BEADONS	35	2.49	0.54	0.40	* * *	* * *	* * *
VEXTON	13	3.62	0.38	0.47	* *	* * *	* *
EGG ISLAND	32	1.33	0.97	0.67	* * *	* * *	* * *
LEDGE	25	1.95	0.88	0.40	* * *	* * *	* * *

Table 11. Tests for non-randomness in runs above and below the median for several variables from seed bed condition samples. The probabilities are derived from Wald-Wolfowitz runs tests. Each significant probability (in **boldface**) indicates that the temporal sequence of annual means had too few runs above and below the median value to be a likely result of random changes. This indicates that non-random sequences occur in the respective variable for extended intervals of time.

	REGIONS				
VARIABLES	ALL BEDS	UPPER BEDS	UPPER MIDDLE BEDS	LOWER MIDDLE BEDS	LOWER BEDS
# oysters * $20L^{-1}$	**<0.001**	0.004	**<0.001**	**<0.001**	**<0.001**
# yearlings * $20L^{-1}$	0.200	0.200	0.200	0.055	**<0.001**
# spat * $20L^{-1}$	0.200	1.000	0.522	0.055	**<0.001**
Prop. dead oysters	**0.025**	0.760	**0.001**	**0.004**	0.310
Prop. dead spat	**<0.001**	1.000	**<0.001**	**<0.001**	0.310
Prop. drilled dead spat	**0.004**	0.702	**0.004**	**0.010**	0.176

Table 12. Collection frequency on Delaware Bay New Jersey oyster seed beds during mortality sampling program, 1958-1993. (See Table 1 for key to seed bed abbreviations.)

Year	ARN	BDN	BEN	BSD	COH	EIS	HKN	LDG	MID	NWB	SHR	SHJ	Total
1958	2	---	1	---	1	---	---		1	---	1	1	7
1959	5	---	2	---	6	---	---		---	---	5	---	18
1960	9	10	23	---	9	---	---		1	2	1	---	55
1961	9	10	18	---	9	---	---		---	---	2	---	48
1962	9	10	13	---	10	---	---		---	4	---	---	46
1963	9	9	9	---	9	---	---		---	11	---	---	47
1964	10	11	11	---	10	---	---		---	11	---	---	53
1965	11	10	10	---	11	---	---		---	6	---	---	48
1966	8	3	8	---	14	---	---		1	---	---	1	35
1967	10	---	10	---	20	---	---		---	---	---	---	40
1968	10	---	10	---	14	---	---		---	---	---	---	34
1969	9	---	9	---	9	---	---		---	---	---	---	27
1970	8	---	4	---	8	---	---		---	5	---	---	25
1971	6	---	---	---	6	---	---		---	6	---	---	18
1972	4	---	---	---	4	---	---		---	4	---	---	12
1973	6	---	3	---	6	2	---		---	6	---	---	23
1974	4	---	14	---	5	4	---		---	5	---	---	32
1975	6	---	10	---	5	5	---		---	5	---	---	31
1976	5	---	7	---	5	5	---		---	2	---	---	24
1977	4	---	4	---	4	4	---		---	---	---	---	16
1978	6	---	6	---	6	6	---		---	---	---	---	24
1979	5	---	6	---	6	6	---		---	---	---	---	23
1980	4	---	5	---	4	6	---		---	---	---	---	19
1981	5	---	10	---	5	14	---	2	---	1	---	---	37
1982	4	---	7	---	4	8	---		---	---	---	---	23
1983	6	---	9	---	6	9	---	5	---	4	---	---	39
1984	3	---	9	---	3	9	---	4	---	7	---	---	35
1985	5	1	7	---	5	6	---		---	10	2	---	36
1986	6	---	6	---	6	5	---		---	3	6	---	32
1987	4	---	4	---	4	5	---		---	---	2	---	19
1988	1	---	2	---	2	2	---		---	---	---	---	7
1989	2	---	2	---	2	2	---		---	---	---	---	8
1990	1	---	1	---	1	1	---		---	---	---	---	4
1991	1	---	---	1	2	1	1		1	1	2	---	10
1992	---	---	---	---	---	---	---		1	6	---	---	7
1993	1	---	1	---	1	---	---		---	2	1	---	6
Total	198	64	197	1	222	100	1	11	5	101	22	2	968

Table 13. Mean Recent Mortality Intervals (MIR), by month, calculated from Delaware Bay New Jersey mortality samples where corroborative or experiential information was available.

MONTH	RECENT MORTALITY INTERVAL (MIR) (weeks)	
	Range	Mean
January	5 - 15	8.8
February	5-20	10.3
March	4 - 20	10.8
April	4 - 26	10.1
May	2-20	6.7
June	2 - 10	4.2
July	3 - 6	4.0
August	2.5 - 5.5	3.9
September	3.5 - 8	4.6
October	4 - 10	4.9
November	4 - 10	5.7
December	4 - 15	6.8

Table 14. Relative Oyster Mortality-Recent (ROM$_R$) calculated from dredge samples taken on the same date from several locations on individual Delaware Bay New Jersey oyster seed beds and showing spatial variability within a bed.

SEED BED	GRID	DATE	RECENT MORTALITY	
			Explained	Unexplained
Egg Island Bed	64	05-May-81	0.0%	8.70%
Egg Island Bed	99	"	0.0%	48.8%
Egg Island Bed	100-101	18-May-81	1.1%	16.8%
Egg Island Bed	42	"	0.0%	6.4%
Egg Island Bed	61	"	0.0%	9.3%
Egg Island Bed	80 + West	"	0.0%	13.6%
Egg Island Bed	81	"	0.0%	44.3%
Egg Island Bed	82 to 65	"	0.0%	45.4%
Bennies Bed	1	27-May-81	0.0%	44.9%
Bennies Bed	2	"	0.0%	23.6%
Bennies Bed	4	"	0.0%	9.0%
Bennies Bed	Sanctuary	"	0.0%	20.1%

Table 15. Numbers of gaping oysters examined for presence and intensity of *Haplosporidium nelsoni* (MSX) during the study period. AUT = summer and autumn collections; SPR = winter and spring collections. Sampling was not conducted on Egg Island Bed until 1973.

	Arnolds		Cohansey		Ben-NewBed		Egg Island		Total	
Year	AUT	SPR	AUT	SPR	AUT	SPR	AUT	SPR	AUT	SPR
1958	0	0	0	0	0	0			0	0
1959	1	27	0	16	0	0			1	43
1960	2	20	1	8	0	12			3	40
1961	1	14	0	6	0	4			1	24
1962	0	22	0	19	0	1			0	42
1963	0	25	2	11	0	0			2	36
1964	0	6	0	0	0	0			0	6
1965	5	34	1	16	0	9			6	59
1966	0	17	1	12	0	4			1	33
1967	0	18	0	3	0	8			0	29
1968	0	5	1	10	0	4			1	19
1969	1	4	0	2	1	2			2	8
1970	0	8	0	8	0	14			0	30
1971	0	2	0	3	0	2			0	7
1972	0	6	2	2	0	4			2	12
1973	0	2	0	1	0	2			0	5
1974	0	9	1	4	0	3	1	3	2	19
1975	1	7	1	4	0	0	0	2	2	13
1976	1	8	1	4	1	4	1	1	4	17
1977	0	13	0	8	0	11	12	1	12	33
1978	1	4	0	6	0	7	0	3	1	20
1979	3	14	1	8	0	3	0	1	4	26
1980	0	5	0	11	1	7	1	5	2	28
1981	0	12	0	11	0	8	0	5	0	36
1982	1	0	0	1	0	1	1	3	2	5
1983	3	5	4	0	0	8	1	6	8	19
1984	1	0	3	4	5	8	6	10	15	22
1985	9	10	2	0	3	0	2	2	16	12
1986	3	0	1	0	1	0	0	2	5	2
1987	0	0	0	0	0	0	0	0	0	0
1988	1	0	1	0	1	0	0	2	3	2
1989	0	0	0	0	0	1	0	0	0	1
1990	0	0	1	1	0	0	0	0	1	1
1991	0	0	0	0	0	0	0	0	0	0
1992	0	0	0	0	0	0	0	0	0	0
Total	34	297	24	179	13	127	25	46	96	649
Grand Total										**745**

Table 16. Sampling frequency of the Delaware Bay New Jersey oyster seed beds for MSX disease prevalence and intensity. See text for details of sampling and laboratory procedures. None = seasons when no samples were taken. Spg = spring samples taken, aut = autumn samples taken.

YEAR	ARNOLDS		COHANSEY		BENNIES		NEW		EGG ISLAND	
1958	none	none	none	none	none	none	none	none	none	none
1959	none	aut	none	aut	none	aut	none	none	none	none
1960	spg	aut	spg	aut	none	aut	none	none	none	none
1961	spg	aut	spg	aut	spg	aut	none	none	none	none
1962	spg	aut	spg	aut	spg	aut	none	aut	none	none
1963	spg	aut	spg	aut	spg	aut	spg	aut	none	none
1964	spg	aut	spg	aut	spg	aut	spg	aut	none	none
1965	spg	aut	spg	aut	spg	aut	spg	none	none	none
1966	spg	aut	spg	aut	spg	aut	none	none	none	none
1967	spg	aut	spg	aut	spg	aut	none	none	none	none
1968	spg	aut	spg	aut	spg	aut	none	none	none	none
1969	spg	aut	spg	aut	spg	aut	none	none	none	none
1970	spg	aut	spg	aut	spg	aut	none	aut	spg	none
1971	spg	aut	spg	aut	spg	none	spg	aut	spg	none
1972	spg	aut	spg	aut	none	none	spg	aut	spg	none
1973	spg	aut	spg	aut	spg	aut	spg	aut	spg	aut
1974	spg	aut	spg	aut	spg	aut	spg	aut	spg	aut
1975	spg	aut	spg	aut	spg	aut	spg	aut	spg	aut
1976	spg	aut	spg	aut	spg	aut	spg	none	spg	aut
1977	spg	aut	spg	aut	spg	aut	none	none	spg	aut
1978	spg	aut	spg	aut	spg	aut	none	none	spg	aut
1979	spg	aut	spg	aut	spg	aut	none	none	spg	aut
1980	spg	aut	none	aut	spg	aut	none	none	spg	aut
1981	spg	aut	spg	aut	spg	aut	none	none	spg	aut
1982	spg	aut	spg	aut	spg	aut	none	none	spg	aut
1983	spg	aut	spg	none	spg	aut	spg	aut	spg	aut
1984	none	aut	none	aut	spg	aut	spg	none	spg	aut
1985	spg	aut	spg	aut	spg	aut	none	none	spg	aut
1986	spg	aut	spg	aut	spg	aut	spg	none	spg	aut
1987	spg	none	spg	none	spg	none	none	none	spg	none
1988	none	aut	none	aut	none	aut	none	none	none	aut
1989	spg	aut	spg	aut	spg	aut	none	none	spg	aut
1990	spg	aut	spg	aut	spg	aut	none	none	spg	aut
1991	spg	aut	spg	aut	spg	aut	none	none	spg	aut
1992	none	aut	none	aut	none	aut	none	none	none	aut

Table 17. Percent Total and Systemic prevalence (TP and SPi) of *Haplosporidium nelsoni* (MSX) infections on New Jersey planted grounds in lower Delaware Bay, 1958-1990. SWL - Southwest Line; DPW = Deepwater; Various = various grounds (Fig. 1).

MSX		**SWL**		**DPW**		**VARIOUS**	
YEAR	**SEASON**	**TP**	**SPi**	**TP**	**SPi**	**TP**	**SPi**
1958	AUTUMN			50	50		
"	SPRING			20	50		
1959	AUTUMN	30	100	50	60		
"	SPRING	10	100	40	25		
1960	AUTUMN	50	20	10	100		
"	SPRING			10	100		
1961	AUTUMN	10	100	10	100		
"	SPRING			25	0		
1962	AUTUMN	0		25	60		
"	SPRING	0		5	100		
1963	AUTUMN	25	100	65	92		
"	SPRING			20	50		
1964	AUTUMN	20	75	75	67		
"	SPRING			65	69		
1965	AUTUMN			55	18		
"	SPRING			75	80		
1966	AUTUMN	40	75	75	67		
"	SPRING	40	88	65	85		
1967	AUTUMN	30	67	80	81		
"	SPRING	40	25	85	76		
1968	AUTUMN	55	55	65	62		
"	SPRING	38	83	55	55		
1969	AUTUMN	35	71	25	60		
"	SPRING	20	25	40	25		
1970	AUTUMN	40	50	65	54		
"	SPRING	15	67	35	29		
1971	AUTUMN	5	0	53	75		
"	SPRING	0		50	67		
1972	AUTUMN	70	0	95	68		
"	SPRING	75	0	80	75		
1973	AUTUMN	25	40	60	58		
"	SPRING	40	63	25	20		
1974	AUTUMN	55	64	65	62		
"	SPRING	60	75	65	54		
1975	AUTUMN	75	40	70	50		
"	SPRING	65	62	65	85		
1976	AUTUMN	55	45				
"	SPRING	45	44				
1977	AUTUMN	55	36				
"	SPRING	20	0				
1978	AUTUMN	5	100	35	86		
"	SPRING	5	100	45	89		
1979	AUTUMN	90	56	85	65		
"	SPRING	90	61	100	85		
1980	AUTUMN	85	65	60	67		
"	SPRING	10	0				
1981	AUTUMN	80	56	70	79		
"	SPRING	70	29	70	71		
1982	AUTUMN	90	67	95	63		
"	SPRING	65	69	60	58		
1983	AUTUMN	55	73	90	44		
"	SPRING	35	29				
1984	AUTUMN	85	53				
"	SPRING	90	94				
1985	AUTUMN	60	33				
"	SPRING						
1986	AUTUMN						
"	SPRING					56	29
1987	AUTUMN					65	54
"	SPRING					60	67
1988	AUTUMN					35	14
"	SPRING					30	17
1989	AUTUMN					50	80
"	SPRING					30	100
1990	AUTUMN					25	20
"	SPRING					55	36
1991	AUTUMN					30	17
"	SPRING					45	67
1992	AUTUMN					20	0

Table 18. Pearson correlations of MSX prevalences between seasons within years, between seasons between years, and between total prevalence and systemic prevalence within seasons. Proportion infected (prevalence) is the number of live oysters showing any degree of MSX infection divided by the total number of live oysters examined. Proportion systemic is the number of live oysters showing systemic infections divided by the number of live oysters showing any level of MSX infection. No between seasonal correlations are available for New Beds systemic infections because all eight spring infections were 0%. All probabilities are Bonferroni-adjusted to control for multiple comparisons. All proportions were angular transformed prior to calculating correlations.

Bed	n	Pearson r	Probability	n	Pearson r	Probability
	Prop. infected in the spring vs. prop. infected in the autumn			Prop. systemic in the spring vs. prop. systemic in the autumn		
Arnolds	26	0.12	1.000	26	-0.01	1.000
Cohansey	24	0.26	1.000	24	0.29	1.000
Bennies	20	0.42	0.389	20	0.25	1.000
New	8	-0.38	1.000	8	---	---
Egg Island	13	0.48	0.599	13	0.42	0.915
	Prop. infected in the spring vs. prop. systemic in the spring			Prop. infected in the autumn vs. prop. systemic in the autumn		
Arnolds	27	0.98	<0.001	29	0.90	<0.001
Cohansey	27	0.81	<0.001	27	0.73	<0.001
Bennies	24	0.80	<0.001	23	0.91	<0.001
New	12	0.52	0.520	10	0.86	0.009
Egg Island	15	0.87	<0.001	15	0.74	0.009
	Prop. infected in the autumn vs. prop. infected in the spring$_{(t+1)}$			Prop. infected in the autumn vs. prop. systemic in the spring$_{(t+1)}$		
Arnolds	27	0.40	0.223	27	0.32	0.635
Cohansey	26	0.11	1.000	26	0.21	1.000
Bennies	21	0.52	0.101	21	0.38	0.541
New	10	0.50	0.852	10	0.20	1.000
Egg Island	14	0.65	0.070	14	0.44	0.705
	Prop. systemic in the autumn vs. prop. infected in the spring$_{(t+1)}$			Prop. systemic in the autumn vs. prop. systemic in the spring$_{(t+1)}$		
Arnolds	27	0.53	0.028	27	0.46	0.088
Cohansey	26	0.29	0.921	26	0.41	0.220
Bennies	21	0.54	0.068	21	0.45	0.251
New	10	0.22	1.000	10	0.31	1.000
Egg Island	14	0.65	0.068	14	0.61	0.129

Table 19. Total annual oyster seed harvest, in thousands of liters, from Delaware Bay New Jersey oyster seed beds, 1958-1991. Solid black indicates closed beds. Grey shading indicates partial bed closings. Harvests from Strawberry beds were included with New Beds.

Year	RIS	UAR	ARN	UMD	MID	COH	SHJ	SHR	BNS	BEN	NPT	HGS	NWB	HKN	BDN	VEX	EIS	LDG	TOTAL
1958	0	0	1337	66	3055	3669	2033	2613	10	0	0	0	0	0	0	0	0	0	12783
1959																			
1960																			
1961	0	0	6	141	1076	3324	703	1217	0	0	0	0	0	0	0	0	0	0	6468
1962	20	0	376	184	1281	2796	1138	916	36	54	69	13	63	0	0	0	0	0	6947
1963																			
1964	0	0	690	138	1841	2565	697	0	0	0	0	0	0	0	0	0	0	0	5931
1965																			
1966	816	0	1153	257	1080	1790	167	287	0	9	677	137	16	0	137	0	0	0	6526
1967	647	544	2336	28	698	296	376	24	0	11	63	9	1	0	0	0	0	0	5033
1968	37	0	69	130	1031	3507	293	16	0	0	53	0	21	0	0	0	0	0	5156
1969	2	127	318	159	788	1538	44	71	0	14	83	3	4	0	0	0	0	0	3151
1970	1023	115	427	115	603	1978	124	235	0	25	0	32	0	0	0	0	0	0	4676
1971	0	0	44	91	128	1180	373	40	1	4	550	2155	2167	0	10	0	11	0	6753
1972	0	0	0	53	372	1207	282	3217	0	0	16	596	716	31	0	0	0	193	6683
1973	0	0	0	18	24	2009	540	2193	0	10	132	1526	2787	0	0	0	0	0	9239
1974	0	0	0	56	1195	1306	1220	2902	0	2067	138	928	4848	106	0	0	1188	28	15983
1975	0	0	0	14	305	1354	619	1286	0	5515	16	235	5331	36	0	0	296	71	15078
1976	0	0	0	0	374	733	0	912	0	4050	10	455	3940	195	5	1174	1532	245	13626
1977	0	0	0	0	0	523	65	948	0	2678	14	329	4933	286	2	503	927	916	12125
1978	0	0	0	0	0	0	21	3681	931	3501	0	65	6645	102	0	503	86	5	15541
1979	0	0	0	0	149	1515	968	5124	1020	3627	0	1069	4252	72	0	546	0	12	18353
1980	0	0	37	0	260	416	633	1463	788	7238	323	2602	1961	0	0	0	0	1678	17397
1981	0	0	0	63	311	2509	578	720	521	1632	0	187	8355	68	0	673	2536	176	18330
1982	46	0	546	28	1052	3065	1369	1858	489	2059	0	274	2111	26	6	49	271	3	13252
1983	35	0	301	132	738	1670	693	1422	734	2446	9	72	4332	7	0	15	398	50	13054
1984	0	0	144	99	757	1888	1339	703	587	2123	24	99	4009	38	14	349	1034	47	13255
1985	24	0	0	0	12	0	128	3457	1365	3034	30	201	4054	10	0	128	176	54	12675
1986	416	0	395	6	12	9	0	961	102	426	0	40	528	0	0	28	4	2	2928
1987																			
1988																			
1989																			
1990	0	0	0	0	22	251	123	4209	1710	63	0	0	0	0	0	0	0	0	6378
1991	0	0	70	76	450	2636	1727	2309	1042	355	268	241	1423	144	28	82	485	0	11338
TOTAL	3066	787	8249	1855	17617	43735	16251	42784	9335	40941	2476	11270	62496	1121	203	4051	8945	3479	278659

Table 20. Summary of Delaware Bay New Jersey oyster seed bed season, oyster boats, and total harvests, 1958-1991.

YEAR	SEASON LENGTH (days)	BOAT DAYS	BOATS WORKING	BOATS REGISTERED	POTENTIAL HARVEST (L x 10^6)	ACTUAL HARVEST (L x 10^6)	ACTUAL/ POTENTIAL HARVEST
1958	15	885	128	152	24	14	0.59
1959	0	0	0	29	0	0	-----
1960	0	0	0	21	0	0	-----
1961	10	633	68	78	12	7	0.56
1962	10	1132	124	127	15	7	0.46
1963	0	0	0	44	0	0	-----
1964	10	957	104	144	13	6	0.45
1965	0	0	0	27	0	0	-----
1966	10	632	72	118	12	7	0.60
1967	10	560	64	81	10	6	0.58
1968	15	532	42	66	15	6	0.39
1969	10	517	53	59	6	3	0.55
1970	15	647	47	52	12	5	0.42
1971	15	564	40	43	11	7	0.66
1972	15	549	38	44	11	7	0.62
1973	18	710	47	53	15	9	0.62
1974	20	836	47	56	24	16	0.67
1975	20	737	43	55	20	15	0.75
1976	20	647	41	50	20	14	0.67
1977	20	776	43	54	19	12	0.63
1978	20	1043	57	65	22	16	0.70
1979	20	1282	73	79	29	19	0.65
1980	20	1213	67	81	28	18	0.64
1981	20	1247	68	106	30	19	0.63
1982	20	853	50	82	22	13	0.60
1983	20	845	48	98	20	13	0.66
1984	20	878	52	97	22	13	0.61
1985	20	953	57	97	21	13	0.61
1986	10	329	43	94	5	3	0.64
1987	0	0	0	91	0	0	-----
1988	0	0	0	96	0	0	-----
1989	0	0	0	96	0	0	-----
1990	10	308	35	94	9	6	0.74
1991	15	776	59	95	17	12	0.70

Table 21. Summary of harvest activity on Delaware River New Jersey Upper region seedbeds from 1958-1991.

YEAR	BOATS WORKING	BOAT DAYS	ACTUAL HARVEST (L x 10^3)	POTENTIAL HARVEST (L x 10^3)	ACTUAL/ POTENTIAL HARVEST
1958	21	40.0	1324.8	1788.8	0.74
1959	0	0.0	0.0	0.0	------
1960	0	0.0	0.0	0.0	------
1961	2	1.0	6.1	14.2	0.43
1962	27	51.5	396.3	840.5	0.47
1963	0	0.0	0.0	0.0	------
1964	32	73.0	659.3	1234.2	0.53
1965	0	0.0	0.0	0.0	------
1966	25	86.0	1968.9	2447.5	0.80
1967	43	271.5	3527.2	5839.4	0.60
1968	10	7.5	105.9	394.8	0.27
1969	27	30.3	446.9	535.4	0.83
1970	23	77.0	1564.9	2018.7	0.78
1971	2	3.0	43.8	69.2	0.63
1972	0	0.0	0.0	0.0	------
1973	0	0.0	0.0	0.0	------
1974	0	0.0	0.0	0.0	------
1975	0	0.0	0.0	0.0	------
1976	0	0.0	0.0	0.0	------
1977	0	0.0	0.0	0.0	------
1978	0	0.0	0.0	0.0	------
1979	0	0.0	0.0	0.0	------
1980	1	1.0	36.6	36.6	1.00
1981	0	0.0	0.0	0.0	------
1982	8	16.5	592.2	670.5	0.88
1983	6	15.0	335.8	376.5	0.89
1984	4	10.0	144.5	189.3	0.76
1985	1	1.0	24.4	24.4	1.00
1986	6	28.0	810.9	991.0	0.82
1987	0	0.0	0.0	0.0	------
1988	0	0.0	0.0	0.0	------
1989	0	0.0	0.0	0.0	------
1990	0	0.0	0.0	0.0	------
1991	3	3.0	70.2	90.6	0.78

Table 22. Summary of oyster harvest activity on Delaware Bay New Jersey Lower region seed beds, 1958-1991.

YEAR	BOATS WORKING	BOAT DAYS	ACTUAL HARVEST (L x 10^3)	POTENTIAL HARVEST (L x 10^3)	ACTUAL/ POTENTIAL HARVEST
1958	0	0.0	0.0	0.0	------
1959	0	0.0	0.0	0.0	------
1960	0	0.0	0.0	0.0	------
1961	0	0.0	0.0	0.0	------
1962	0	0.0	0.0	0.0	------
1963	0	0.0	0.0	0.0	------
1964	0	0.0	0.0	0.0	------
1965	0	0.0	0.0	0.0	------
1966	0	0.0	0.0	0.0	------
1967	0	0.0	0.0	0.0	------
1968	0	0.0	0.0	0.0	------
1969	0	0.0	0.0	0.0	------
1970	0	0.0	0.0	0.0	------
1971	1	1.5	11.2	52.9	0.21
1972	8	14.5	192.8	370.4	0.52
1973	0	0.0	0.0	0.0	------
1974	28	97.0	1216.8	2578.8	0.47
1975	10	21.0	367.3	583.0	0.63
1976	26	100.5	1777.6	3224.5	0.55
1977	30	154.0	1842.5	3180.7	0.58
1978	10	14.0	91.4	230.0	0.40
1979	2	1.0	11.7	34.6	0.34
1980	34	109.0	1677.6	2673.0	0.63
1981	54	230.8	2712.0	5412.1	0.50
1982	18	44.5	274.1	912.7	0.30
1983	21	71.0	447.7	1019.5	0.44
1984	28	112.7	1081.5	2272.1	0.48
1985	18	28.0	229.5	536.2	0.43
1986	4	3.0	5.7	25.4	0.22
1987	0	0.0	0.0	0.0	------
1988	0	0.0	0.0	0.0	------
1989	0	0.0	0.0	0.0	------
1990	0	0.0	0.0	0.0	------
1991	25	39.0	485.3	838.4	0.58

Table 23. Summary of oyster harvest activity on Delaware Bay New Jersey Upper Middle region seed beds, 1958-1991.

YEAR	BOATS WORKING	BOAT DAYS	ACTUAL HARVEST (L x 10^3)	POTENTIAL HARVEST (L x 10^3)	ACTUAL/ POTENTIAL HARVEST
1958	118	734.0	11435.7	19430.2	0.59
1959	0	0.0	0.0	0.0	------
1960	0	0.0	0.0	0.0	------
1961	68	556.0	6462.1	11311.1	0.57
1962	122	943.0	6283.6	14267.8	0.44
1963	0	0.0	0.0	0.0	------
1964	104	813.5	5241.7	12442.0	0.42
1965	0	0.0	0.0	0.0	------
1966	63	351.0	3433.3	6729.5	0.51
1967	47	157.0	1236.4	2559.0	0.48
1968	39	395.5	4977.0	12716.9	0.39
1969	48	389.4	2600.2	5202.9	0.50
1970	42	417.7	2897.6	9001.0	0.32
1971	33	138.0	1761.1	2959.9	0.59
1972	35	337.0	5131.2	7537.6	0.68
1973	39	276.5	4703.1	6819.3	0.69
1974	33	263.0	6678.9	8860.4	0.75
1975	22	138.0	3578.5	4619.5	0.77
1976	19	82.5	1988.7	2893.8	0.69
1977	18	60.5	1535.9	2046.2	0.75
1978	32	210.0	3702.5	4920.6	0.75
1979	71	449.0	7755.7	11125.3	0.70
1980	35	132.0	2772.2	3895.0	0.71
1981	41	171.5	4181.9	5341.9	0.78
1982	44	360.0	7165.2	10549.4	0.68
1983	39	205.0	4634.5	6303.4	0.74
1984	44	222.0	4514.4	6474.4	0.70
1985	40	187.0	3597.9	5161.8	0.70
1986	30	109.0	988.1	1475.4	0.67
1987	0	0.0	0.0	0.0	------
1988	0	0.0	0.0	0.0	------
1989	0	0.0	0.0	0.0	------
1990	34	188.5	4604.9	6338.0	0.73
1991	53	376.2	7198.0	10129.2	0.71

Table 24. Summary of oyster harvest activity on Delaware Bay New Jersey Lower Middle region seed beds, 1958-1991.

YEAR	BOATS WORKING	BOAT DAYS	ACTUAL HARVEST (L x 10^3)	POTENTIAL HARVEST (L x 10^3)	ACTUAL/ POTENTIAL HARVEST
1958	1	1.0	10.2	12.2	0.83
1959	0	0.0	0.0	0.0	------
1960	0	0.0	0.0	0.0	------
1961	0	0.0	0.0	0.0	------
1962	29	37.0	132.9	492.3	0.27
1963	0	0.0	0.0	0.0	------
1964	0	0.0	0.0	0.0	------
1965	0	0.0	0.0	0.0	------
1966	22	40.0	293.0	769.2	0.38
1967	5	6.5	17.3	37.6	0.46
1968	11	39.0	64.5	244.8	0.26
1969	4	4.0	7.6	37.0	0.21
1970	8	8.0	31.9	163.2	0.20
1971	40	338.0	4332.6	6485.5	0.67
1972	35	164.5	1343.3	3142.0	0.43
1973	46	398.5	4313.1	7991.4	0.54
1974	44	425.0	7439.0	12169.1	0.61
1975	43	570.0	11116.2	15089.5	0.74
1976	40	454.0	9819.2	14294.9	0.69
1977	42	552.5	8731.9	14099.5	0.62
1978	57	801.0	11747.1	17490.8	0.67
1979	73	780.5	10545.6	17172.3	0.61
1980	67	876.5	12179.2	19980.6	0.61
1981	68	762.7	11436.1	19772.1	0.58
1982	49	381.0	4990.5	10107.0	0.49
1983	48	522.5	7593.0	12627.0	0.60
1984	52	492.3	7103.3	12737.1	0.56
1985	57	686.5	8677.4	15822.1	0.55
1986	40	168.0	1071.0	2219.6	0.48
1987	0	0.0	0.0	0.0	------
1988	0	0.0	0.0	0.0	------
1989	0	0.0	0.0	0.0	------
1990	33	97.5	1710.5	2744.2	0.62
1991	55	242.5	3197.8	5684.8	0.56

Table 25. Pearson correlations between measures of MSX infection and mean oyster abundance or estimates of oyster mortality. Oyster change equals the difference between the mean number of oysters * $20L^{-1}$ in $year_{(t)}$ and the mean number of oysters * $20L^{-1}$ in $year_{(t-1)}$. Oyster mortality is the mean sum of gapers, new boxes, and old boxes * $20L^{-1}$ of dredge sample. Relative mortality is the mean of oyster mortality divided by the sum of mean oyster mortality and mean numbers of oysters *

	SPRING				AUTUMN			
VARIABLE	Prop. Inf.	Prob.	Prop. Syst.	Prob.	Prop. Inf.	Prob.	Prop. Syst.	Prob.
ARNOLDS (n)	27		27		28		28	
Oysters * $20L^{-1}$	0.06	n s	0.08	n s	-0.07	n s	-0.11	n s
Oyster change	0.16	n s	0.13	n s	0.00	n s	0.14	n s
Oyster mortality	0.45	n s	0.43	n s	0.29	n s	0.19	n s
Rel. mortality	0.30	n s	0.26	n s	0.28	n s	0.25	n s
COHANSEY (n)	27		27		26		26	
Oysters * $20L^{-1}$	-0.35	n s	-0.31	n s	-0.02	n s	-0.17	n s
Oyster change	-0.18	n s	-0.08	n s	0.09	n s	-0.04	n s
Oyster mortality	0.35	n s	0.52	n s	0.17	n s	0.24	n s
Rel. mortality	0.60	*	0.73	* * *	0.18	n s	0.36	n s
BENNIES (n)	23		23		23		22	
Oysters * $20L^{-1}$	-0.18	n s	-0.21	n s	0.04	n s	-0.17	n s
Oyster change	-0.18	n s	-0.18	n s	0.19	n s	0.12	n s
Oyster mortality	0.20	n s	0.07	n s	0.41	n s	0.22	n s
Rel. mortality	0.48	n s	0.41	n s	0.51	n s	0.46	n s
NEW (n)	11		11		9		9	
Oysters * $20L^{-1}$	-0.09	n s	-0.39	n s	0.38	n s	0.27	n s
Oyster change	-0.23	n s	0.20	n s	-0.21	n s	-0.25	n s
Oyster mortality	0.22	n s	0.67	n s	0.30	n s	0.51	n s
Rel. mortality	0.00	n s	0.68	n s	-0.31	n s	-0.08	n s
EGG I. (n)	15		15		14		14	
Oysters * $20L^{-1}$	-0.02	n s	-0.03	n s	-0.58	n s	0.57	n s
Oyster change	-0.29	n s	-0.33	n s	-0.28	n s	-0.34	n s
Oyster mortality	-0.34	n s	-0.37	n s	0.18	n s	-0.22	n s
Rel. mortality	-0.11	n s	-0.12	n s	0.57	n s	0.52	n s
ALL BEDS (n)	103		103		100		99	
Oysters * $20L^{-1}$	-0.42	* * *	-0.38	* *	-0.38	* *	-0.47	* * *
Oyster change	0.16	n s	0.08	n s	0.10	n s	0.16	n s
Oyster mortality	-0.09	n s	-0.08	n s	-0.10	n s	-0.14	n s
Rel. mortality	0.36	* *	0.36	* *	0.41	* * *	0.45	* * *

Table 26. Pearson correlations of seed bed harvest intensity versus seed bed abundances of oysters, yearlings, and spat. Correlations with a Bonferroni - adjusted probability less than 0.05 occur in boldface. All values were ln-transformed prior to determining the correlation except for proportional values which were angular transformed and oyster change and seedbed harvest which remained untransformed. Variable definitions are in Table 24 or in the text. The beds are listed from the furthest up the bay to the lowest in the bay. Evidence of drill caused spat mortality was never found on Round Island, Upper Arnolds, and Upper Middle beds in this study. No records of seedbed harvest were available for Strawberry bed.

	ABUNDANCES			**MORTALITY**							
	# oysters $* 20L^{-1}$	# yearlings $* 20L^{-1}$	# spat $* 20L^{-1}$	Oyster mortality	Oyster change	Relative oyster mortality	Drill spat mortality	Non-drill spat mortality	Relative spat mortality	Relative drill spat mortality	n
ROUND ISLAND	-0.11	-0.11	0.03	-0.18	0.08	-0.05	- - -	0.05	0.16	- - -	26
UPPER ARNOLDS	0.08	0.22	-0.36	-0.10	-0.08	-0.16	- - -	-0.22	-0.22	- - -	30
ARNOLDS	-0.20	0.04	-0.11	-0.24	0.02	-0.01	-0.10	0.00	0.01	-0.10	35
UPPER MIDDLE	0.33	0.28	0.49	0.14	0.42	-0.19	- - -	-0.08	-0.18	- - -	17
MIDDLE	-0.12	-0.24	0.14	-0.09	0.12	-0.03	0.19	0.11	-0.06	0.15	34
COHANSEY	-0.01	-0.14	0.18	-0.19	0.30	-0.13	0.02	0.16	-0.13	-0.02	35
SHIP JOHN	0.09	0.05	-0.06	-0.04	0.32	-0.07	-0.18	0.06	-0.01	-0.29	35
SHELL ROCK	0.40	0.27	0.37	0.07	0.36	-0.34	-0.22	0.03	-0.38	-0.27	35
BENNIES SAND	-0.15	0.16	0.17	-0.11	0.30	0.00	0.01	-0.02	-0.12	0.04	18
BENNIES	0.67	0.38	0.32	0.39	0.65	-0.60	-0.23	0.23	-0.39	-0.37	34
NANTUXENT PT.	-0.02	-0.01	0.34	0.29	0.21	0.33	0.30	0.33	0.05	0.07	29
HOG SHOAL	0.39	0.49	0.22	0.27	0.02	-0.22	-0.19	0.17	-0.18	-0.28	30
NEW	0.68	0.35	0..25	0.29	0.54	-0.58	-0.27	0.06	-0.39	-0.29	32
STRAWBERRY	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -
HAWK'S NEST	0.43	0.08	-0.13	0.17	0.07	-0.35	-0.30	-0.05	-0.09	-0.19	25
BEADONS	-0.16	-0.22	0.02	0.19	0.19	0.28	-0.08	-0.05	-0.02	0.08	33
VEXTON	-0.04	-0.27	-0.39	-0.18	0.12	-0.14	0.08	-0.10	0.57	0.16	16
EGG ISLAND	0.46	0.20	0.10	0.39	0.36	-0.29	0.07	0.05	-0.15	-0.06	30
LEDGE	0.31	0.07	0.12	0.34	0.30	-0.18	0.19	0.36	-0.07	0.01	27

Table 27. Results of multivariate regressions of adult oyster abundance onto several independent variables. The first four columns give the regression parameters for each independent variable. The r^2 and significance for each entire model are presented in the last two columns. The number of observations (n) in the model is presented after the area name.

AREA (n)	**Coefficient**	**Std. Coef.**	**Tolerance**	**Probability**	**r^2**	**Prob.**
ALL BEDS (94)					0.66	<0.001
constant	-2.82	0.00	- - -	0.131		
yearlings(t-1)	0.42	0.70	0.88	0.001		
annual flow	0.68	0.22	0.93	0.001		
spring infections	-0.80	-0.25	0.69	0.001		
autumn infections	0.07	0.03	0.69	0.706		
harvest	-0.00	-0.04	0.89	0.499		
ARNOLDS (27)					0.66	<0.001
constant	-5.81	0.00	- - -	0.062		
yearlings(t-1)	0.24	0.53	0.86	0.003		
annual flow	1.10	0.63	0.71	0.002		
spring infections	0.53	0.13	0.76	0.463		
autumn infections	0.44	0.22	0.85	0.194		
harvest	-0.00	-0.01	0.92	0.934		
COHANSEY (25)					0.66	0.001
constant	-6.74	0.00	- - -	0.027		
yearlings(t-1)	0.25	0.50	0.70	0.005		
annual flow	1.15	0.67	0.59	0.001		
spring infections	-0.24	-0.07	0.66	0.670		
autumn infections	0.55	0.36	0.82	0.026		
harvest	-0.00	-0.20	0.69	0.223		
BENNIES (20)					0.81	<0.001
constant	-8.21	0.00	- - -	0.203		
yearlings(t-1)	0.41	0.67	0.63	<0.001		
annual flow	1.18	0.28	0.58	0.088		
spring infections	0.17	0.05	0.59	0.758		
autumn infections	0.10	0.00	0.77	0.980		
harvest	0.00	0.26	0.67	0.087		
NEW (8)					0.91	0.218
constant	-11.82	0.00	- - -	0.671		
yearlings(t-1)	0.20	0.36	0.46	0.379		
annual flow	1.70	0.60	0.05	0.612		
spring infections	-1.45	-0.26	0.08	0.769		
autumn infections	-0.93	-0.15	0.10	0.848		
harvest	0.00	0.30	0.10	0.705		
EGG I. (14)					0.79	0.013
constant	-2.82	0.00	- - -	0.672		
yearlings(t-1)	0.35	0.84	0.79	0.002		
annual flow	0.64	0.23	0.49	0.356		
spring infections	-0.31	-0.12	0.39	0.660		
autumn infections	0.13	0.06	0.62	0.767		
harvest	0.00	0.23	0.67	0.285		

Table 28. Coefficients and probabilities for a multivariate regression of adult oyster abundance onto several independent variables after use of a stepwise procedure. The first four columns give the regression parameters for each independent variable. The number of observations (n), r^2, and significance for the entire model are presented in the last two columns.

Variable	Coefficient	Std. Coef.	Tolerance	Probability	n	r^2	Prob.
ALL BEDS					94	0.62	<0.001
constant	-3.55	0.00	- - -	0.077			
yearlings$_{(t-1)}$	0.44	0.68	0.94	<0.001			
annual flow	0.74	0.22	0.98	0.001			
spring infections	-0.64	-0.20	0.92	0.002			