

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/230689149>

# Long-term Trends in Oyster Population Dynamics in Delaware Bay: Regime Shifts and Response to Disease

Article in *Journal of Shellfish Research* · December 2008

DOI: 10.2983/0730-8000(2008)27[729:LTIOPD]2.0.CO;2

CITATIONS

55

READS

151

5 authors, including:



[Kathryn Ashton-Alcox](#)

Rutgers, The State University of New Jersey

44 PUBLICATIONS 843 CITATIONS

[SEE PROFILE](#)



[David Bushek](#)

Rutgers, The State University of New Jersey

106 PUBLICATIONS 1,517 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Minimizing Risks of Vibrio Bacteria [View project](#)

## LONG-TERM TRENDS IN OYSTER POPULATION DYNAMICS IN DELAWARE BAY: REGIME SHIFTS AND RESPONSE TO DISEASE

ERIC N. POWELL,\* KATHRYN A. ASHTON-ALCOX, JOHN N. KRAEUTER,  
SUSAN E. FORD AND DAVID BUSHEK

*Haskin Shellfish Research Laboratory, Rutgers University, 6959 Miller Ave., Port Norris,  
New Jersey 08349*

**ABSTRACT** We evaluate a 54-y survey time series for the Delaware Bay oyster beds in New Jersey waters to identify the characteristics of regime shifts in oyster populations and the influence of MSX and Dermo diseases on population stability. Oyster abundance was high during the 1970s through 1985. Oyster abundance was low at the inception of the time series in 1953, remained low through 1969, and has been low since 1985 and very low since 2000. Natural mortality was low in most years prior to the appearance of MSX in 1957. From 1957 through 1966, natural mortality generally remained above 10% annually and twice exceeded 20%. Natural mortality remained well below 15% during the 1970s and into the early 1980s when oyster abundance was continuously high. The largest mortality event in the time series, an MSX epizootic that resulted in the death of 47% of the stock, occurred in 1985. Mortality rose again with the incursion of Dermo in 1990 and has remained above 15% for most years since that time and frequently has exceeded 20%. The primary impact of MSX and Dermo diseases has been to raise natural mortality and ultimately to cause a dispersed stock to retreat into its habitat of refuge in the moderately low salinity reach of the bay. The time series of oyster abundance on the New Jersey oyster beds of Delaware Bay is dominated by two regime shifts, the 1970 abundance increase that was maintained for about 15 y thereafter, and the 1985 abundance decrease that continues through today. These two regime shifts ushered in long-term periods of apparent constancy in population dynamics. The 1985 regime shift was induced by the largest MSX epizootic on record that produced high mortalities throughout a population distributed broadly throughout its habitat range after 15 y of high abundance. A putative new regime commenced circa 2000 as a consequence of a series of Dermo epizootics. Mortalities routinely exceeded 20% of the population annually during this period, with the consequence of a greater degree of stock consolidation than any previous time in the 54-y record. Extreme consolidation of the stock would appear to be a characteristic of the population's response to Dermo disease. The 1970–1984 and post-1985 regimes each were ushered in by a confluence of events unique in the 54-y time series. Each was characterized by a period of relative stability in population abundance. However, the stability in total population abundance belies a more dynamic process of stock redistribution during both time intervals, demonstrating that the appearance of constancy in stock abundance is not necessarily a result of invariant stock dynamics. Rather, the Delaware Bay oyster time series suggests that regime shifts delimit periods during which differential, often offsetting, local trends impart similar abundance levels, and thus constancy at the level of the stock masks substantive changes in local population dynamics potentially fostering future catastrophic changes in population-level attributes. Understanding such regime shifts will likely determine the success of decadal management goals more so than measures designed to influence population abundance.

**KEY WORDS:** oyster, *Crassostrea*, regime shift, time series, population dynamics, stock survey, refuge habitat, spatial distribution

### INTRODUCTION

Many states depend on the use of publicly owned oyster resources to sustain oyster fisheries and low-intensity aquaculture (e.g., Hofstetter 1983, Dugas 1988, MacKenzie 1989, Hargis & Haven 1994). The range of uses varies. Some states use publicly owned oyster beds as seed resources. Some use them to support direct-market fisheries; activities in which market-size oysters are caught and taken directly, or after a short depuration period, to market. Some, through more intensive manipulation, use the public beds in both activities (Hofstetter 1990, Berrigan et al. 1991, Fegley et al. 1994, Krantz & Jordan 1996, MacKenzie 1996). Regardless, these beds often suffer the fate of any common-use resource: overharvesting. Sustainability has sometimes been achieved because oysters can rapidly repopulate in some harvested areas, particularly in the southern portion of their range (e.g., Ingle & Dawson 1950, Hopkins 1954, Hayes & Menzel 1981), but increased rates of mortality accompanying the onset of MSX and Dermo diseases abetted by poorly constrained fishing rates have resulted in

population declines, sometimes catastrophic in nature, in many more temperate regions (Rothschild et al. 1994, Mann 2000, Jordan & Coakley 2004).

Oysters maintain their own habitat and this activity is dynamic as shell is continually added by natural mortality and degraded and lost through the process of taphonomy (Powell et al. 2006, Powell & Klinck, 2007). Unsurprisingly, the decline in abundance, whether by overfishing or disease, normally is associated with habitat degradation (Marshall 1954, Smith et al. 2001, Smith et al. 2005, Woods et al. 2005, Bergquist et al. 2006) as the declining rate of shell addition ceases to compensate for the perpetual loss of shell (Powell et al. 2006, Powell & Klinck 2007). A plethora of papers, reports, and workshops have evaluated and proposed management strategies for these public beds (e.g., MacKenzie 1981, Andrews & Ray 1988, Ford & Haskin 1988, Hargis & Haven 1994, Krantz & Jordan 1996, Jordan et al. 2002, Jordan & Coakley 2004). These have, in most cases, recognized the influence of the disease process in oyster population dynamics, but some also have emphasized variable recruitment and the failure to control fishing, and a few have dealt with the shell balance. One of the overarching themes through much of this work has been the assumption that proper

\*Corresponding author. E-mail: eric@hsrl.rutgers.edu.

management can change the population structure of the stock. Dramatically increased abundance is an oft-mentioned goal, as is increased commercial harvest. But, the question remains: what is the range of options available to the manager and how is this range constrained? Neither is well understood because only limited attention has been given to the range in stock dynamics revealed by long-term survey time series, although both are necessary conditions for successful management.

A number of long-term time series exist documenting key stock indices such as abundance, biomass, natural and fishing mortality, and recruitment. These include surveys conducted by the states of Virginia (Austin et al. 1996, Mann & Evans 1998), Maryland (Rothschild et al. 1994, Jordan et al. 2002), Texas (Hofstetter 1977, 1983), Delaware, and New Jersey (Fegley et al. 1994, 2003). The New Jersey survey began as a response to overfishing that had reduced stock abundance by the early 1950s (Haskin 1953). By 2006, this 54-y record covered a number of unique periods, including the period of time after the onset of MSX disease circa 1957 (Haskin & Andrews 1988, Ford 1997) and the period of time after the onset of Dermo disease circa 1990 (Ford 1996, Cook et al. 1998). The purpose of this analysis is to present a quantitative reconstruction of this survey time series and, then, to describe the range of oyster population dynamics observed over the 54 y, with particular emphasis on time segments of unique and coherent population characteristics. We

then use this information to consider the population's response to increased mortality associated with disease and the relationship between regime shifts, periods of stability in population abundance, and the underlying degree of constancy in the essential components of the oyster's population dynamics.

## SURVEY QUANTIFICATION AND TIME SERIES RECONSTRUCTION

### Overview

The first rigorously-designed stock survey of oysters in Delaware Bay was carried out in 1953. This survey, which has been carried out each year subsequently, predates the onset of MSX by a few years (Ford & Haskin 1982, Haskin & Andrews 1988, Ford 1997). The survey is of stratified random design implemented on a grid system depicted in Figure 1. Details of the survey can be found in Fegley et al. (1994, 2003) and HSRL (2007). The oyster stock in the New Jersey waters of Delaware Bay is partitioned into twenty oyster beds that are sufficiently large to be included in the sampling program. Allocation of grids to strata has varied over the years (e.g., Fegley et al. 1994). A recent detailed resurvey of beds from Middle downbay, with the exception of Ledge, Egg Island, and New Beds, has permitted division of each of these beds into three strata based on

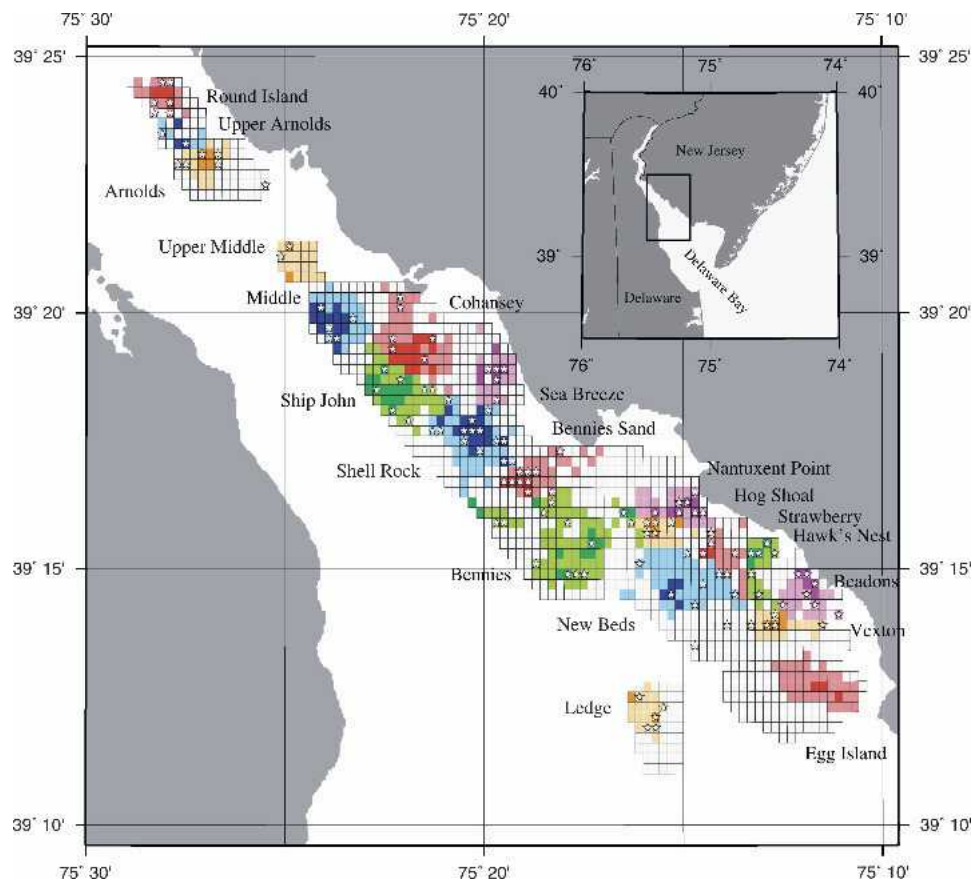


Figure 1. Natural oyster beds in the New Jersey waters of Delaware Bay showing the locations of the 2006 survey sampling sites (white stars) and the bed footprint defined by the high-quality (dark shade) and medium-quality grids (light shade). Low-quality grids are shown in white. The footprints for Middle downbay, excepting New Beds, Egg Island, and Ledge, are updated from resurveys in 2005 and 2006. The footprints for the remaining beds are based on Fegley et al. (1994).

post-2004 population distributions: a low-quality stratum contributing in aggregate only 2% of the stock; a medium-quality stratum consisting of grids with moderate levels of oyster abundance contributing about 48% of the stock; and a high-quality stratum consisting of grids with high levels of oyster abundance contributing the remaining approximately 50% of the stock. Figure 1 shows that low-quality strata account for a large fraction of bay area and generally occupy the bed margin. High-quality strata, by comparison, are few in number and generally occupy the bed core. Medium-quality strata comprise much of the bed proper and contribute much of the fishable area of the bed. Samples are distributed randomly within each stratum on each bed; however, most of the sampling effort is directed at the medium- and high-quality strata, and this has been true over the history of the survey, as the total number of samples taken is constrained financially and logistically. The present analysis is based on an assumption of uniformitarianism; namely that the high- and medium-quality strata shown in Figure 1 describe the regions contributing most of the stock over the history of the survey.

The survey has been conducted in similar fashion since 1953. A significant change in gear, from a small survey dredge to a larger commercial dredge, occurred in 1989. Gear intercalibration experiments were not undertaken and, so, no explicit conversions are available; however some independent dredge efficiency estimates are available for both dredges. Some beds were sampled more routinely than others over the years. A number of changes in sample density on each bed also occur throughout the record. Nevertheless, sampling was relatively comprehensive throughout the history of the survey. Of greatest consequence are two changes in sampling protocol. (a) Size frequencies were not obtained prior to 1989. As a consequence, biomass cannot be reconstructed prior to this date. (b) Catchability coefficients were not available prior to 1997. Thus, quantitative abundance was not overtly measured prior to 1997. As a consequence of the limited size-frequency data, the analyses provided herein focus on the numerical abundance of spat and oysters, oysters herein defined as animals  $\geq 1$  y old. Neither biomass, spawning stock biomass, nor the abundance of market-size animals can be reconstructed over the entire time series. As a consequence of the limits of survey quantification, swept area of survey tows and catchability coefficients must be reconstructed retrospectively.

#### Fishing Styles and Bay Region Terminology

The analysis that follows will make reference to four distinctive types of stock manipulation that have been pursued on the Delaware Bay oyster beds of New Jersey. From 1953 through 1995, a "bay-season" fishery was prosecuted. In this mode, some portion of the beds was opened for usually 2–6 wk in the spring. Oysters were removed *en masse* and transplanted to leased grounds most of which are downbay of Egg Island bed (Fig. 1). Cull laws limited the amount of cultch moved downbay, but no size limitation existed. Based on recent dredge efficiency estimates for transplant activities of this type (Powell & Ashton-Alcox 2004), the bay-season fishery likely was relatively nonselective and moved oysters more or less in proportion to their abundance in the population's size-frequency distribution. In most years, the fishery was limited by the 40% rule. When the volume of live oysters dropped to <40% of the

bushel haul, the bed was closed (Fegley et al. 2003). As a consequence, target beds varied during the program from year to year as the relative abundance of the resource varied and in 12 of the 43 y from 1953–1995, all beds were closed because of low oyster volume.

Since 1996, a direct-market fishery has taken place. In this fishery, market-size oysters are taken directly off the beds and marketed immediately or stored for a time on leased grounds prior to marketing. Although no size limit is rigorously enforced, the vast majority of animals removed by this fishery exceed 63 mm (Powell et al. 2005, HSRL 2007). For the most part, the direct-market fishery has targeted beds from Shell Rock downbay (Fig. 1).

Since 1997, an intermediate transplant program has been conducted. Oysters are removed from beds upbay, transplanted downbay to selected market beds for fattening (Kraeuter et al. 2003), and then the number supported by the transplant marketed six or more weeks later, but typically within the same year. No effort is made to focus marketing on the transplants. Rather, the procedure increases the number of market-quality oysters on the bed available for harvest and thus increases the total harvest from that region. With one exception, all donor beds have been upbay of Shell Rock. Although efforts have been made to focus the transplant on oysters  $\geq 63$  mm, recent evidence suggests that the program moves oysters downbay more or less in proportion to their size-frequency distribution in the donor population (Powell & Ashton-Alcox 2004). To what extent this program diverges from the bay-season fishery in its impact on the population structure of the donor bed is unclear.

In 2003, a "juvenile-enhancement" program was initiated. A suction dredge was used to move spat shell upbay from high setting regions to enhance recruitment on the market beds. Additionally, beginning in 2005, shell was planted directly on selected beds to enhance recruitment. This latter activity recapitulates a program carried out sporadically in the 1950s–1970s, but with limited recording of impact.

In the following discussions, these activities will be referred to as bay-season, direct-market, intermediate-transplant, and recruitment-enhancement activities. In addition, the analyses that follow will often delineate four bay groups based on the long-term average rates of natural mortality, productivity, and influence on survey catchability. Analyses of the Delaware Bay oyster resource of New Jersey routinely reveal a division between the upbay group of eight beds (Round Island, Upper Arnolds, Arnolds, Upper Middle, Middle, Sea Breeze, Cohansey, and Ship John [Fig. 1]) and the downbay group of 12 beds (Shell Rock, Bennies Sand, Bennies, New Beds, Nantuxent Point, Hog Shoal, Hawk's Nest, Strawberry, Vexton, Beadons, Egg Island, and Ledge). Salinity, natural mortality rate, and growth rate are higher downbay. Dredge efficiencies are significantly higher downbay (Powell et al. 2002a, Powell et al. 2007). Both regions can be subdivided based on natural mortality rate and productivity. In the upbay region, natural mortality rates and growth rates are significantly lower for the upper three beds, Round Island, Upper Arnolds, and Arnolds; than for the remainder. This trend is dictated by the salinity gradient. Over the long term, salinity averages around 12‰ on the upper group of beds and closer to 15‰ on the lower group of beds (Haskin & Ford 1982). Henceforth these two groups will be termed the low-mortality and medium-mortality beds



TABLE 1.

The bed groups referred to in the text. Bed locations are shown in Figure 1.

<b>Upbay group</b>	
Low mortality	Round Island, Upper Arnolds, Arnolds
Medium mortality	Upper Middle, Middle, Sea Breeze, Cohansey, Ship John
<b>Downbay group</b>	
Medium mortality	Shell Rock
High mortality	Bennies Sand, Bennies, New Beds, Hog Shoal, Hawk's Nest, Strawberry, Vexton, Ledge, Egg Island, Nantuxent Point, Beadons

(Table 1). In the downbay region, growth rates and mortality rates are lower for Shell Rock, leading to its designation as a medium-mortality bed; the remainder being high-mortality beds (Table 1). Salinities for most beds downbay of Shell Rock average around 18‰ with salinities tending to exceed 20‰ on the lowermost two, Egg Island, and Ledge (Haskin & Ford 1982). Shell Rock is unique in consistently achieving the highest productivity today of any New Jersey bed. This is because of an auspicious coincidence of relatively high recruitment and growth and relatively low mortality on this bed.

For the purposes of the following analyses, the stock is defined as those oysters on the twenty natural oyster beds shown in Figure 1. Oysters are also found on the Delaware side of the bay, although the total bed area is much less (Moore 1911, Maurer et al. 1971, Maurer & Watling 1973), as well as in many of the river mouths, and an unknown, but during certain periods of history (MacKenzie 1996, Ford 1997) significant number have been present on leased grounds, most of which occur downbay of Egg Island (see Fig. 1 of Haskin & Ford 1982). Inadequate survey data exist to include the oysters in bay margin habitats and on leased grounds in the stock analysis. Delaware maintains an independent survey, but these data are not yet available on a per-m<sup>2</sup> basis.

#### Time Series Reconstruction—Catchability Coefficient

Population abundance  $N$  is related to survey abundance  $n_s$  by a catchability coefficient:

$$N = qn_s. \quad (1)$$

An estimate of  $q$ , the catchability coefficient, requires four variables:  $A$ , the area surveyed;  $d$ , the distance traveled per tow;  $w$ , the cross-section sampled by the dredge (the dredge width); and  $e$ , the efficiency of capture by the dredge. Thus

$$q = \frac{A}{dwe}. \quad (2)$$

The term  $dw$  is normally referred to as swept area (m<sup>2</sup>). For convenience, we first standardize the catch of all survey tows to 1 m<sup>2</sup>; that is, we set  $A = 1$  and  $n_s = v/dw$ , where  $v$  is any survey variable. Then,  $q$  in Eq. (1) is the reciprocal of dredge efficiency:  $q = 1/e$ . Tow-based measures of swept area are obtained from 5-sec DGPS position logs and a known estimate of dredge efficiency (Powell et al. 2002a, Powell et al. 2007) and these are

used to standardize bushel-sample constituents to per-m<sup>2</sup> values. The summation of total abundance is subsequently conducted in four steps: (1) a mean catch is obtained by averaging all survey tows in a given bed and stratum; (2) the mean catch is multiplied by stratum area; (3) the strata are summed to provide a value for each oyster bed; and (4) the beds are summed to provide total values for bed groups and the entire survey domain.

The raw survey data, beginning in 1953, are available in terms of the number of oysters or spat per bushel (1 New Jersey bushel = 37 liquid quarts = 35 L) sample. Estimating a catchability coefficient for pre-1997 survey tows requires (1) using the post-1996 quantified measures for a temporally stable constituent of the survey sample and then (2) using that stable constituent to retrospectively estimate tow-based catchability coefficients.

The measured dredge efficiencies obtained in 2001 and 2003, although temporally variable (e.g., Powell & Ashton-Alcox 2004, Powell et al. 2002a, Powell et al. 2007), are likely representative of the commercial dredge in all years that it has been used, namely 1989 to 2006. Additional checks of dredge efficiency in 2005 and 2006 have conformed to these more comprehensive analyses (HSRL 2006, 2007). The smaller survey dredge was evaluated in the early 1950s; estimates of dredge efficiency varied around 25% (Haskin, hand-written notes). This value falls within the range of efficiencies for the commercial dredge (Powell et al. 2007). Commercial dredge efficiency varies significantly and predictably between beds, however, and this variance seems to be temporally stable over time periods of a few years (Powell et al. 2007). Unfortunately, equivalent data for the smaller survey dredge do not exist. Furthermore, dredge efficiency may vary temporally over a period of years as a function of spatial changes in industry effort (Powell & Ashton-Alcox 2004, Powell et al. 2007). Although the dispersion of industry effort across the 20 oyster beds has been relatively constant in the post-1996 period, being concentrated on the beds downbay of Ship John and Cohansey (Fig. 1), this was not always true and the total dredging impact of the direct-market fishery (e.g., Banta et al. 2003) likely exceeds any year's effort for the bay-season fishery. Therefore, an average catchability coefficient cannot be implemented across the entire survey, all beds and all years.

What is needed is a surrogate measure of sample swept area provided, for example, by a conservative property of the sample. Such a constituent would vary more by the difference in swept area than by the inherent yearly variation of the constituent. Thus, its abundance could be used to estimate retrospectively the swept area of the tow. The survey sample contains four principal components: (1) live oysters, (2) boxes, dead articulated shells likely representing recent mortality (Christmas et al. 1997, Powell et al. 2001, Ford et al. 2006); (3) debris, miscellany such as rocks, gravel, and detached bionts such as sponges and erect hydroid/bryozoan colonies; and (4) cultch, shells including clumps, single valves, and shell fragments without attached live oysters or boxes. Debris is inherently volatile, as to a lesser degree are boxes that come from widely varying yearly mortality rates. Cultch has been moved around the bay over the last 54 y; however culling regulations have minimized this movement in comparison with live oysters and boxes. Live oysters have generation times of 4–7 y, judging from recent estimates of size at age (Kraeuter et al. 2007), but fishing

adds significant year-to-year volatility as does varying natural mortality rates. Most boxes disarticulate relatively rapidly after death (Ford et al. 2006, Powell et al. 2006).

We have only a minimal understanding of the temporal stability of oyster shell (e.g., Gunter et al. 1957, Warburton 1958, Hopkins 1962, Frérotte et al. 1983, DeAlteris 1988). Although oyster shell might be believed to be more resistant than most molluscan shells to the vicissitudes of taphonomy because of its construction and thickness (Callender et al. 1994, Zuschin & Stanton 2001, Lescinsky et al. 2002, Powell et al. 2002b), recent analyses have shown otherwise (Powell et al. 2006). Oyster shell degrades relatively rapidly, with shell half-lives on the order of 3–10 y being commonplace (Powell et al. 2006) and comparable to oyster generation times (Powell & Klinck 2007). However, comparison of the volatility of shell, relative to boxes or live oysters, by Powell & Klinck (2007) reveals that surficial shell content available to an oyster dredge will change slowly relative to the remaining bed constituents and likely not vary unidirectionally unless the input rate of boxes were to persistently increase or decrease over many years. Recent time series analysis by Soniat et al. (in press) resolves cyclic changes in oyster abundance and mortality, with important periodicities at 4 and 8 y. A 4-y periodicity is insufficient to produce a large shift in surficial shell content (Powell & Klinck 2007). An eight-year periodicity may be adequate, although variation in surficial shell content by a factor of two over this time period seems unlikely. We are cognizant that multidecadal changes in shell content have occurred in other bays (e.g., Powell et al. 1995, Smith et al. 2005). Nevertheless, whereas we have no way to confirm that long-term cycles or directional shifts in shell content have not occurred over the 54-y history of record, shell is certainly the most temporally stable bed component measured in the survey.

A constant-cultch assumption permits time series standardization in that a measure of cultch volume per bushel from a survey tow can be related to a density of cultch  $m^{-2}$  on the bottom. We use this ratio to convert retrospectively a semiquantitative measure of oysters per bushel for each survey tow to oysters per  $m^2$ :

$$(\text{oysters } m^{-2})_{bij} = \frac{(\text{oysters } bu^{-1})_{bij}}{(\text{cultch } bu^{-1})_{bij}} * (\text{cultch } m^{-2})_{b,\bar{i}\bar{j}} \quad (3)$$

where  $b$  is the bed,  $i$  is the year,  $\bar{i}\bar{j}$  is the 1998 to 2004 average,  $j$  is the survey tow, and the final variable on the right-hand side,  $(\text{cultch } m^{-2})_{b,\bar{i}\bar{j}}$ , is obtained as the average of the 1998 to 2004 survey tows using the average of catchability coefficients,  $q_{\text{cultch}}$ , provided by Powell et al. (2002a) and Powell et al. (2007):

$$(\text{cultch } m^{-2})_{b,\bar{i}\bar{j}} = \frac{\left( \sum_{j=1}^{\eta_i} \sum_{i=1}^7 (\text{cultch } bu^{-1})_{bij} * (\text{bu caught } m^{-2})_{bij} * q_{\text{cultch}} \right)}{\sum_{i=1}^7 \eta_i} \quad (4)$$

where  $\eta_i$  is the yearly number of survey tows. The 1998 to 2004 time period is used because 1998 is the first year of quantitative field estimate of oyster abundance and the initiation of a shell-planting program in 2005 may modify locally the amount of surficial shell. To the extent that the constant-cultch assumption is invalid, perusal of time series data suggest that abundance is likely to be overestimated historically because surficial shell

content, if anything, has been higher at times in the past than present-day. The absence of shell planting for at least a score of years prior to 2005 and the low oyster abundance that followed the onset of Dermo disease limiting shell addition rate conspire to limit surficial shell content in recent years.

#### Time Series Reconstruction—Total Shell Volume

The next question concerns the wisdom of including boxes with cultch as a measure of the total shell to be used for quantification. Dredge efficiencies are lower for cultch than for live oysters (Powell et al. 2002a, Powell et al. 2007, Powell & Ashton-Alcox 2004, Mann et al. 2004). Presumably, some cultch is more difficult to remove from the bottom than live oysters or is sufficiently small to pass between the dredge teeth. Interestingly, dredge efficiencies for boxes routinely fall in-between live oysters and cultch (Powell et al. 2002a, Powell et al. 2007, Powell & Ashton-Alcox 2004). This suggests that some fraction of boxes have the catchability properties of cultch.

Since 1989, cultch has been separated from boxes in the survey. Prior to this time, boxes were lumped in with cultch volumetrically in most years. Luckily, in these years, single shell and box counts are usually available. Accordingly, the proportion of total shell volume, hereafter defined as the volume of cultch plus boxes, contributed by cultch could be estimated by either the ratio  $(\text{box volume})/(\text{total shell volume})$  or  $(\text{box counts} * 2)/(\text{total shell counts})$ . However, in some cases, no apportionment can be made and these tows would be lost if only cultch were used. As important, dredge efficiency estimates indicate that some boxes should be treated as cultch. As a consequence, we use total shell for standardization. Because total shell includes boxes and cultch, the catchability coefficient used for the final quantification must be prorated according to the relative contribution of cultch and boxes to total shell:

$$\bar{q} = \left( \frac{\# \text{ boxes} * 2}{\# \text{ total shells}} * (q_{\text{box}} - q_{\text{cultch}}) \right) + q_{\text{cultch}} \quad (5)$$

As shells normally outnumber boxes by at least a factor of 10 (Powell et al. 2006), this correction, and the inclusion of boxes in the first place, adds only a minor correction to subsequent estimates of oyster density.

In addition, the dredge efficiency for live oysters is higher than boxes and substantially higher than cultch. As a consequence, a correction factor is required to take into account this bias of the dredge. Eq. (3) is therefore modified, in the case of shell counts for example, as

$$\text{oysters } m^{-2} = \frac{\text{oysters } bu^{-1}}{\text{cultch } bu^{-1}} * \text{cultch } m^{-2} * \frac{q_{\text{live}}}{\bar{q}} \quad (6)$$

Oysters  $\geq 63$  mm tend to be caught with higher efficiency, although not all dredge calibration measurements provide uniform results (Powell et al. 2007). Spat, however, certainly must be caught with the efficiency of the substrate upon which they attach, be it cultch, box, or live oyster. Accordingly, spat densities were reconstructed piecemeal based on the distribution of spat on these three constituents and the respective catchability coefficients.

No data exist prior to 1998 to directly test the accuracy of this retrospective quantification. However, for 1998 to 2004,

oyster densities were directly measured and these direct measurements can be compared with the densities inferred from the amount of shell present per bushel and average shell densities (Fig. 2). The predicted oyster densities overall are biased neither high nor low (binomial test,  $\alpha = 0.05$ ). In 50 out of 103 cases, the observed oyster density is higher than the predicted oyster density. An ANOVA using year and bay region as main effects revealed a significant year effect in the residuals ( $P = 0.0006$ ) and a significant interaction with bay region ( $P < 0.0001$ ) because the upbay group in 2003 and 2004 tended to have negative residuals; the predicted value exceeded the observed value. Powell et al. (2007) demonstrated that commercial dredging tends to increase dredge efficiency for live oysters significantly in the short term (Powell et al. 2002a, Powell & Ashton-Alcox 2004). Industry effort was higher upbay in 2003 and 2004 than in other years of the 1998–2004 time series (HSRL 2007) and increased efficiency for live oysters would produce the effect observed. Indeed, the three beds contributing most to the significant main effect are Cohansey, Ship John, and Middle, beds purposely targeted for exploitation since 2002 (HSRL 2006, 2007). An ANCOVA with year as the main effect and landings (the term landings is used although some few oysters may have been moved to leased grounds and not subsequently marketed) normalized by bed area as the covariate confirms the importance of landings in revealing nonsignificance for the year main effect or the landings covariate, but with a significant interaction term ( $P = 0.03$ ) between the two.

Likely, the same phenomenon occurred in previous years as dredging effort varied significantly from one bay region to another over time. Unfortunately, reconstruction of the effect of past harvests on dredge efficiency is not feasible. Industry effort can be estimated for the 1996 to 2004 direct-market fishery (Banta et al. 2003) and its stability over that time is likely the most important contributor to the accuracy of the retrospective estimates of cultch density. However, an effort measure

does not exist for the 1997 to 2004 intermediate transplant program or the bay-season fishery pre-1996. The analyses suggest, however, that the use of cultch to retrospectively estimate catchability provides a reasonable quantitative reconstruction of survey data (Fig. 2). Subsequent time series analyses will provide additional support for this conclusion.

#### Time Series Reconstruction—Cultch Subsampling

Since 1989, a subsample of cultch has been taken from each bushel sample and re-examined for missed oysters, boxes, and spat as a measure of sorting error. Examination of these errors reveals that oysters were originally undercounted by an average of 1.1 oyster per bushel, cultch volume underestimated by an average of 0.5%, and spat undercounted by 4.7 spat per bushel. Although 1989 to 2003 samples were corrected for this degree of inaccuracy, the corrections are inconsequential. We cannot evaluate sorting efficiency prior to 1989, but presumably the data were obtained with no less accuracy.

#### Time Series Reconstruction—Spat on Cultch in Oyster Sampling

The only significant data issue, besides retrospective quantification, arises from the 1953 to 1989 practice of lumping spat on cultch with oysters in the volumetric measurements. The technique for quantification requires that spat on cultch volume be allocated to cultch volume, not oyster volume. No simple method exists to partition the cumulated volume. A simple conversion might be obtained by assuming that the ratio of the number of spat on shell to the number of spat on oysters, both data being available, equals the ratio of cultch volume to oyster volume. However, no *a priori* reason exists to expect that spat choose live oysters and shell in proportion to their volumetric contribution. Some cultch is buried. The inside valves of boxes may recruit spat disproportionately because of lower illumination or a cleaner surface (Butler 1955, Ritchie & Menzel 1969). That oyster spat preferentially settle on certain substrata is well documented (e.g., Haven et al. 1987, Soniat et al. 1991). Spat may also respond to spat already settled (Hidu 1969, Hidu et al. 1978), as do some other bivalve larvae (Peterson & Black 1993, McGrorty & Goss-Custard 1993). Thus, the validity of the primary assumption of indiscriminate setting on cultch and live oysters cannot be blithely accepted.

Consequently, we first examined the validity of the assumption that spat settle indiscriminately on live oysters and shell. On the average,  $0.9 \pm 0.15$  spat (bay average  $\pm$ SD of 20 beds) settled on an oyster for each spat on a shell (boxes were counted as two shells in summing shells) or shell fragment. This value is significantly less than 1 (*t*-test,  $P = 0.016$ ). The relationship is linear over a wide range of spat densities (Fig. 3), suggesting a slight bias for spat settlement favoring shell; however, the average surface area of a shell may be greater than the average surface area of an oyster. On the average  $1.59 \pm 0.26$  more oysters were present than shells for each unit volume of oyster or shell. The value of 1.59 is significantly greater than 1 (*t*-test,  $P < 0.0001$ ), indicating that live oysters average smaller in size than shells. The relationship was relatively consistent over a wide range of volumes and shell numbers (Fig. 4). Small oyster shells are likely not caught as efficiently by the dredge and their taphonomic decay rates must be greater than larger shells (Cummins et al. 1986b, Powell & Klinck 2007). These rates of

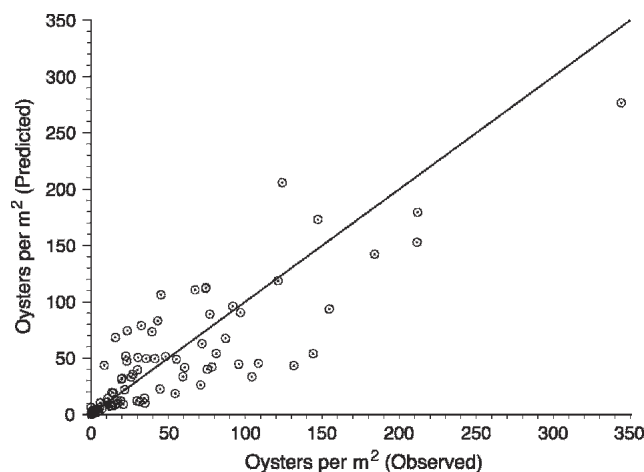


Figure 2. Comparison between oyster density during 1998–2004 obtained by direct quantification using survey catch, directly-measured swept area, and dredge efficiency for live oysters from Powell et al. (2007) with the oyster density predicted from total shell (boxes + cultch) catch, swept area predicted from total shell catch, and dredge efficiencies for boxes and cultch from Powell et al. (2007). The line marks the expected trajectory if the ratio of the two plotted variables is one.



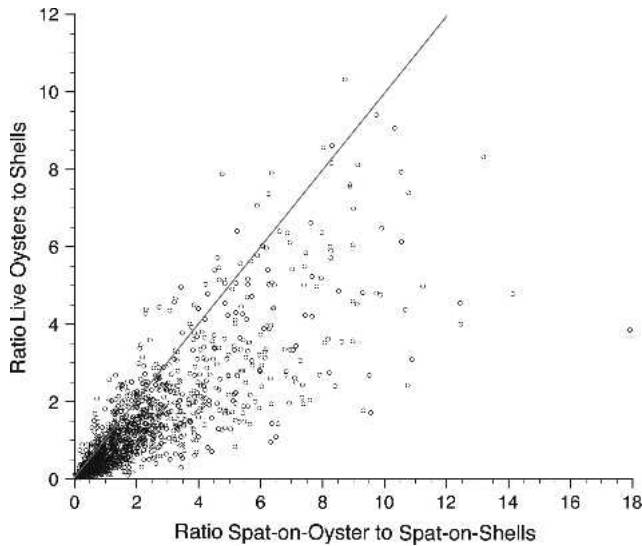


Figure 3. Comparison of the ratio of spat on live oysters to spat on shells (cultch + boxes) and the ratio of the number of live oysters to the number of shells (cultch + 2\*boxes). The line marks the expected trajectory if the ratio of the two plotted variables is one.

taphonomic decay may be substantial (Powell et al. 2006, Powell & Klinck 2007); thus shells might be expected to average larger than live oysters. Taking into account the greater abundance of live oysters per unit volume,  $1.41 \pm 0.15$  spat are found on a unit volume of live oysters for each spat found on a unit volume of shell. The value significantly exceeds 1 ( $t$ -test,  $P < 0.0001$ ), suggesting a distinct settling bias favoring live oysters.

Spatted cultch was split from a cumulated spatted cultch + oyster volume using these two relationships:

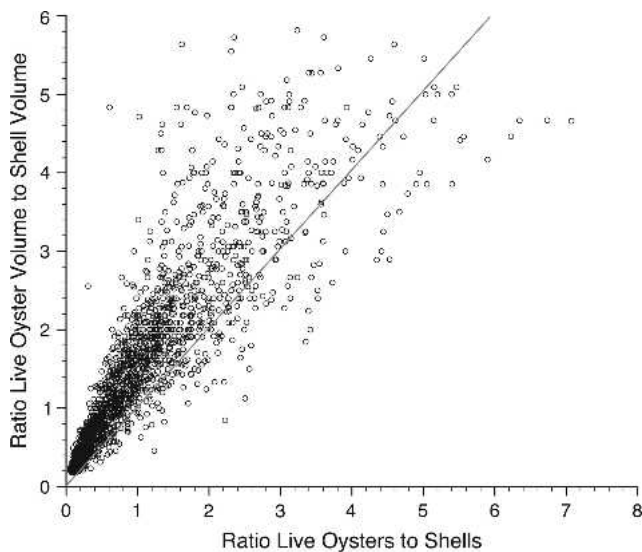


Figure 4. Comparison of the ratio of the number of live oysters to the number of shells (cultch + 2\*boxes) and the ratio of live oyster volume to shell volume (cultch + boxes). The line marks the expected trajectory if the ratio of the two plotted variables is one.

$$\frac{\# \text{ spat oysters}^{-1}}{\# \text{ spat shells}^{-1}} = \epsilon \frac{\# \text{ oysters}}{\# \text{ shells}} \quad (7)$$

and

$$\frac{\# \text{ oysters}}{\# \text{ shells}} = \epsilon \zeta \left( \frac{v_{(\text{oyster} + \text{spatted cultch})} - v_{\text{spatted cultch}}}{v_{\text{cultch}} + v_{\text{spatted cultch}}} \right) \quad (8)$$

where  $\epsilon$  and  $\zeta$  are the two correction factors, the first from Eq. (7) and the second correcting oyster and shell numbers to oyster and shell volume, and  $v$  is the bushel volume contributed by the sample constituent.

#### Time Series Reconstruction—Borrowing of Strata

The previous calculations provide an estimate of oyster and spat abundance for each sampled grid for each bed for each stratum. Stratum values are then calculated as the average of the sampled grids within a bed and year times the number of grids in that stratum on that bed. Obtaining bed, bay region, and bay tallies, however, requires that each stratum have a value in each bed for each year. (Bay-scale estimates as given herein will always be estimates for the entire stock as previously defined; namely, those oysters on the 20 natural oyster beds in the New Jersey waters of Delaware Bay shown in Figure 1.) This is not the case and tends to be less the case for surveys in earlier years. Empty strata were filled by borrowing (NEFSC 2000, 2001, 2003). Borrowing is a technique used to apply neighboring data in time and space to the estimate of unknown values. For live oysters, the following two rules applied. (1) The value assigned to the unsampled stratum was taken as the arithmetic mean of the first four borrowed numbers chosen by sequential search following a prioritized series. (2) Borrowing priorities for high-quality and medium-quality strata, listed in order, were: (a) a value for a high-quality or medium-quality stratum from the same bed and year; (b) a value for a high-quality or medium-quality stratum from a neighboring bed, taking in succession the four nearest bed neighbors; (c) a value for a high-quality or medium-quality stratum for that bed in the previous or subsequent year; and (d) a value for a high-quality or medium-quality stratum from a neighboring bed in the previous or subsequent year, taking in succession the four nearest bed neighbors. Low-quality strata were similarly filled, except that only values for other low-quality strata were used (e.g., HSRL 2006); however, these estimates will not be considered subsequently in this study. Selected examples are provided in Table 2.

Spat values were obtained for unsampled strata similarly, except borrowing was restricted to the sampling year. As a consequence, the six nearest bed neighbors were searched.

The complete dataset for the 54-y time series requires 3,240 values: 3 strata, 20 beds, and 54 y. Of these, 2,160 are high-quality or medium-quality stratal values. Of the 2,160 values required, 1,456 are present in the original dataset; the remaining 704 were borrowed. Thus, 33% of the stratal values were borrowed for the high-quality and medium-quality strata. Of the 704 borrowed stratal values, all but 10 could be filled after one round of borrowing. These few unfilled strata existed in a space-time position with relatively few temporal or spatial neighbors and so failed to obtain the necessary four borrowed values. Thus, the missing values for most medium- and high-quality strata could be estimated directly from survey data or



TABLE 2.

Examples of borrowing to fill unsampled strata for live oyster abundance. Estimated values in *italics* are obtained from the four subsequent set of borrowed values.

	Bed	Stratum	Year	#Oysters
Missing value	Arnolds	High	1960	<i>176.1</i>
Value obtained from	Arnolds	Medium	1960	112.6
	Arnolds	Medium	1959	194.9
	Arnolds	High	1959	238.0
	Upper Arnolds	Medium	1961	158.9
Missing value	Shell Rock	High	2001	<i>30.8</i>
Value obtained from	Shell Rock	Medium	2001	22.4
	Shell Rock	Medium	2000	23.9
	Shell Rock	High	2000	62.3
	Shell Rock	Medium	2001	14.7
Missing value	Round Island	Medium	1969	<i>437.6</i>
Value obtained from	Round Island	Medium	1968	144.9
	Round Island	High	1968	168.6
	Round Island	Medium	1970	689.1
	Round Island	High	1970	747.9
Missing value	New Beds	Medium	1965	<i>2.9</i>
Value obtained from	New Beds	Medium	1964	4.1
	New Beds	High	1964	2.8
	New Beds	Medium	1966	1.9
	New Beds	High	1966	2.8

with a single borrowing of values from adjacent strata and/or previous and subsequent years' samples for that stratum. After a second round of borrowing using the same sequential search, all medium- and high-quality strata were filled.

The situation with spat was more difficult because borrowing was only permitted within years. Thus, 159 of the original 718 strata remained unfilled after one round of borrowing. In the end, bay-wide mean values were imposed for a final 4 missing stratal values that could not otherwise be filled.

#### Time Series Reconstruction—Mortality Rate

Natural mortality fractions were obtained from box counts ( $bc$ ) under the assumption that

$$\# \text{ oysters}_{t-1} = \# \text{ boxes}_t + \# \text{ live oysters}_t, \quad (9)$$

hence,

$$\Phi_{bc} = \frac{\# \text{ boxes}_t}{\# \text{ boxes}_t + \# \text{ live oysters}_t}, \quad (10)$$

where  $\Phi_{bc}$  is the fraction of the individuals that died during a given year. We use the term "fraction" rather than "rate" for Eq. (10). Rates are expressed in exponentials and have units of  $\text{time}^{-1}$ .

In Delaware Bay, boxes appear to remain intact, on the average, for a little less than one year (Powell et al. 2001, Ford et al. 2006). On the other hand, dredge efficiencies suggest that some boxes may be old (Powell et al. 2007). The degree to which the two biases counterweigh is unclear; however, box counts are clearly adequate to identify significant changes in yearly mortality rates (Ford et al. 2006). We consider box counts as

the best available basis for estimating the natural mortality rate of adult oysters.

Boxes very likely do not adequately measure the mortality of juvenile animals. Juvenile shells are taphonomically more active (Cummins et al. 1986a, Cummins et al. 1986b, Powell et al. 1986, Glover & Kidwell 1993) and, thus, can be expected to remain intact for only a relatively short time. In addition, deaths of smaller animals do not leave intact boxes as often because increased predation rates include increased predation by predators that break shells (Powell et al. 1994, Alexander & Dietl 2001, Milke & Kennedy 2001). Inasmuch as the mortality rate of juvenile animals is likely to be underestimated by box counts, the fraction dying not recorded by box counts,  $\Phi_0$ , was obtained by difference:

$$\Phi_0 = \frac{(N_t - N_{t-1}) - (R_{t-1} - \Phi_{bc}N_{t-1} - \Phi_f N_{t-1})}{N_{t-1} + R_{t-1}} \quad (11)$$

where  $\Phi_f$  is the fraction taken by the fishery,  $R$  is the number of recruits into the population, and the first two terms on the right-hand side represent the difference in abundance between two consecutive surveys.

#### Time Series Reconstruction—Harvest Data

Fishing mortality was calculated as the fraction of the population present at the beginning of the year removed during that year by the fishery:

$$\Phi_f = \frac{\text{catch}_t}{N_{t-1}}. \quad (12)$$

Two fractions were calculated, apparent ( $\Phi_f$ ) and real ( $\Phi_r$ ). Prior to 1997, all removals from any bed were real removals. Prior to 1995, these animals were transplanted to downbay leases and permanently lost from the surveyed population. From 1996 on, the direct-market fishery produced the analogous effect, in that animals caught were permanent removals from the surveyed population. The intermediate transplant program that began in 1997, however, removes oysters from one bed, but places them on another. Thus, the real fraction removed by the fishery,  $\Phi_r$ , is related to the apparent fraction removed,  $\Phi_f$ , as

$$\Phi_{f_r} = \Phi_{f_t} - \frac{I_r}{N_{r,t-1}}, \quad (13)$$

where  $I_r$  is the number of individuals transplanted to the receiver bed  $r$  by intermediate transplant and

$$\Phi_{f_{dt}} = \frac{C_{dt} + I_{dt}}{N_{d,t-1}} \quad (14)$$

where  $C$  is the direct-market catch from the donor bed  $d$  and  $I_d$  represents the number of individuals removed for intermediate transplant.

Catches, for all three fisheries, are reported in bushels. A conversion to oyster number is therefore required. A direct-market bushel was assumed to contain 279 oysters (HSRL 2007). Of these, 263 are >63.5 mm in size. Since 1999, bed-specific direct counts are available for the intermediate transplant program. These estimates ranged from 295–693 oysters per bushel transplanted. The number of animals moved in 1997 and 1998 was obtained by taking bushel counts for beds after 1998 and applying them to these earlier two years. Bushel

counts for bay-season transplants were available for 1961 to 1978 and 1980. These counts ranged from 274–1,702 oysters per bushel removed, depending on bed and year. Estimates for other years were borrowed using the previously described rules.

## RESULTS AND EVALUATION OF TIME SERIES

### Abundance

Oyster abundance was high during the 1970s through 1985, low prior to 1969, and low since 1985 (Fig. 5). MSX became epizootic in Delaware Bay in 1957 and Dermo in 1990 (Ford & Haskin 1982, Cook et al. 1998, Ford et al. 1999).

In the earliest years of the 1950s, as in the late 1970s and early 1980s, oysters were distributed more evenly throughout the low-, medium-, and high-mortality beds; in the former case, in low abundance. The pre-1957 period is the only period of low abundance so characterized in the time series (Fig. 6). The 1970 to 1984 period was characterized by high abundances throughout the bay. The high-mortality beds and the low-mortality beds (Table 1) had unusually high abundances during this period (Fig. 5), with the low-mortality beds contributing a greater proportion of the population as time progressed. Since 1953, the medium-mortality beds have contributed, on the average, 44.4% of the stock, with a median of 41.7% (Fig. 7). Prior to the onset of MSX, the proportion of the stock on these beds fell below the 54-y median. Beginning in 1957, and extending through 1978, the fraction of the stock on the medium-mortality beds fell above the long-term median in 15 of 22 y. From 1978 until 1995, the medium-mortality beds contributed less than the long-term median fraction to the stock. The initial increase in total abundance in 1970 did not coincide with the change in

stock distribution that occurred 8 y later in 1978. The dramatic increase in the proportion of the stock on these beds after 1995 occurred five years after the onset of Dermo in 1990 and nearly 10 y after the crash in total abundance in 1985–1986.

Substantial changes in abundance over a 1-y period occurred rarely (Fig. 8). The greatest increases in abundance occurred in 1959 (this is likely a survey artifact), 1970, 1973, and 1979. Greatest declines occurred in 1960 (this is likely a survey artifact), 1975, and 1985. Proportional one-year changes indicate greater volatility relative to start-of-year abundance, particularly early in the time series (Fig. 8). This is likely a symptom of lesser survey precision, as navigational accuracy has increased substantively over the 54-y period. The number of declines outnumbers the number of expansions by 29 to 24. This allotment can readily be obtained by chance (binomial test,  $P > 0.10$ ). During the post-1988 period, oyster abundance declined in 10 of 17 y. This rate of occurrence is also no different than expected by chance (binomial test,  $P > 0.10$ ). Over 54 y, a large two-year expansion has occurred only once, 1969 to 1970. Proportional changes exceed 0.6 in both years. Since 1953, a large decline in abundance has occurred thrice. The 1960 event is likely a survey artifact imposed by the aberrant survey index of 1959. The 1975 event follows a record recruitment in 1972 and marks the failure of most of this recruitment to influence abundance more than a few years thereafter. Only the 1985 event had a long-term impact on the stock. This was an MSX epizootic.

### Recruitment

The recruitment time series is dominated by the 1972 set (Fig. 9); however, recruitment was relatively good in most years

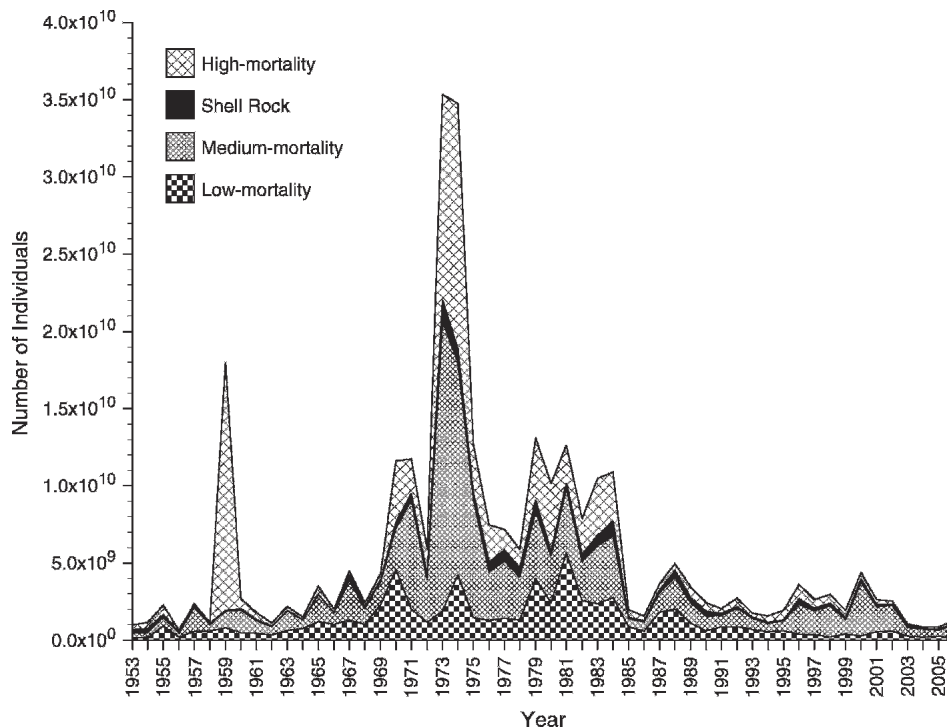


Figure 5. Time series of oyster abundance for the New Jersey oyster beds in Delaware Bay, by bay region. Each shaded region represents that region's contribution to total stock abundance, the summation being the cumulative value. Bed groups are defined in Table 1. Bed locations are shown in Figure 1. The value for 1959 is likely a survey artifact.

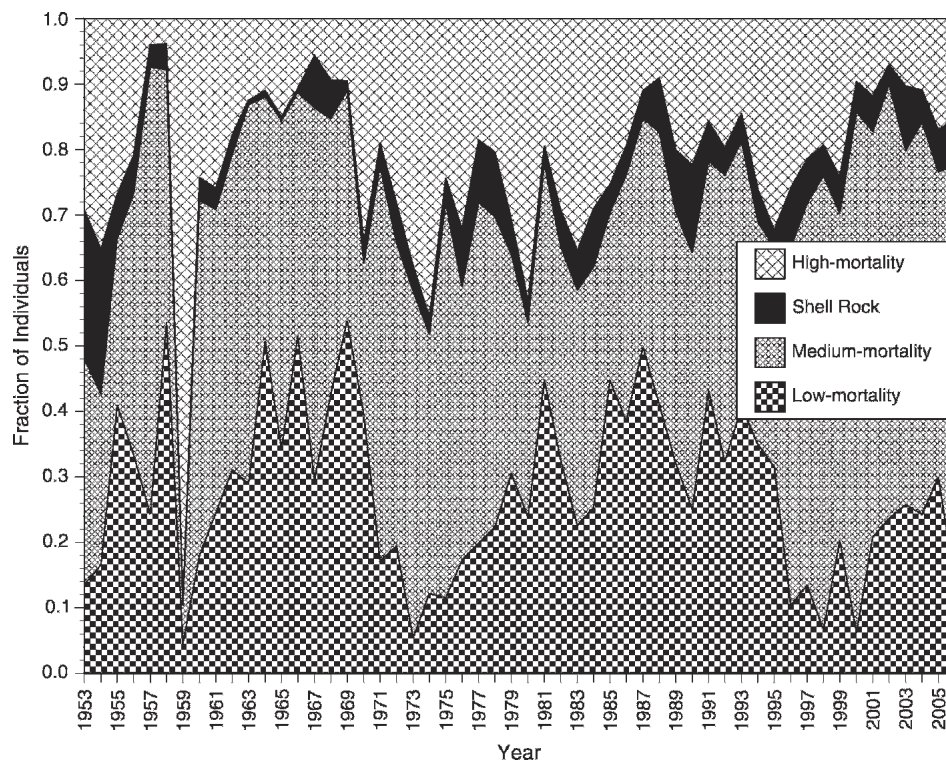


Figure 6. Time series of the fractional distribution of oyster abundance for the New Jersey oyster beds in Delaware Bay, among bay regions. Bed distributions by region are given in Table 1. Unusual values for 1959 are a survey artifact.

from 1964 through 1986. Prior to 1964 and subsequent to 1991, recruitment was relatively low, with the exception of the 1997 to 1999 time period. Since 2000, recruitment has been at near-historical lows. The ratio of spat to 1+-yr animals has exceeded

a ratio of 1 in 15 of the 54 y (Fig. 10). A value above 0.5 has occurred in 31 of 54 y. Values exceeding 1 were common in two time periods, 1962 to 1972 and 1986 to 1999. Only three such values exist in the high-abundance period 1970 to 1984. Values

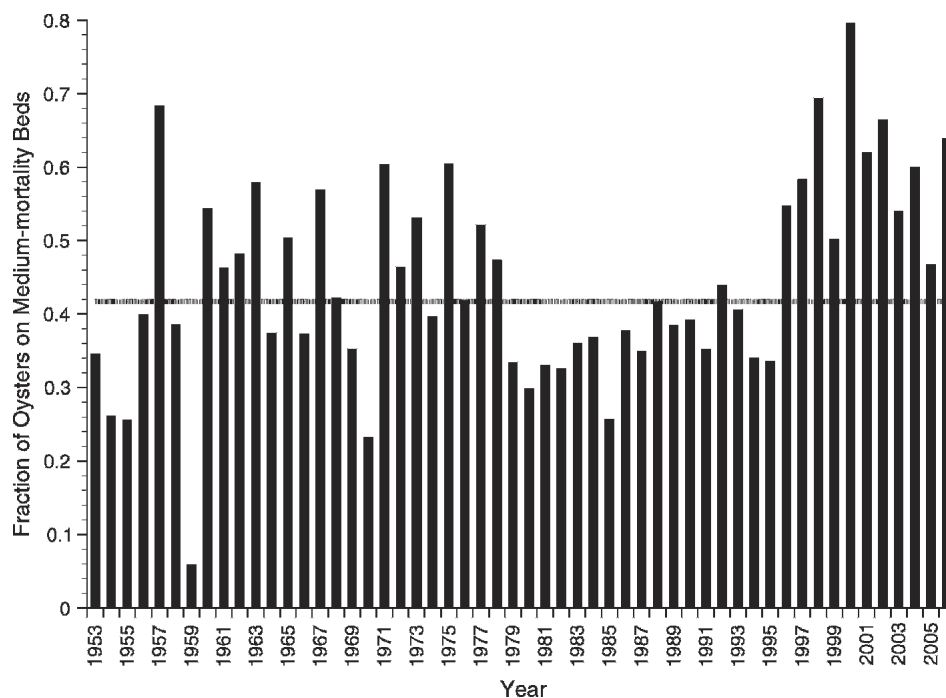


Figure 7. The fraction of the total oyster stock, by number, on the medium-mortality beds. The horizontal bar represents the 54-y median of 0.417. See Table 1 for bed groups.

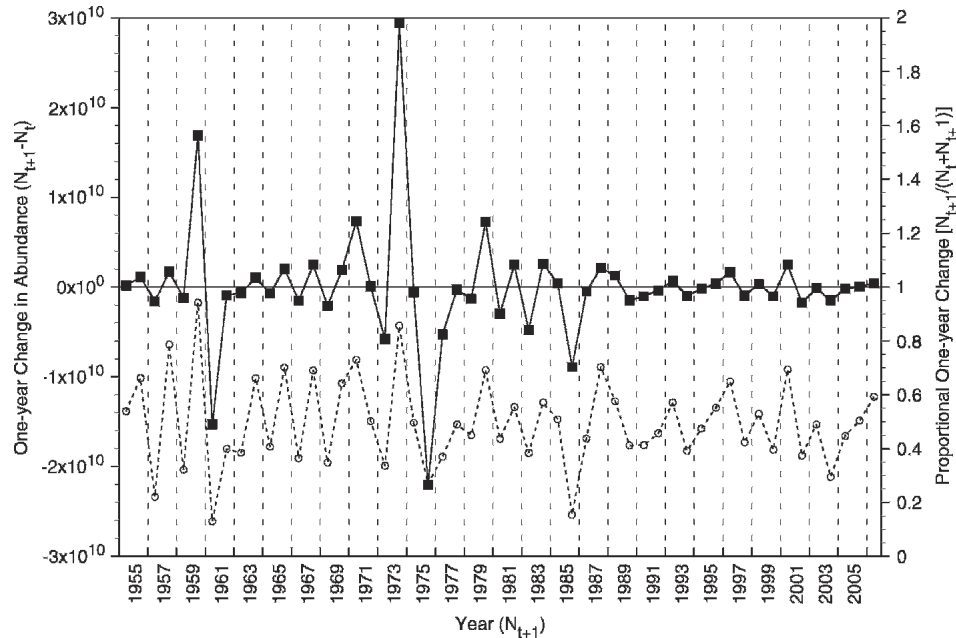


Figure 8. Solid line: Year-to-year trends in oyster abundance for the New Jersey oyster beds in Delaware Bay, estimated by the one-year change in live oyster abundance ( $N_{t+1} - N_t$ ). Dotted line: Succeeding year oyster abundance relative to the abundance for both years using the ratio estimator:  $(N_{t+1}) / (N_{t+1} + N_t)$ . A value of 0.5 indicates that abundance did not change between years. Values of 0.45–0.55 bracket ~20% changes; 0.4–0.6, 33% changes; 0.2–0.8, 50% changes.

exceeding 0.5 have been relatively frequent throughout the time series except since 1999. Only a single year has seen a recruitment event that exceeded 0.5 recruits per 1+-yr animals in the 2000s.

Trends have varied substantially between bay regions. The high-mortality beds have received a set exceeding 1 recruit per

1+-yr individual 21 times in 54 y, whereas the equivalent event has occurred only 10 times on the low-mortality beds (Fig. 11). A recruitment event of this magnitude has not occurred on the low-mortality beds since 1986, a 20-y period. Large recruitment events have occurred periodically on the medium-mortality beds with such events being commonplace between 1962 and

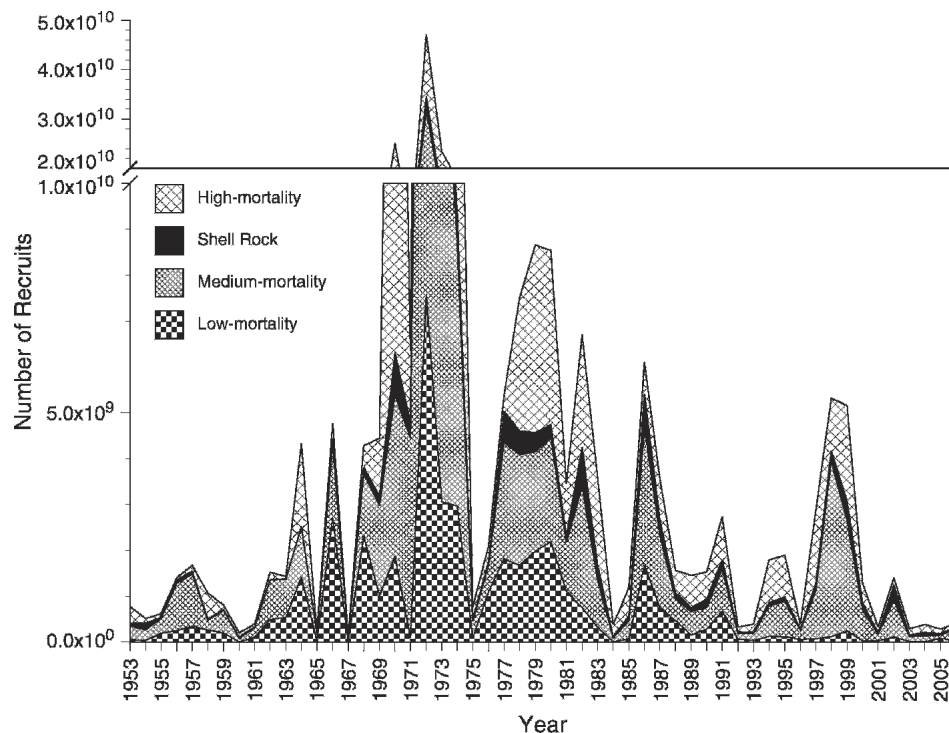


Figure 9. Number of spat recruiting per year for the 1953–2006 time series, by bay region. Each shaded region represents that region's contribution to total stock recruitment, the summation being the cumulative value. Bay regions are defined in Table 1.



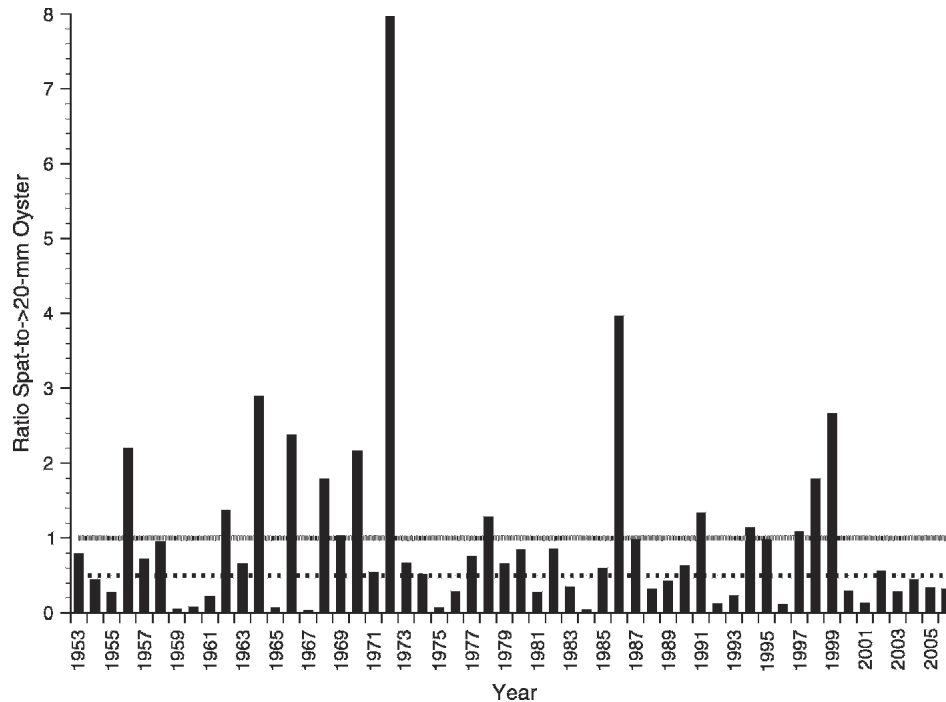


Figure 10. The number of spat recruiting per >20-mm oyster per year for the New Jersey oyster beds in Delaware Bay. Solid and dashed lines mark the 1.0 and 0.5 ratio boundaries, respectively.

1972 and 1986 through 1999. The same general trend exists for the high-mortality beds; however, these beds are characterized by events of this scale as well between 1972 and 1986 and post-1999. The high-mortality beds are also unique in that the likelihood of a recruitment event exceeding 0.5 recruits per 1+-yr animals was higher in the post-1989 time period after the onset of Dermo in comparison with the 1950s, whereas the opposite was true for the medium-mortality beds.

#### Fishing

Early in the time series, the bay-season fishery routinely removed 10% to 20% or more of the oysters yearly from the high-quality and medium-quality strata (Fig. 12). This high per-year fishing rate was compensated for by closure of the beds that occurred almost every other year through 1965, so that biannual fishing mortality was about half the yearly values. The early 1950s' concern about overfishing was responsible for the beginning of the survey and our retrospective estimates of high rates of fishing mortality agree with estimates of Harold Haskin in laboratory notes of that period retained in laboratory archives. This level of fishing declined during the 1970s and early 1980s except for 1979, peaked again in 1991, and was just under 5% in the last year of the bay-season fishery, 1995. Because the direct-market fishery began in 1996, the highest apparent catch occurred in 2004, 5.2%, but some of this catch was contributed by the intermediate transplant program. The highest real catch was 1.8% of the standing stock on the high-quality and medium-quality strata, in 2004 and 2006.

The beds have not routinely contributed the same fraction to the fishery (Fig. 13). Prior to 1970, most oysters landed after transplant to downbay leases by the bay-season fishery originated from the medium-mortality beds. During the 1970s and

early 1980s, the high-mortality beds contributed the bulk of the landings, albeit indirectly after transplant to leases downbay. This trend continued into 1995. Oysters for the direct-market fishery conducted since 1996 have come primarily from the medium-mortality beds, partly because of the intermediate transplant program that has moved oysters downbay to Shell Rock and the high-mortality beds from which they were subsequently harvested. Most of the oysters removed by the direct-market fishery have been fished from Shell Rock and the high-mortality beds. With the exception of 2004, the low-mortality beds have not contributed substantively to the bay fishery since the late 1960s.

#### Mortality

Annual mortality was estimated from box counts for the population as a whole and for each of the four bay regions. For the population as a whole, mortality typically fell above 10% of the stock after the onset of MSX in 1957 until after the 1966 epizootic (Fig. 14). For nearly a score of years succeeding this event, mortality rarely rose as high as 15% of the stock. Mortality fraction notably dropped several years prior to the stock abundance increase of 1970. The 1985 to 1986 MSX epizootic remains a unique event, reaching 47% of the stock in 1985. Another 36% succumbed in 1986. Since the onset of Dermo disease in 1990, annual mortality of the entire stock has never fallen to 10% and has generally exceeded 15%. Mortalities have exceeded 20% in 8 of 16 y post-1989, a record not observed previously. Interestingly, mortalities have averaged lower since 2002.

Regional divisions reveal that the low-mortality beds have often maintained a pattern of mortality distinct from the remainder of the bay (Fig. 15). Increased episodes of mortality

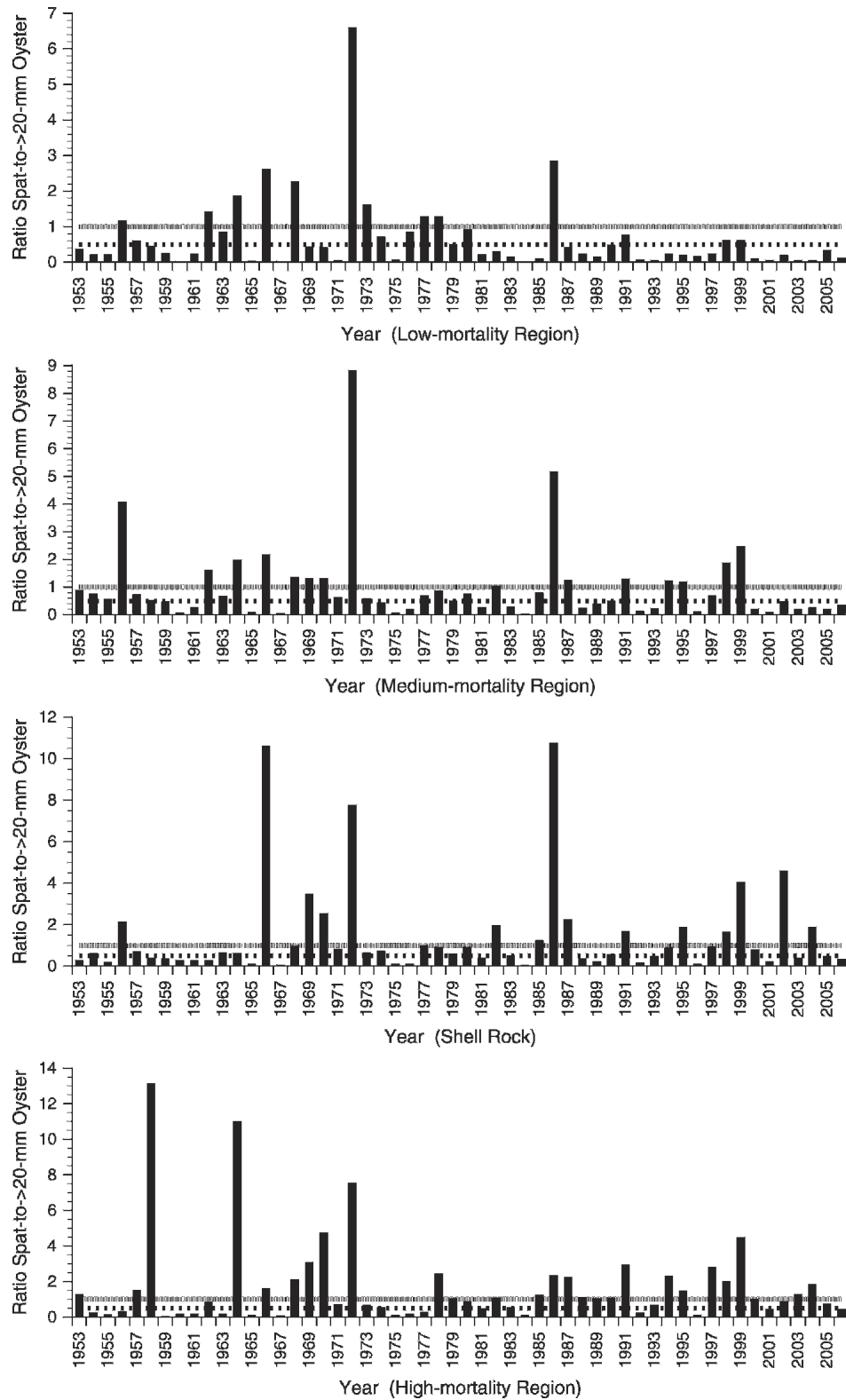


Figure 11. The number of oyster spat recruiting per  $\geq 20$ -mm oyster per year by bay section. Bay sections are defined in Table 1. Solid and dashed lines mark the 1.0 and 0.5 ratio boundaries, respectively.

upbay in 1956, 1961, 1971, and 1972 likely mark low-salinity kills. The 1956 event resulted from high Delaware River flow in August–November, 1955, produced by the passage of two hurricanes. The 1971 to 1972 event stems from high river flows

from December to April, 1971, followed by passage of Hurricane *Agnes* in 1972 (Boesch et al. 1976). The event in 1985 to 1986 is different in that it coincided with the MSX epizootic that occurred throughout the bay at that time. During periods of

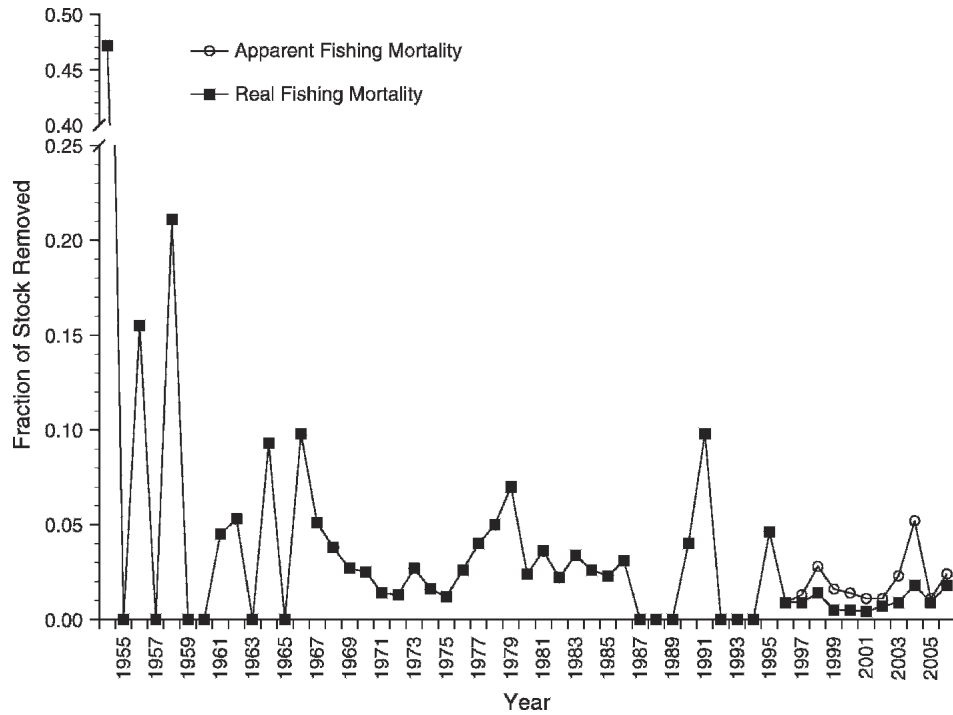


Figure 12. Fishing mortality rates during the 1953–2006 time period on the New Jersey oyster beds in Delaware Bay. The total stock manipulation since 1996, including intermediate transplant and direct-market, is identified as the apparent rate; those oysters landed are identified as the real rate. Prior to 1996, all oysters were permanently removed from the stock and thus only 'real' removals occurred. Zeros represent years of fishery closure.

relatively low-mortality, prior to the onset of MSX in 1957 and during the 1967–1984 time period, the bay regions were characterized by relatively equivalent mortality rates (Fig. 15). MSX and Dermo disease epizootics typically raised the mor-

tality rates disproportionately downbay. The mid-1960s mortality event was an MSX epizootic likely triggered by the mid-1960s drought and increased downbay mortality fractions above 30%. The largest mortality event in the time series, an MSX

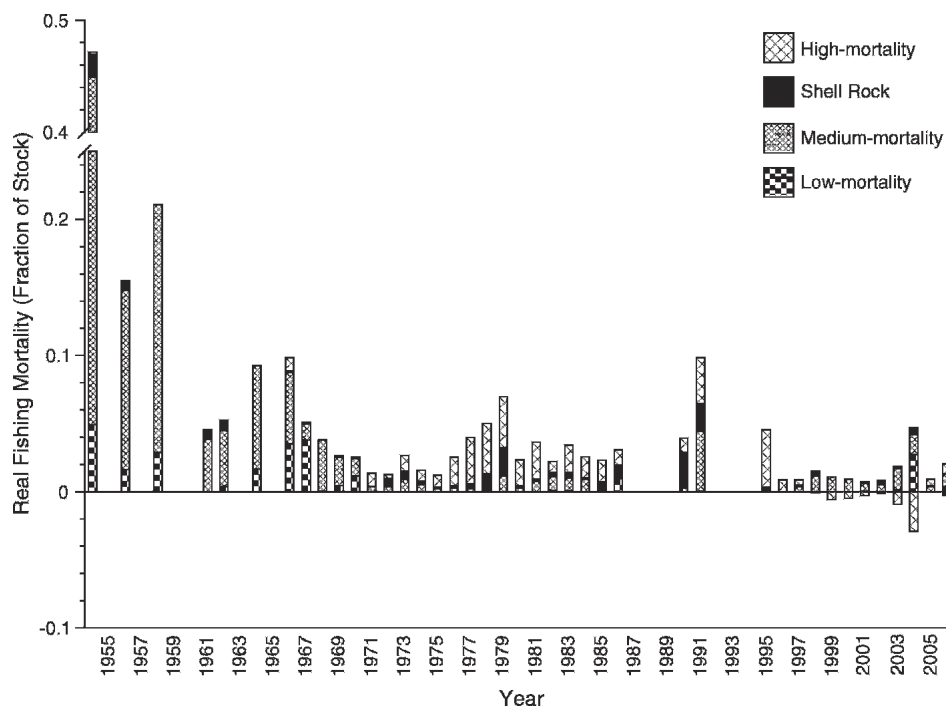


Figure 13. The distribution of catch among bay sections. Negative rates represent occurrences when more animals were transplanted to a bay region than removed. Zeros represent years of fishery closure.

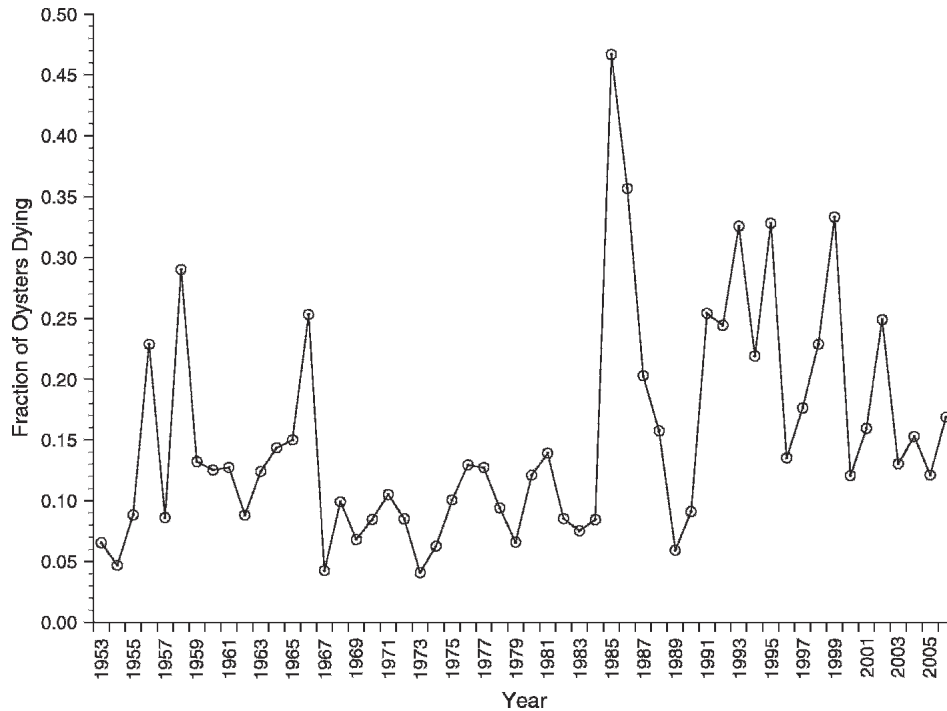


Figure 14. The fraction of animals naturally dying each year in the oyster population in the New Jersey waters of Delaware Bay.

epizootic, occurred in 1985 to 1986 and this epizootic was unique in increasing mortality throughout all four bay regions. Mortality rose again with the incursion of Dermo in 1990 and has remained above 20% for most years since that time. During this time frame, as earlier in the 1960s, oysters in the downbay regions suffered a disproportionate increase in mortality (Fig. 15).

Stock-wide estimates of mortality are controlled as much by the distribution of animals among the bay regions as by the regional mortality rates. Thus, a high mortality rate in a region with low abundance will contribute little to the total number of deaths in the population. To a degree, deaths on the low-mortality beds as a proportion of cumulative bay oyster mortality have remained relatively constant since 1953. Prior to

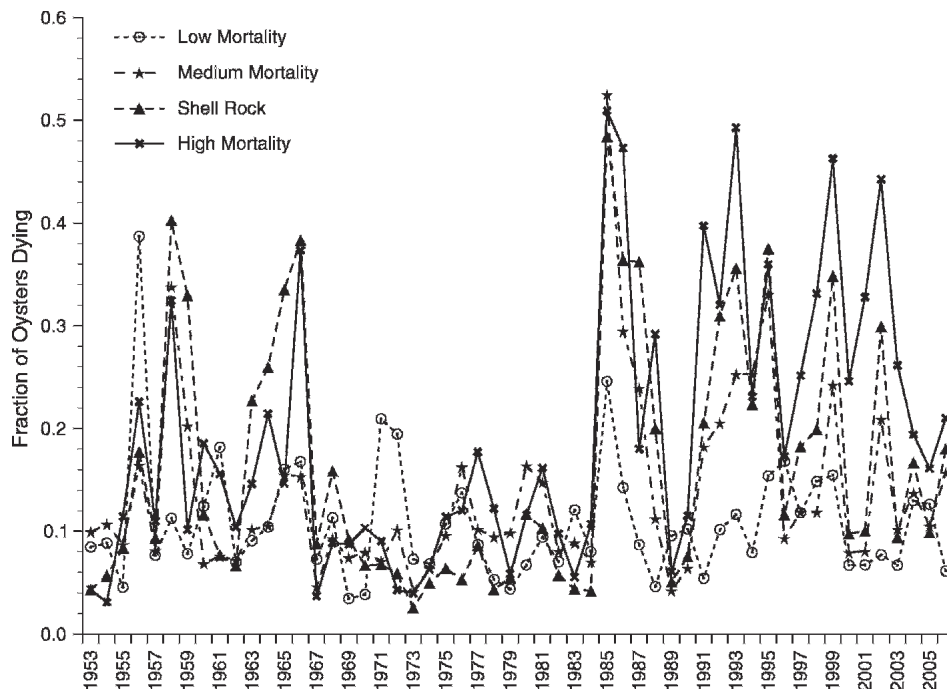


Figure 15. The fraction of animals naturally dying each year for each bay section, as measured by box counts. The fraction dying is estimated for each bay section based upon the number of oysters and boxes in that section.



1960, the greatest number of deaths occurred on the medium-mortality and low-mortality beds (Fig. 16) because the greatest concentrations of oysters were on these beds, even though the fraction dying on those beds relative to the number living there was lower in many years than on the high-mortality beds (Fig. 15). During much of the 1960s, the deaths on the high-mortality beds contributed most to the population total number of deaths even though more of the stock was concentrated on the medium-mortality beds (Fig. 5). During the 1970 to 1984 period of high abundance, the oysters on the high- and medium-mortality beds contributed the bulk of the animals dying naturally—that is, by means other than fishing—because of the larger numbers present on these beds and because natural mortality was not substantially higher on the beds farther downbay. The decline in abundance that occurred in 1985 and the subsequent shift in population distribution to proportionately higher abundances on the medium-mortality beds occurred in part because the fraction of total deaths contributed by animals on the high-mortality beds increased. This shift began in MSX years and continued after the incursion of Dermo. In the first decade after the onset of Dermo, the high-mortality beds routinely matched or exceeded the medium-mortality beds in the number of oysters dying despite lower abundance (Figs. 7 and 16). Toward the end of the time series, as abundance fell to even lower levels on the high-mortality beds, relative to the medium-mortality beds, animals on the medium-mortality beds again began to contribute the majority of the deaths in the population, as they had during the late 1950s and late 1970s; however, the high degree of contribution since 2000 is unusual in comparison with the remainder of the time series.

The fraction of total deaths contributed by animals on the high-mortality beds has a long-term median of 0.48 (Fig. 17). That is, in about half of the years, half or more of the total oyster deaths in the population were contributed by the portion of the population in this bay region. The fraction contributed falls below the median in three periods. Prior to 1960, before and during the initial phases of the 1950s' MSX epizootic, more of the animals dying came from regions upbay of these beds. During the 1970 to 1984 high-abundance period, the fraction of deaths contributed by animals on the high-mortality beds fell above the median in only 5 of 15 y. Thus, in most of these years, animals on the medium- and low-mortality beds contributed a disproportionate share to total population mortality. Since 2001, animals on the high-mortality beds have persistently contributed a lower fraction of total deaths in the population than the 54-y median (Fig. 17).

#### Unrecorded Mortality

On the average, the abundance in any year should equal the abundance in the prior year decremented by the landings and box-count mortalities and incremented by recruitment. In most years, this calculation does not balance, and, in fact, yields a negative value (Fig. 18). The average offset is equivalent to an unrecorded fraction of mortality of 27.4%, excluding the 1959 outlier. The imbalance in inputs and losses documents an otherwise unmeasured loss. The obvious outlier, 1959, likely records a bias in the sampling program in that year.

Most of this additional mortality unmeasured by box counts is likely juveniles dying in their first year or two of life, most through predatory means. Drills, crabs, and *Stylochus*

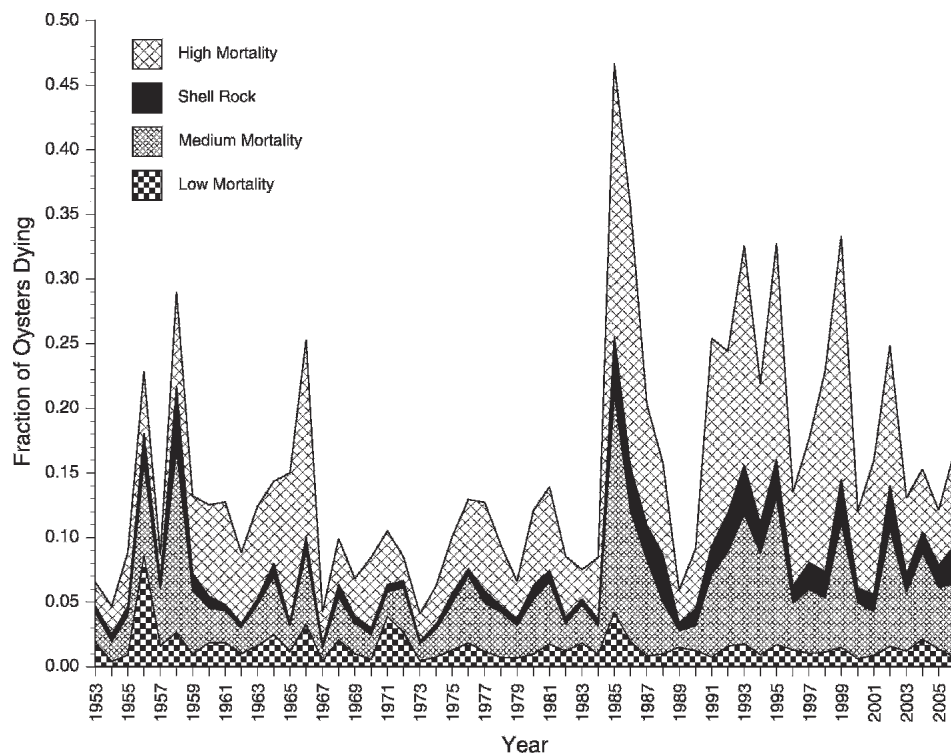


Figure 16. The distribution among bay sections of animals >20 mm dying naturally as measured by box counts, in terms of the cumulative fraction dying. The cumulative fraction of the population matches the stock value given in Figure 14. The proportion of deaths contributed by each bay section represents the contribution of the population in that bay section to mortality in the total population (Figure 14).

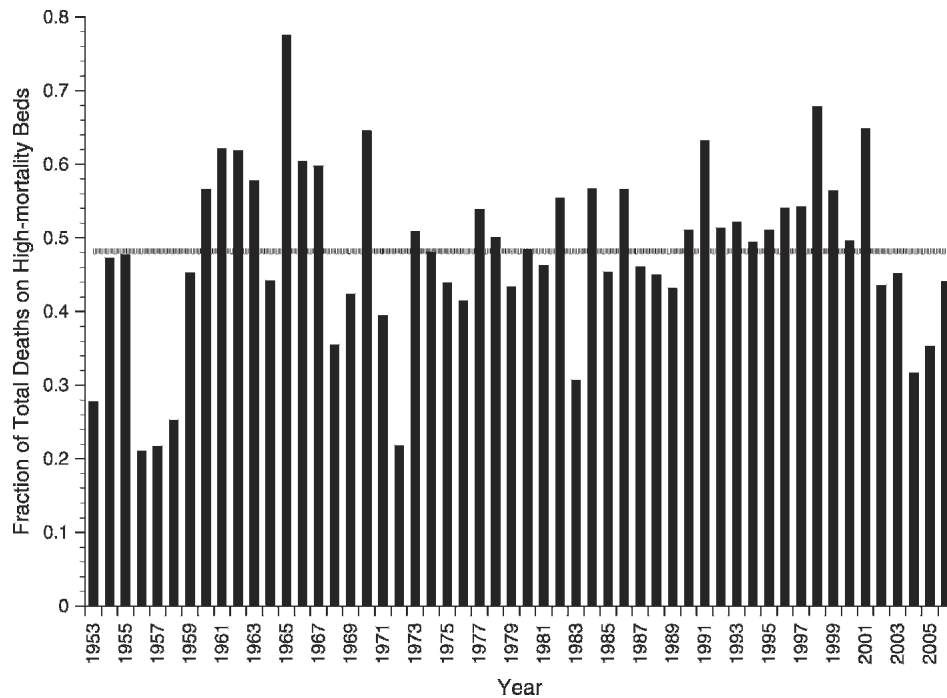


Figure 17. The fraction of total deaths in the population contributed by the population component on the high-mortality beds. See Table 1 for bed groups. The horizontal bar represents the 54-y median fraction of 0.482.

turbellarians are all active predators in Delaware Bay (Stauber 1943, McDermott & Flower 1952, Maurer & Watling 1973, Ismail 1985) and likely do not leave boxes behind when they die or leave behind boxes of small individuals that rapidly disarticulate. Applying this assumption, juvenile mortality normally would vary between 50% and 100% of the set, with a 54-y average of 90.0%. This is not an unrealistic estimate based on known mortality rates for juvenile bivalves (Powell et al. 1984, Osman et al. 1989). One-year survival of spat can be directly calculated for the period 1953 to 1988 when yearling numbers were recorded as part of the survey. The mean yearling-to-spat ratio is 0.371 rather than 0.100, indicating that some portion of the unrecorded mortality is contributed by older animals that either do not leave boxes behind when they die or contribute boxes that rapidly disarticulate after death; however, the bulk of this mortality can still be explained by the higher rate of death of animals in their first year of life.

## DISCUSSION

### *Trends in Abundance and Putative Regime Shifts*

The most dominant trend in the 54-y time series of oyster abundance in Delaware Bay is the increment in abundance in 1970 and the decrement in 1985. These two events bound a multidecadal period of low abundance prior to 1970, a 16-y period of high abundance between 1970 and 1985, and a multidecadal period of low abundance subsequently. Such discontinuities bounding periods of population stability have recently been referred to as regime shifts (Collie et al. 2004, Rothschild & Shannon 2004). Increasingly, these transitions are recognized as an important long-term component of population variation (e.g., Botsford 1981, Steele & Henderson 1984, Ware

2000, Jackson et al. 2001, Choi et al. 2004, Collie et al. 2004, Breitburg & Fulford 2006). Inherent in the alternate stable state hypothesis is the premise that such states are self-reinforcing for protracted periods of time and bounded by catastrophic shifts, oft-proposed as products of climatic change. The time periods delineated by these two shifts in abundance in Delaware Bay have attributes of alternate stable states (*sensu* Gray 1977, Peterson 1984, Knowlton 2004). They are multigenerational and demonstrably not of anthropogenic origin (see Knowlton 2004), as the fishing mortalities have been much below the natural mortalities over much of this time. [We recognize that the earlier introduction of MSX (Bureson et al. 2000) that subsequently played a critical role in the 1985 regime shift, likely was anthropogenic.] The intervening periods are persistent and transcend a range of climatology (Soniati et al. in press).

The influence of climate change has received increasing attention as an important driver of long-term changes in fish and shellfish populations (e.g., Kim & Powell 1998, Powell et al. 1992, Attrill & Power 2002, Choi et al. 2004, Oviatt 2004, Valero et al. 2004, Zuur & Pierce 2004, Soniat et al. 2006), but application of the concept of regime shifts principally has been applied in the interpretation of long-term variations in finfish population dynamics. One reason for this is the likely association between disease epizootics and extreme transitions in abundance in shellfish. Periods of rapid change in abundance are often associated with epizootics in animal populations (e.g., Mangel & Tier 1994, Young 1994, Boero 1996, Harvell et al. 1999), including shellfish, but regime shifts are most often associated with changes in abundance of more subtle or mysterious origin. Well-documented exceptions exist, however, where large-scale catastrophic changes in shellfish abundance are not associated with a disease process (e.g., Weinberg et al. 2002, Kim & Powell 2004). Moreover, disease as an instigator of

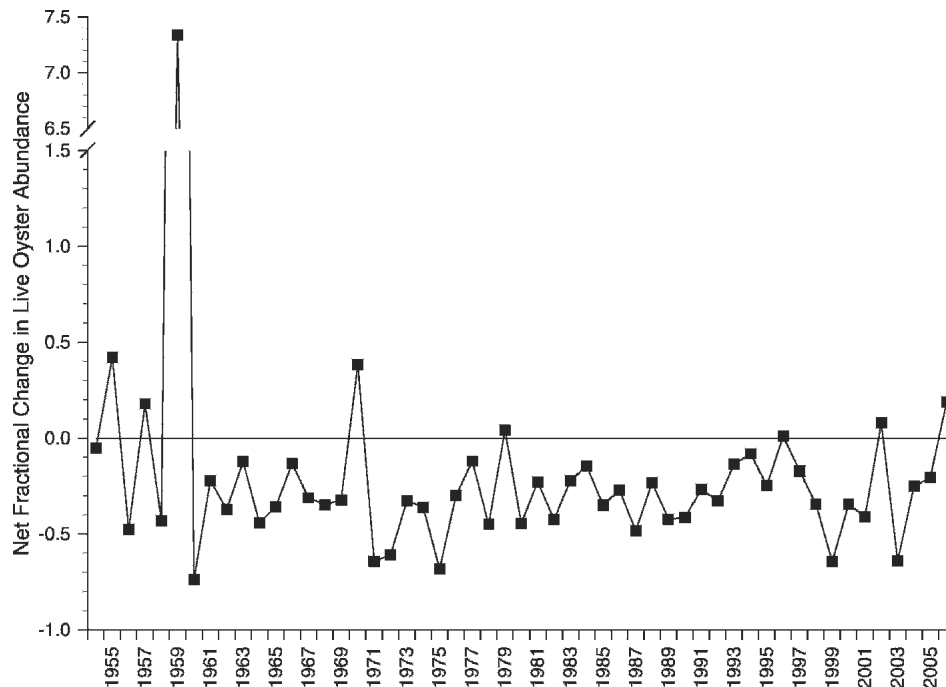


Figure 18. The ratio of the degree of change in population abundance unrecorded by box counts, catch, and recruitment to the abundance present at the beginning of the year, including the recruits. A negative value is equivalent to an unrecorded mortality removing this fraction of the population during the year. The value for 1959 is likely a survey artifact.

regime shifts perhaps should be more explored, as most disease models inherently produce multiple stable states (e.g., Kermack & McKendrick 1991, Godfray & Briggs 1995)—this is the basis for parasite control of pests (e.g., Reeve & Murdoch 1985, McCallum & Singleton 1989, Jaenike 1998)—and most diseases can mediate the influence of climate change on host population abundance just as do other biological processes, such as the timing of reproduction (Cushing & Dickson 1976) and changes in food supply (Kim & Powell 2004, Richardson & Schoeman 2004).

The 1970 to 1984 high-abundance period occurred despite the presence of MSX disease. This period of high oyster abundance encompasses a period of high abundance in a number of other species of commercial importance (Gabriel 1992, Link et al. 2002), including many finfish species in the Gulf of Maine and Mid-Atlantic Bight, as well as hard clams along the Long Island coast (Kraeuter et al. 2005, Hofmann et al. 2006), and *Illex* squid off Newfoundland (Dawe et al. 2000). In many of these cases, the 1970s high abundance was rapidly impacted by overfishing (e.g., Kraeuter et al. in press), thus artificially limiting its duration. This did not occur in the Delaware Bay. In other cases, the abundance high began a few years after 1970 rather than at the start of the decade (e.g., Dawe et al. 2000). However, the coincidence of bay and shelf species, temperate and boreal, bespeaks of a large-scale climatic event that influenced the bulk of the northeast region of the U.S. coastline. Soniat et al. (in press) examined the influence of specific climatic phenomena on the Delaware Bay oyster. Chief in importance was the North Atlantic Oscillation (NAO) that influences primarily temperature (Soniat et al. in press; see also Sutton & Hodson 2003, Hurrell & van Loon 1997, Hurrell et al. 2003). Soniat et al. (in press) identified 4 and 8-y cycles in the Delaware Bay time series correlated with shifts in NAO and related to changes in temperature, as

well as a 4-y signal related to salinity that was independent of the NAO. Notaro et al. (2006) implicates the Pacific North American (PNA) teleconnection in modulating precipitation in the Delaware River watershed. The years 1970 to 1985 coincide with a cold period in the northern North Atlantic (Reverdin et al. 1997), a transition period in the NAO (Hurrell et al. 2003), and the beginning of a cool phase in the Atlantic Multidecadal Oscillation (AMO) (Enfield et al. 2001, McCabe et al. 2004).

The proximate factor initiating the post-1984 low-abundance period was a true extreme event (*sensu* Taylor 1934) in the form of a bay-wide MSX epizootic. This was a unique event in that it raised mortality rates throughout the bay, including on the low-mortality beds (Fig. 15). Soniat et al. (in press) showed that this event was likely the product of a unique confluence of the 4-y temperature and salinity cycles initiated by a unique phase shift in the former. Such a climatic event is unrecorded in the remainder of the 54-y time series. However, the 1985 event was not a typical epizootic, in that the population did not recover in abundance after the event. Thus, the 1985 event was put in motion by disease, triggered by unique climatic conditions, but it yielded a persistent stable state of lower abundance and thus conforms to the general model of a regime shift. Whether this outcome would have occurred without the onset of Dermo in 1990 that likely abetted a continued restriction in abundance cannot be known. The factors inducing the increase in abundance in 1970 are less well understood, although its origin in the AMO and/or NAO seems likely. As will be discussed subsequently, factors initiating this shift began in 1967 immediately after the drought of record within the time frame of the Delaware Bay time series, but preceded a period of above average freshwater inflow and warmer temperatures just after the decadal ascension.

The dynamics within the oyster population during the three periods of apparent relative stability in abundance is also interesting (Fig. 5). During each of these periods, substantial shifts in distribution occurred within the population that potentially increased the population's sensitivity to climatic assault. It is noteworthy, for example, that the mid-1960s drought did not initiate a dramatic decline in abundance as did the mid-1980s drought, though more severe climatically. It is also noteworthy that the stock expansion of 1970 was preceded by three consecutive years of relatively good recruitment, as was the 1997 to 1999 period, yet the latter did not lead to an equivalent stock expansion and the abundance high of 1970 to 1985 was maintained by a series of solid, but unremarkable, years of recruitment that were sustained through many generations. Thus the initiation of regime shifts may not be purely climatological and the abetting agents not solely disease. Furthermore, the stable states may not be because of constancy (*sensu* Stearns, 1981) in population dynamics.

#### *Population Dispersion and The Influence of Disease*

Neither the onset of MSX nor the advent of Dermo is well documented by a shift in abundance (Fig. 5). The well-documented decline in the oyster fishery brought on by MSX in the late 1950s (Ford & Haskin 1988, Ford et al. 1995, Ford 1997) was primarily caused by loss of oysters downbay of the natural beds, on leased grounds maintained in production by active farming practices of the industry (Ford 1997, Powell et al. 1997, Kraeuter et al. 2003). Neither is the onset of either disease associated with a shift in distribution of the stock, yet proportional increases and decreases in abundance on the medium-mortality beds occur periodically and nevertheless are persistent, though out of phase with the regime shifts exposed by the time series of population abundance. It is the dispersion and contraction of the Delaware Bay population that offers explanation for the apparent stability of the population abundance throughout most of the time series and, perhaps, modulates the sensitivity of the population to catastrophic shifts in abundance that occurred twice during the 54-y record.

#### **The Pre-1970 Period of Low Abundance**

For the four years of record prior to 1957, the Delaware Bay oyster population was characterized by an unremarkable rate of recruitment (Fig. 10), relatively low natural mortality (Fig. 14), and a spatial distribution in which the fraction of the stock on the medium-mortality beds was relatively low in comparison with the 54-y median (Fig. 7). The dispersion of the stock was likely maintained by overfishing, as the bay-season fishery dominantly targeted the medium-mortality beds during this time (Fig. 13). Although only speculative, given that the natural mortality rates averaged below 10% during this period and the fishing rates routinely exceeded 10%, it is likely that had fishing rates typical of later years in the time series been in vogue at that time, a much more contracted stock distribution would have been present produced by a proportionately higher abundance on the medium-mortality beds.

MSX entered the picture circa 1957 with the following consequences. Abundance on the natural beds was little affected. This was in part achieved by the implementation of the 40% rule during this time frame that commensurately curtailed overfishing. The highest fishing mortality rate ob-

served post-1958 was about 10% of the stock. By circa-1960, the effect of an increase in natural mortality, on the order of 5% to 10% of the stock, had been ameliorated by a decrease in fishing mortality at least that large. From 1957 through 1966, natural mortality neared 15% of the stock in most years with fractions exceeding 20% in two. Mortality substantively increased downbay, and, by 1960, animals on the high-mortality beds were contributing a disproportionate share of total mortality to the population. As a consequence of this differential mortality, the population contracted. During the 1960s, the medium-mortality beds contributed more than the long-term median to the total stock in 8 of 10 years (Fig. 7). Although the fishery continued to target these beds (Fig. 13), the reduction in total removals minimized the influence of the fishery on the stock.

Thus, stock stability in the MSX era pre-1970 was achieved first by a trade-off between natural and fishing mortality and second by a contraction of the stock that limited total population mortality. Although the change in stock dispersion is not manifested in a change in stock range, as in range shifts, it is the upbay and downbay margins of the stock that are most susceptible to variability in stock abundance in Delaware Bay. This phenomenon is a well-described characteristic of populations existing over a broad environmental gradient (e.g., Svensson et al. 2005, Guo et al. 2005, Holt et al. 2005). The medium-mortality beds, by being less susceptible to the many mortality factors coincident with higher salinities, such as predation and disease, yet also insulated from the influence of freshets, represent the refuge habitat for oysters in Delaware Bay.

#### **The 1970 Population Expansion**

In 1970, population abundance expanded by more than a factor of three and this high level of abundance was maintained for the succeeding 15 y. Three noteworthy events preceded this expansion. First, the period 1968 to 1970 was noteworthy in producing three successive years of relatively high recruitment (Fig. 10). Only one other similar three-year period exists in the time series, 1997 to 1999. Secondly, the three consecutive years of relatively high recruitment occurred in three of four bay regions [medium-mortality, Shell Rock, and high-mortality (Fig. 11)]. No equivalent coincidence of years and coverage occurs in the time series. Third, beginning in 1967, natural mortality dropped below 10% and remained at or below this level through 1975. This drop followed the largest MSX epizootic of the 1960s. The dramatic shift in mortality pattern is reminiscent of the 1985 to 1990 time period, though the scale of effect is much muted with respect to the latter. The coincidence of dramatically lower natural mortality and a triplex of high recruitment years is unique in the time series and certainly provides the proximate conditions for the population expansion of 1970, but the single largest recruitment event, in 1972, did not substantively influence the population dynamics and thus was not a causative factor. The rarity and aperiodicity of large recruitment events in oyster populations is well known (Oviatt 2004, Loosanoff 1966) and rarely are they so insignificant in the succeeding history of the population. The continuing relatively good recruitment throughout much of the 1970s, recruitment indices exceeding 0.5 spat per adult in eight of ten years, may be responsible for the limited impact of the 1972 event.



### The 1970 to 1985 High Abundance Interval

The 1970 to 1985 time period is remarkable for its persistent high level of oyster abundance (Fig. 5), but the implied constancy in population dynamics is more apparent than real. The period was characterized by a lower contribution of animals on the high-mortality beds to total population mortality and natural mortalities rarely exceeding 13% (Fig. 15). During this period, the fraction of deaths on the high mortality beds exceeded the long-term median only five times (Fig. 17). The change in yearly mortality and distribution of deaths do not offer a simple explanation for population persistence in the high-abundance state, however. In the first half of the interval, the population was in a contracted state; that is, a higher proportion of the stock was on the medium-mortality beds. This stock distribution was not obviously different from most of the MSX-dominated decade that preceded it (Fig. 7). Very late in the preceding decade of the 1960s, a proportional increase in abundance upbay and downbay transiently increased the dispersion of the stock, but the dynamics of the 1970 expansion rapidly returned the population to a more contracted state. Although the population expansion that occurred in 1970 occurred over all bay regions, higher increases were recorded downbay of the low-mortality beds. As a result, the medium-mortality beds again supported a disproportionate portion of the stock. The relatively contracted distribution of the stock shifted dramatically in the 1977 to 1979 period with a dispersion of the stock over a few years first upbay and then onto its more environmentally sensitive downbay margin (Fig. 5).

The readjustment of the population dispersion pattern circa 1979 is the initial event establishing increased susceptibility to epizootic disease mortality that was realized in the coincidence of climatic events that occurred in 1985 to 1986. However, unlike previous epizootics, this epizootic extended into the low-mortality reach. It is interesting that this stock collapse was not obviously associated with any unusual trends in recruitment immediately before or after, neither did the distribution of death, nor the dispersion of the stock much change. The event merely reduced total abundance; however, this reduction was permanent.

### The Post-MSX Period

The few years immediately preceding the onset of Dermo and after the 1985 to 1986 MSX epizootic are not unusual in any way, nor with one exception is the first half-decade after Dermo became an important contributor to population mortality. Total abundance remained relatively stable from 1987 through 2001 (Fig. 5). Recruitment was not unusual from 1987 to 1996 (Fig. 10). Natural mortality rose dramatically however, from the 10% level immediately post-1986 to routinely exceed 20% to 30% throughout the 1990s (Fig. 14). The fraction of the deaths contributed by the high-mortality beds did not change markedly over the 1990s, though incrementing in 1990 from the few years preceding (Fig. 17). The dispersed stock distribution of the 1980s remained through 1995, despite the increased mortality rate on the high-mortality beds post-1989 (Fig. 7).

The response of the stock to Dermo became more apparent after 1995. During this time, the stock contracted rapidly to its refuge on the medium-mortality beds. This occurred coincident with a strong recruitment event on these beds in 1998 to 1999 that counterweighed the accumulating losses of individuals

farther downbay. As a consequence, and with the continuing low recruitment on the low-mortality beds upbay, total abundance did not much change.

### The Post-2000 Era

Although the time series is still limited, a third regime shift is suggested circa 2000. Beginning in 2000, recruitment rate declined precipitously and remained low thereafter (Fig. 9). Total abundance declined with continuing high mortality on the high-mortality beds, but stock consolidation continued, reducing mortality in the population as a whole. The fraction of total mortality contributed by the high-mortality beds declined to levels not consistently recorded since the 1950s and remained low (Fig. 17). This occurred because of the increased concentration of the population on the medium-mortality beds that limited the number of individuals available to die on the high-mortality beds (Fig. 7).

### Environmental Time Series

Figures 19 and 20 show the deviations from the mean monthly temperature and freshwater inflow records over most of the survey time series for Delaware Bay. Water temperature anomalies are estimated from air temperature anomalies at Wilmington, DE. Freshwater inflow anomalies are estimated from Delaware River flow at Trenton. Delaware River flow is a good predictor of changes in bay salinity (Haskin 1972).

River flow records show that the first six years of the 1960s were dry (Fig. 19). River inflow increased to a more nearly normal level in the late 1960s. The 1970s were generally wetter than normal and so, river inflow averaged above and often well above the long-term mean. Dry periods occurred again in 1980, 1985, 1991 to 1992, 1999, and 2001 to 2002. Only the 1980 event failed to generate an epizootic of either MSX or Dermo.

Temperatures were generally cooler than the long-term mean through approximately 1970 (Fig. 20). The first half of the 1970s was generally warm but the last few years of the 1970s were characterized by unduly cold winters. Cold winters generally diminish the prevalence of MSX (Ford et al. 1999). The failure of drought to generate an MSX epizootic in 1980 is likely because of the series of preceding cold winters. The 1980s were generally characterized by more normal conditions, with a slight tendency for warmer conditions after the 1990s.

The events of 1967 to 1970 leading up to the 1970 regime shift are marked by the degeneration of the 1960s drought, but are otherwise unexceptional. The first half of the 1970 to 1984 high-abundance period is characterized by a unique confluence of warm and wet conditions: these conditions, however, did not extend into the 1980s, although abundance remained high. The time of the shift in population dispersion circa 1979 (Fig. 7) is exceptional environmentally only in the occurrence of a series of unusually cold winters during that time. The time of the contraction in population dispersion in 1996, a time also characterized by a triplet of years with relatively high recruitment, is likewise characterized by an unremarkable set of environmental conditions, although river flow was well above normal for a few months toward the end of 1996. The absence of clearly unique climatic events in the proximate climatic modulators of temperature and precipitation at the time of the two regime shifts and also at the time of the two dramatic changes in population dispersion is consistent with the observation of Collie et al.

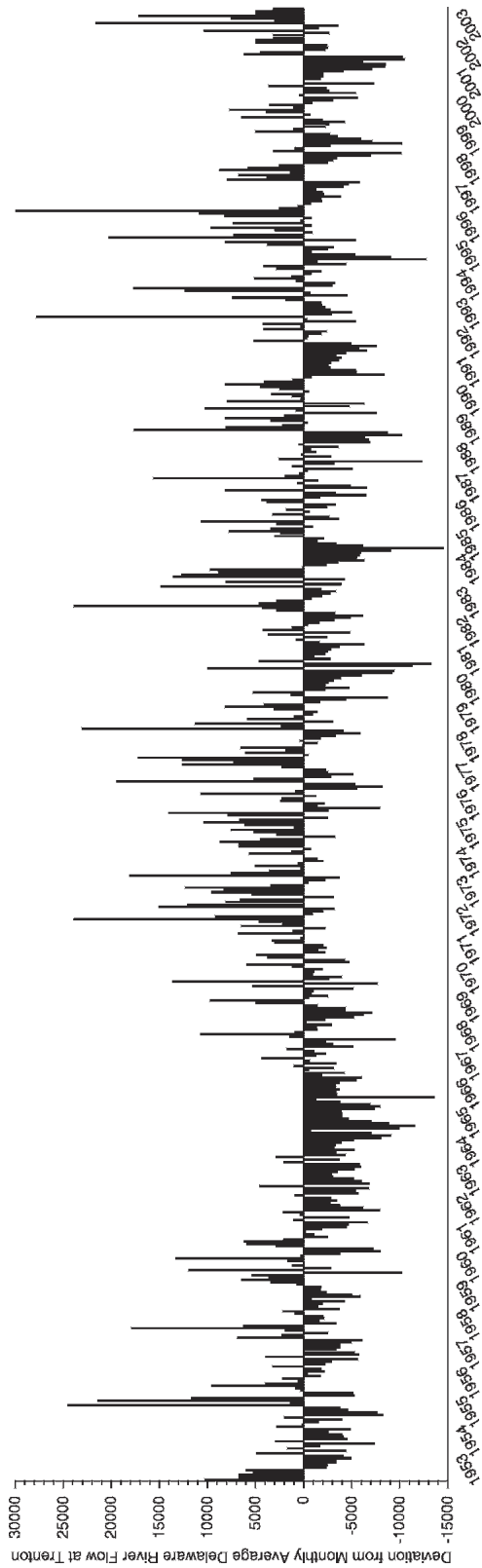


Figure 19. The deviation from the long-term monthly mean for Delaware River flow, measured at Trenton ( $\text{ft}^3 \text{s}^{-1}$ ).

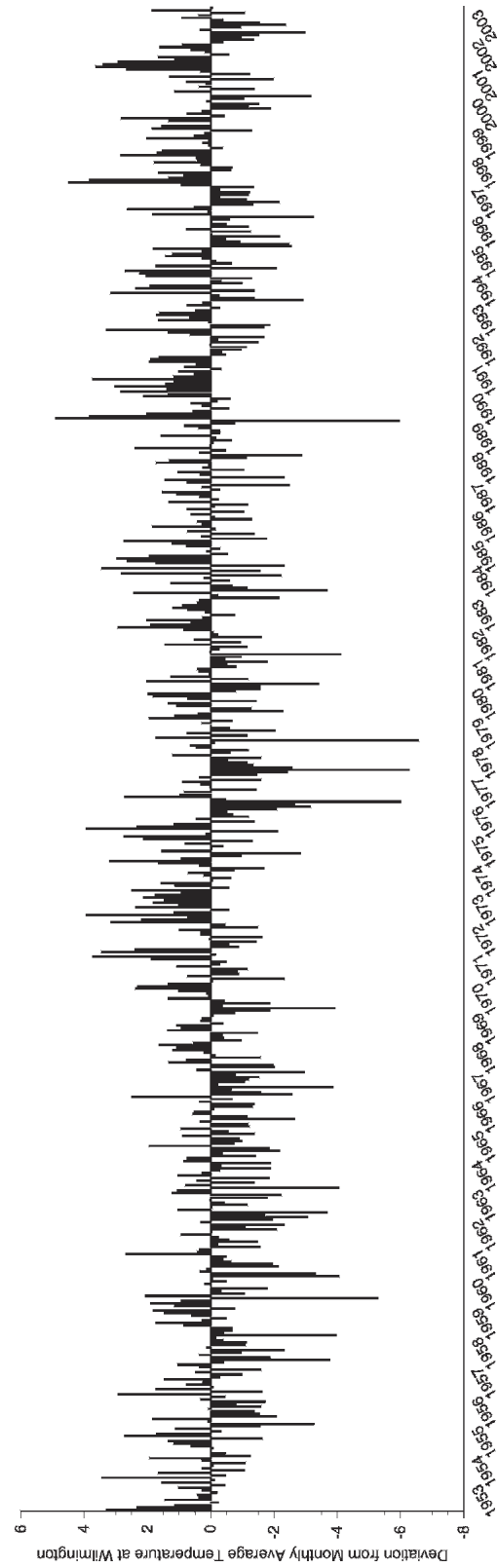


Figure 20. The deviation from the long-term monthly mean for surface air temperature, measured at Wilmington ( $^{\circ}\text{C}$ ).

(2004) that poor correlations between the response variable and potential forcing variables is a common characteristics of large-scale changes in species' population dynamics and consistent with models of catastrophic events ([DeAngelis & Waterhouse 1987](#), [Deakin 1990](#)).

#### *Comparison of MSX and Dermo*

The primary impact of MSX and Dermo disease has been to raise natural mortality and to modify the dispersion of the population. Limited evidence from the early years of the time series suggests that prior to the onset of MSX, a typical level of natural mortality for Delaware Bay oysters was 5% to 10% of the stock yearly, and this is in agreement with the natural mortality rate expected from an animal with a life span of 10–15 y ([Hoenig, 1983](#)).

During the period of 1957 to 1967, natural mortality hovered around 13% to 15% of the stock with excursions above 25% in two years. When the influence of disease relaxed late in the 1960s and into the 1970s, the oyster population reverted to the lower level of natural mortality characteristic of years preceding the onset of MSX. Post-1990, natural mortality rarely fell as low as 13% to 15% with 7 of 15 y exceeding 20%. The increased level of mortality for the population as a whole during this period is partly the result of higher mortality rates on the high-mortality beds, but more important is the increase in mortality rate on the medium-mortality beds. Yearly losses in this region averaged around 15% during the 1960s in comparison with losses routinely exceeding 20% and often exceeding 25% in the 1990s. The ability of Dermo to tolerate lower salinities than MSX and to be an effective agent of mortality at lower salinities than MSX are the likely explanations (e.g., [Andrews 1979](#), [Powell et al. 1996](#), [Paraso et al. 1999](#)).

The consequence of increased mortality from Dermo disease is an enhanced consolidation of the stock. During the 1960s, the fraction of the stock on the medium-mortality beds ranged from just below the 41.7% long-term median to as high as approximately 60% (Fig. 7). Values have reached near 80% since 1996 and six of the last 10 y have reached or exceeded 60%, a value reached or exceeded in only three years prior to 1997 (1957, 1971, 1975), and only once during a low-abundance period. This extreme consolidation of the stock would appear to be a characteristic of the population's response to Dermo disease.

#### *The Characteristics of Regime Shifts—and the Illusion of Constancy*

Regime shifts are routinely synonymized with large and persistent changes in abundance or biomass. Typical, by implication, is the assumption that the persistent subsequent state is a product, to a nontrivial extent, of biological determinism, although the change itself may be environmentally triggered. The Delaware Bay oyster population evinces two regime shifts, a shift to high abundance circa 1970 and a shift to low abundance in 1985–1986. The latter was clearly caused by MSX disease and a coincidence of climatic cycle phasing not recorded previously or since. The former most certainly originated in climatic factors, as the scale of this event encompassed at least the northeast region and influenced similarly estuarine, coastal, and shelf species. Causation for the 1970s high-abundance period remains enigmatic, although the concordance with a shift in AMO is noteworthy.

Regardless, the two regimes themselves had interesting and unexpected characteristics. Each was ushered in by a series of events over a number of years. The 1970 expansion was initiated by a decline in mortality in 1967 and three consecutive, immediately succeeding, years of good recruitment. The 1985 MSX epizootic was ushered in by several years of low recruitment followed by an unusual coincidence of climatic conditions, and the expansion of the population from its refuge state into a less defensible spatial distribution, so that more of the population was exposed to the higher mortality rates.

Each regime was characterized by a period of relative stability in population abundance. However, the population was not as constant as appearance might warrant the inference in either case. During the 1970s, whereas population abundance was reasonably stable, the population changed from a relatively condensed state early in the period, with the fraction of the total population on the medium-mortality beds routinely above the long-term median, to a more dispersed state with the fraction of the population on the medium-mortality beds routinely below the long-term median. In the post-1986 low-abundance period, the opposite trend occurred. The stability in total population abundance belies a more dynamic process of stock redistribution during both time intervals that demonstrates that the appearance of constancy in stock abundance is not necessarily a result of invariant stock dynamics.

The time series is 54 y long and can be divided into a 17-y initial segment, a 16-y high-abundance segment, and a 16-y low-abundance segment. The final five years are relatively unique in being characterized by very low abundance. Whether by chance or not, each of these three longer segments falls into two segments of about eight years defined by changes in stock abundance and distributional pattern. This 8-y signal coincides with an 8-y pattern in the NAO ([Soniati et al. in press](#), see also [Bojariu & Gimeno 2003](#)). The tendency for this periodicity to alternately influence abundance and spatial dispersion is also apparent. The inference is the expectation that the change in recruitment rate in 2000, the decline in mortality in 2003, and the decrease in the fraction of total deaths contributed by the high-mortality beds in 2002 identify another regime shift with the outcome being a period of persistently very low abundance. Certainly, the population dynamic post-2000 is unique for the 54-y time series.

#### *The Concept of Carrying Capacity*

Carrying capacity typically is defined in the context of the stock ([Rice 2001](#), [Hilborn 2002](#)) and assumed to delimit the upper range of stock abundance that might be observed over a substantial time frame. However, the concept is encumbered by the dynamic nature of abundance at the edge of the species' range ([Svensson et al. 2005](#), [Guo et al. 2005](#)) or, for an estuarine species, the sequestration of population units in smaller bodies of water each with habitat margins and habitat refuges (e.g., [Luo et al. 2001](#)). [Botsford \(1981\)](#) suggested that carrying capacity might be valued differentially for alternate stable states (see also [Parvinen 2002](#)). The 54-y time series for Delaware Bay oysters supports that belief. Since 1958, fishing mortality has been lower, and usually much lower, than natural mortality in most years. Thus, the fishery has been relatively inconsequential in the population dynamics of the oysters for over 40 y. The change in plateaus of abundance bespeaks a change in carrying capacity as a product of regime shift. Certainly, the oyster is an

unusual case in that the diseases, MSX and Dermo, impede the population dynamic equilibrium of a typical species at carrying capacity; nevertheless, the time series strongly suggests that the environment, which included MSX disease, permitted a substantially larger population to exist pre-1985 as compared with subsequently and the post-1990 Dermo era demonstrates a wide range in abundance under a continuing high mortality rate. Furthermore, the data are consistent with the involvement of the disease process as an instrument of regime shift, as opposed to the classic quasi-cyclical nature of epizootic and recovery (e.g., Patterson, 1996) that may occur within the larger constraint on the species' population dynamics imposed by the regime shift itself.

Analysis of the Delaware Bay oyster time series suggests that regime shifts usher in substantive changes in carrying capacity for populations. These are marked by apparent equilibria between recruitment and mortality leading to relatively stable population abundance. Analysis of the Delaware Bay oyster time series suggests, however, that stock status is a complex summation of relatively independent local dynamics. Population-level trends may be composites of differential, often offsetting, local trends, and thus constancy in stock abundance may mask substantive changes in population dynamics fostering future catastrophic changes in population-level attributes. Hilborn (2002) has questioned the wisdom of managing populations relative to carrying capacity, as maximum sustainable yield is often related to this measure (Mangel et al. 2002, see also Rice 2001). Using the 1970s high-abundance period as an estimate of carrying capacity for today is a tempting contrivance, but evidence exists in the 54-y time series as to the uniqueness of this period, at least since 1953, and the likely impossibility of developing management measures to reconstitute its essential population attributes must be considered. Regime shifts must constrain management goals. Certainly in Delaware Bay, if a maximum-sustainable-yield goal exists, it is a goal shifting on the order of every 8 or so years within a given bay region and about half that often for the stock as a whole. The former is an order of time less than the rebuilding

requirements of the Magnuson-Stevens Fishery Conservation and Management Act (Anonymous 1996), shorter than most time series analysis would permit adequate prediction (e.g., Stearns 1981, Hilborn & Walters 1992), no more than twice the likely generation time (*sensu* Felsenstein 1971) for oysters in Delaware Bay, and cautionary for the tendency to establish decadal management goals (e.g., the Chesapeake 2000 agreement: <http://www.chesapeakebay.net/agreement.htm>). Moreover, the quasi-decadal dynamic constrains the application of the classic Schaefer model of surplus production (Ricker 1975, Hilborn & Walters 1992). This model, which underlies modern fisheries management, presupposes an increase in secondary production with incremental reduction in population abundance below carrying capacity, with a maximum value at biomass-maximum-sustainable-yield. But, achieving such an equilibrium below carrying capacity takes time and requires the expectation of constancy in the ambit of population dynamics, an expectation impossibly illusory for oysters, at least in Delaware Bay.

#### ACKNOWLEDGMENTS

The authors recognize the many people who contributed over the years to the collection of the 54 years of survey data analyzed in this report, with particular recognition of the contributions by Harold Haskin, Don Kunkle, and Bill Richards. The authors also wish specifically to recognize Harold Haskin whose original survey design in 1953, with relatively few modifications, has continued through today. The analyses presented here show that even the first year of the survey, 1953, conducted at a time when the methodology for randomized surveys was not well established, provided sufficient information for this retrospective quantification. The study was funded by an appropriation from the State of New Jersey to the Haskin Shellfish Research Laboratory, Rutgers University and authorized by the Oyster Industry Science Steering Committee, a standing committee of the Delaware Bay Section of the Shell Fisheries Council of New Jersey.

#### LITERATURE CITED

- Alexander, R. R. & G. P. Dietl. 2001. Shell repair frequencies in New Jersey bivalves: A recent baseline for tests of escalation with Tertiary, Mid-Atlantic congeners. *Palaios* 16:354–371.
- Andrews, J. D. 1979. Oyster diseases in Chesapeake Bay. *Mar. Fish. Rev.* 41(1-2):45–53.
- Andrews, J. D. & S. M. Ray. 1988. Management strategies to control the disease caused by *Perkinsus marinus*. *Am. Fish. Soc. Spec. Publ.* 18:257–264.
- Anonymous. 1996. Magnuson-Stevens Fishery Conservation and Management Act. *NOAA Tech. Mem. NMFS-F/SPO-23*. 121 pp.
- Attrill, M. J. & M. Power. 2002. Climatic influence on a marine fish assemblage. *Nature* 417:275–278.
- Austin, H. M., D. Evans & D. S. Haven. 1996. A retrospective time series analysis of oyster, *Crassostrea virginica*, recruitment (1946 to 1993). *J. Shellfish Res.* 15:565–582.
- Banta, S. E., E. N. Powell & K. A. Ashton-Alcox. 2003. Evaluation of dredging effort by the Delaware Bay oyster fishery in New Jersey waters. *N. Am. J. Fish. Manage.* 23:732–741.
- Bergquist, D. C., J. A. Hale, P. Baker & S. M. Baker. 2006. Development of ecosystem indicators for the Suwanee River estuary: Oyster reef habitat quality along a salinity gradient. *Estuaries Coasts* 29:353–360.
- Berrigan, M., T. Candies, J. Cirino, R. Dugas, C. Dyer, J. Gray, T. Herrington, W. Keithly, R. Leard, J. R. Nelson & M. van Hoose. 1991. The oyster fishery of the Gulf of Mexico, United States: A regional management plan. Ocean Springs, Mississippi: Gulf States Marine Fisheries Commission.
- Boero, F. 1996. Episodic events: Their relevance to ecology and evolution. *P.S.Z.N.I: Mar. Ecol.* 17:237–250.
- Boesch, D., R. Diaz & R. Virnstein. 1976. Effects of tropical storm Agnes on soft-bottom macrobenthic communities of the James and York estuaries and the lower Chesapeake Bay. *Chesapeake Sci.* 17:246–259.
- Bojariu, R. & L. Gimeno. 2003. Predictability and numerical modelling of the North Atlantic Oscillation. *Earth Sci. Rev.* 63:145–168.
- Botsford, L. W. 1981. The effects of increased individual growth rates on depressed population size. *Am. Nat.* 117:38–63.
- Breitbart, D. L. & R. S. Fulford. 2006. Oyster-sea nettle interdependence and altered control within the Chesapeake Bay ecosystem. *Estuaries Coasts* 29:776–784.
- Burreson, E. M., N. A. Stokes & C. S. Friedman. 2000. Increased virulence in an introduced pathogen: *Haplosporidium nelsoni* (MSX) in the eastern oyster *Crassostrea virginica*. *J. Aquat. Anim. Health* 12:1–8.



- Butler, P. A. 1955. Selective setting of oyster larvae on artificial cultch. *Proc. Natl. Shellfish. Assoc.* 45:95–105.
- Callender, W. R., E. N. Powell & G. M. Staff. 1994. Taphonomic rates of molluscan shells placed in autochthonous assemblages on the Louisiana continental slope. *Palaios* 9:60–73.
- Choi, J. S., K. T. Frank, W. C. Leggett & K. F. Drinkwater. 2004. Transition to an alternate state in a continental shelf ecosystem. *Can. J. Fish. Aquat. Sci.* 61:505–510.
- Christmas, J. F., M. R. McGinty, D. A. Randle, G. F. Smith & S. J. Jordan. 1997. Oyster shell disarticulation in three Chesapeake Bay tributaries. *J. Shellfish Res.* 16:115–123.
- Collie, J. S., K. Richardson & J. H. Steele. 2004. Regime shifts: Can ecological theory illuminate the mechanisms? *Prog. Oceanogr.* 60:281–302.
- Cook, T., M. Folli, J. Klinck, S. Ford & J. Miller. 1998. The relationship between increasing sea-surface temperature and the northward spread of *Perkinsus marinus* (Dermo) disease epizootics in oysters. *Estuar. Coast. Shelf Sci.* 46:587–597.
- Cummins, H., E. N. Powell, R. J. Stanton, Jr. & G. Staff. 1986a. The rate of taphonomic loss in modern benthic habitats: How much of the potentially preservable community is preserved? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 52:291–320.
- Cummins, H., E. N. Powell, R. J. Stanton, Jr. & G. Staff. 1986b. The size-frequency distribution in palaeoecology: The effects of taphonomic processes during formation of death assemblages in Texas bays. *Palaeontology (Lond.)* 29:495–518.
- Cushing, D. H. & R. R. Dickson. 1976. The biological response in the sea to climatic changes. *Adv. Mar. Biol.* 14:1–122.
- Dawe, E. G., E. B. Colbourne & K. F. Drinkwater. 2000. Environmental effects on recruitment of short-finned squid (*Illex illecebrosus*). *ICES J. Mar. Sci.* 57:1002–1013.
- Deakin, M. A. B. 1990. Catastrophe modelling in the biological sciences. *Acta Biotheor.* 38:3–22.
- DeAlteris, J. T. 1988. The geomorphic development of Wreck Shoals, a subtidal oyster reef of the James River, Virginia. *Estuaries* 11:240–249.
- DeAngelis, D. L. & J. C. Waterhouse. 1987. Equilibrium and non-equilibrium concepts in ecological models. *Ecol. Monogr.* 57:1–21.
- Dugas, R. J. 1988. Administering the Louisiana oyster fishery. *J. Shellfish Res.* 7:493–499.
- Enfield, D. B., A. M. Mestas-Nunez & P. J. Trimble. 2001. The Atlantic Multidecadal Oscillation and its relation to rainfall and river flows in the continental US. *Geophys. Res. Lett.* 28:2077–2080.
- Fegley, S. R., S. E. Ford, J. N. Kraeuter & H. H. Haskin. 2003. The persistence of New Jersey's oyster seedbeds in the presence of MSX disease and harvest: Management's role. *J. Shellfish Res.* 22:451–464.
- Fegley, S. R., S. E. Ford, J. N. Kraeuter & D. R. Jones. 1994. Relative effects of harvest pressure and disease mortality on the population dynamics of the Eastern oyster (*Crassostrea virginica*) in Delaware Bay. National Oceanic and Atmospheric Administration Final Rpt # NA26FL0588. Bivalve, NJ: Haskin Shellfish Research Laboratory, Rutgers University.
- Felsenstein, J. 1971. Inbreeding and variance effective numbers in populations with overlapping generations. *Genetics* 68:581–597.
- Ford, S. E. 1996. Range extension by the oyster parasite *Perkinsus marinus* into the northeastern United States: Response to climate change. *J. Shellfish Res.* 15:45–56.
- Ford, S. 1997. History and present status of molluscan shellfisheries from Barnegat Bay to Delaware Bay. In: C. L. MacKenzie, Jr., V. G. Burrell, Jr., A. Rosenfield & W. L. Hobart, editors. The history, present condition, and future of the molluscan fisheries of North and central America and Europe, Vol. 1. Atlantic and Gulf Coasts. *NOAA Tech. Rept. NMFS* 127:119–140.
- Ford, S. E., M. J. Cummings & E. N. Powell. 2006. Estimating mortality in natural assemblages of oysters. *Estuaries Coasts* 29:361–374.
- Ford, S. E. & H. H. Haskin. 1982. History and epizootiology of *Haplosporidium nelsoni* (MSX), an oyster pathogen in Delaware Bay, 1957–1980. *J. Invertebr. Pathol.* 40:118–141.
- Ford, S. E. & H. H. Haskin. 1988. Management strategies for MSX (*Haplosporidium nelsoni*) disease in Eastern oysters. *Am. Fish. Soc. Spec. Publ.* 18:249–256.
- Ford, S. E., H. H. Haskin & J. N. Kraeuter. 1995. Eastern oyster. In: L. E. Dove & R. M. Nyman, editors. Living resources of the Delaware Estuary. *Delaware Estuary Program (DELEP)* 95-07. pp. 105–111.
- Ford, S., E. Powell, J. Klinck & E. Hofmann. 1999. Modeling the MSX parasite in Eastern oyster (*Crassostrea virginica*) populations. I. Model development, implementation, and verification. *J. Shellfish Res.* 18:475–500.
- Fr  rotte, B., A. Raguideau & J.-P. Cuif. 1983. D  gradation in vitro d'un test carbonat   d'invert  br  , *Crassostrea gigas* (Thunberg), par action de cultures bact  riennes. Int  r  t pour l'analyse ultrastructurale. *C.R. Acad. Sci. Paris Ser. 2 Mech.-Phys.-Chim. Sci. Univ. Sci. Terre* 297:383–388.
- Gabriel, W. L. 1992. Persistence of demersal fish assemblages between Cape Hatteras and Nova Scotia, northwest Atlantic. *J. Northw. Atl. Fish. Sci.* 14:29–46.
- Glover, C. P. & S. M. Kidwell. 1993. Influence of organic matrix on the post-mortem destruction of molluscan shells. *J. Geol.* 101:729–747.
- Godfray, H. C. J. & C. J. Briggs. 1995. The population dynamics of pathogens that control insect outbreaks. *J. Theor. Biol.* 176:125–136.
- Gray, J. S. 1977. The stability of benthic ecosystems. *Helgol. Wiss. Meeresunters.* 30:427–444.
- Gunter, G., C. E. Dawson & W. J. Demoran. 1957. Determination of how long oysters have been dead by studies of their shells. *Proc. Natl. Shellfish. Assoc.* 47:31–33.
- Guo, Q., M. Taper, M. Schoenberger & J. Brandle. 2005. Spatial-temporal population dynamics across species range: From centre to margin. *Oikos* 108:47–57.
- Hargis, W. J., Jr. & D. S. Haven. 1994. The precarious state of the Chesapeake public oyster resource. In: P. Hill & S. Nelson, editors. Toward a sustainable coastal watershed: The Chesapeake experiment. Proceedings of the conference June 1–3, 1994, Norfolk VA *Chesapeake Research Consortium Publ.* 149:559–584.
- Harvell, C. D., K. Kim, J. M. Burkholder, R. R. Colwell, P. R. Epstein, D. J. Grimes, E. E. Hofmann, E. K. Lipp, A. D. M. E. Osterhaus, R. M. Overstreet, J. W. Porter, G. W. Smith & G. R. Vasta. 1999. Emerging marine diseases—climate links and anthropogenic factors. *Science (Wash. DC)* 285:1505–1510.
- Haskin, H. H. 1953. First annual report on the natural seed beds investigation. Bivalve, NJ: New Jersey Agricultural Experiment Station, Rutgers University. 75 pp.
- Haskin, H. H. 1972. Delaware River flow-bay salinity relationships. Report to the Delaware River Basin Commission: Phase III. Bivalve, NJ: Rutgers University.
- Haskin, H. H. & J. D. Andrews. 1988. Uncertainties and speculations about the life cycle of the Eastern oyster pathogen *Haplosporidium nelsoni* (MSX). *Am. Fish. Soc. Spec. Publ.* 18:5–22.
- Haskin, H. H. & S. E. Ford. 1982. *Haplosporidium nelsoni* (MSX) on Delaware Bay seed oyster beds: A host-parasite relationship along a salinity gradient. *J. Invertebr. Pathol.* 40:388–405.
- Haven, D. S., J. M. Zeigler, J. T. DeAlteris & J. P. Whitcomb. 1987. Comparative attachment, growth and mortalities of oyster (*Crassostrea virginica*) spat on slate and oyster shell in the James River, Virginia. *J. Shellfish Res.* 6:45–48.
- Hayes, P. F. & R. W. Menzel. 1981. The reproductive cycle of early setting *Crassostrea virginica* (Gmelin) in the northern Gulf of Mexico, and its implications for population recruitment. *Biol. Bull.* 160:80–88. (Woods Hole).
- Hidu, H. 1969. Gregarious setting in the American oyster *Crassostrea virginica* Gmelin. *Chesapeake Sci.* 10:85–92.

- Hidu, H., W. G. Valleau & F. P. Veitch. 1978. Gregarious setting in European and American oysters—response to surface chemistry vs. waterborne pheromones. *Proc. Natl. Shellfish. Assoc.* 68:11–16.
- Hilborn, R. 2002. The dark side of reference points. *Bull. Mar. Sci.* 70:403–408.
- Hilborn, R. & C. J. Walters. 1992. Quantitative fisheries stock assessment. Choice, dynamics and uncertainty. New York, NY: Chapman & Hall. 570 pp.
- Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. *Fish. Bull. (Wash. D. C.)* 83:898–903.
- Hofmann, E. E., J. M. Klinck, J. N. Krauter, E. N. Powell, R. E. Grizzle, S. C. Buckner & V. M. Bricelj. 2006. A population dynamics model of the hard clam, *Mercenaria mercenaria*: Development of the age- and length-frequency structure of the population. *J. Shellfish Res.* 25:417–444.
- Hofstetter, R. P. 1977. Trends in population levels of the American oyster *Crassostrea virginica* Gmelin on public reefs in Galveston Bay, Texas. *Tex. Parks Wildl. Dept. Tech. Rept.* 24:1–90.
- Hofstetter, R. P. 1983. Oyster population trends in Galveston Bay 1973–1978. Texas Parks Wildl. Dept. Manage. Data Ser. No 51. 33 pp.
- Hofstetter, R. P. 1990. (revised by C.E. Bryan). 1990. The Texas oyster fishery. *Tex. Parks Wildl. Dept. Bull.* 40:1–21.
- Holt, D., T. H. Keitt, M. A. Lewis, B. A. Maurer & M. L. Taper. 2005. Theoretical models of species' borders: Single species approaches. *Oikos* 108:18–27.
- Hopkins, S. H. 1954. Oyster setting on the Gulf coast. *Proc. Natl. Shellfish. Assoc.* 45:52–55.
- Hopkins, S. H. 1962. Distribution of species of *Cliona* (boring sponge) on the Eastern Shore of Virginia in relation to salinity. *Chesapeake Sci.* 3:121–124.
- HSRL. 2006. Report of the 2006 Stock Assessment Workshop (8th SAW) for the New Jersey Delaware Bay Oyster Beds. Bivalve, NJ: Haskin Shellfish Research Laboratory, Rutgers University. 81 pp.
- HSRL. 2007. Report of the 2007 Stock Assessment Workshop (9th SAW) for the New Jersey Delaware Bay Oyster Beds. Bivalve, NJ: Haskin Shellfish Research Laboratory, Rutgers University. 94 pp.
- Hurrell, J. W., Y. Kushnir, M. Visbeck & G. Ottersen. 2003. An overview of the North Atlantic Oscillation. In: J. W. Hurrell, Y. Kushnir, G. Ottersen & M. Visbeck, editors. The North Atlantic Oscillation: climate significance and environmental impact. *Geophys. Monogr. Ser.* 134:1–35.
- Hurrell, J. W. & H. van Loon. 1997. Decadal variations in climate associated with the North Atlantic Oscillation. *Clim. Change* 36:301–326.
- Ingle, R. M. & C. E. Dawson, Jr. 1950. Variation in salinity and its relation to the Florida oyster. Part One: Salinity variations in Apalachicola Bay. *Proc. Natl. Shellfish. Assoc.* pp. 6–19.
- Ismail, N. S. 1985. The effects of hydraulic dredging to control oyster drills on benthic macrofauna of oyster grounds in Delaware Bay, New Jersey. *Int. Rev. Ges. Hydrobiol.* 70:379–395.
- Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner & R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science (Wash. DC)* 293:629–637.
- Jaenike, J. 1998. On the capacity of macroparasites to control insect populations. *Am. Nat.* 151:84–96.
- Jordan, S. J. & J. M. Coakley. 2004. Long-term projections of eastern oyster populations under various management scenarios. *J. Shellfish Res.* 23:63–72.
- Jordan, S. J., K. N. Greenhawk, C. B. McCollough, J. M. Vanisko & M. L. Homer. 2002. Oyster biomass, abundance, and harvest in northern Chesapeake Bay: Trends and forecasts. *J. Shellfish Res.* 21:733–741.
- Kermack, W. O. & A. G. McKendrick. 1991. Contributions to the mathematical theory of epidemics - I. *Bull. Math. Biol.* 53:33–55.
- Kim, Y. & E. N. Powell. 1998. Influence of climate change on interannual variation in population attributes of Gulf of Mexico oysters. *J. Shellfish Res.* 17:265–274.
- Kim, Y. & E. N. Powell. 2004. Surfclam histopathology survey along the Delmarva mortality line. *J. Shellfish Res.* 23:429–441.
- Knowlton, N. 2004. Multiple “stable” states and the conservation of marine ecosystems. *Prog. Oceanogr.* 60:387–396.
- Krauter, J. N., S. Buckner & E. N. Powell. 2005. A note on a spawner-recruit relationship for a heavily exploited bivalve: The case of northern quahog (hard clams), *Mercenaria mercenaria* in Great South Bay New York. *J. Shellfish Res.* 24:1043–1052.
- Krauter, J. N., S. E. Ford & M. Cummings. 2007. Growth measurement in oysters: A comparison of methods. *J. Shellfish Res.* 26:479–491.
- Krauter, J. N., S. Ford & W. Canzonier. 2003. Increased biomass yield from Delaware Bay oysters (*Crassostrea virginica*) by alteration of planting season. *J. Shellfish Res.* 22:39–49.
- Krauter, J. N., J. M. Klinck, E. N. Powell, E. E. Hofmann, S. C. Buckner, R. E. Grizzle & V. M. Bricelj. Effects of the fishery on the northern quahog (=hard clam, *Mercenaria mercenaria* L.) population in Great South Bay, New York: a modeling study. *J. Shellfish Res.* 27:653–666.
- Krantz, G. E. & S. J. Jordan. 1996. Management alternatives for protecting *Crassostrea virginica* fisheries in *Perkinsus marinus* enzootic and epizootic areas. *J. Shellfish Res.* 15:167–176.
- Lescinsky, H. L., E. Edinger & M. J. Risk. 2002. Mollusc shell encrustation and bioerosion rates in a modern epeiric sea: Taphonomy experiments in the Java Sea, Indonesia. *Palaios* 17:171–191.
- Link, J. S., J. K. T. Brodziak, S. F. Edwards, W. J. Overholtz, D. Mountain, J. W. Jossi, T. D. Smith & M. J. Fogarty. 2002. Marine ecosystem assessment in a fisheries management context. *Can. J. Fish. Aquat. Sci.* 59:1429–1440.
- Loosanoff, V. L. 1966. Time and intensity of setting of the oyster *Crassostrea virginica*, in Long Island Sound. *Biol. Bull.* 130:211–227. (Woods Hole)
- Luo, J., K. J. Hartman, S. B. Brandt, C. F. Cerco & T. H. Rippetoe. 2001. A spatially-explicit approach for estimating carrying capacity: An application for the Atlantic menhaden (*Brevoortia tyrannus*) in Chesapeake Bay. *Estuaries* 24:545–556.
- MacKenzie, C. L., Jr. 1981. Biotic potential and environmental resistance in the American oyster (*Crassostrea virginica*) in Long Island Sound. *Aquaculture* 22:229–268.
- MacKenzie, C. L., Jr. 1989. A guide for enhancing estuarine shellfisheries. *Mar. Fish. Rev.* 51(3):1–47.
- MacKenzie, C. L., Jr. 1996. History of oystering in the United States and Canada, featuring the eight greatest oyster estuaries. *Mar. Fish. Rev.* 58(4):1–78.
- Mangel, M., B. Marinovic, C. Pomeroy & D. Croll. 2002. Requiem for Ricker: Unpacking msy. *Bull. Mar. Sci.* 70:763–781.
- Mangel, M. & C. Tier. 1994. Four facts every conservation biologist should know about persistence. *Ecology* 75:607–614.
- Mann, R. 2000. Restoring the oyster reef communities in the Chesapeake Bay: A commentary. *J. Shellfish Res.* 19:335–339.
- Mann, R. & D. A. Evans. 1998. Estimation of oyster, *Crassostrea virginica*, standing stock, larval production and advective loss in relation to observed recruitment in the James River, Virginia. *J. Shellfish Res.* 17:239–253.
- Mann, R., M. Southworth, J. M. Harding & J. Wesson. 2004. A comparison of dredge and patent tongs for estimation of oyster populations. *J. Shellfish Res.* 23:287–390.
- Marshall, N. 1954. Changes in the physiography of oyster bars in the James River, Virginia. *Natl. Shellfish. Assoc. Conv. Add.* pp. 113–121.
- Maurer, D. & L. Watling. 1973. The biology of the oyster community and its associated fauna in Delaware Bay. In: D. F. Polis, editor. *Lewes, Delaware: College of Marine Studies, University of Delaware Vol. 6. Delaware Bay Report Series.* 97 pp.

- Maurer, D., L. Watling & R. Keck. 1971. The Delaware oyster industry: a reality? *Trans. Am. Fish. Soc.* 100:100–111.
- McCabe, G. J., M. A. Palecki & J. L. Betancourt. 2004. Pacific and Atlantic ocean influences on multidecadal drought frequency in the United States. *Proc. Natl. Acad. Sci. USA* 101:4136–4141.
- McCallum, H. I. & G. R. Singleton. 1989. Models to assess the potential of *Capillaria hepatica* to control population outbreaks of house mice. *Parasitology* 98:425–437.
- McDermott, J. J. & F. B. Flower. 1952. Preliminary studies of the common mud crabs on oyster beds of Delaware Bay. *Natl. Shellfish. Assoc. Conv. Add.* pp. 47–50.
- McGrorty, S. & J. D. Goss-Custard. 1993. Population dynamics of the mussel *Mytilus edulis* along environmental gradients: Spatial variations in density-dependent mortalities. *J. Anim. Ecol.* 62:415–427.
- Milke, L. M. & V. S. Kennedy. 2001. Mud crabs (Xanthidae) in Chesapeake Bay: Claw characteristics and predation on epifaunal bivalves. *Invertebr. Biol.* 120:67–77.
- Moore, H. F. 1911. Condition and extent of the natural oyster beds of Delaware. *U.S. Bur. Fish.* 745:1–29.
- NEFSC. 2000. 30th northeast regional stock assessment workshop (30th SAW): Stock assessment review committee (SARC) consensus summary of assessments. *NMFS NEFSC Ref. Doc.* 00-03. 477 pp.
- NEFSC. 2001. 33rd northeast regional stock assessment workshop (33rd SAW): Stock assessment review committee (SARC) consensus summary of assessments. *NMFS NEFSC Ref. Doc.* 01-18. 281 pp.
- NEFSC. 2003. 37th northeast regional stock assessment workshop (37th SAW): Stock assessment review committee (SARC) consensus summary of assessments. *NMFS NEFSC Ref. Doc.* 03-16. 603 pp.
- Notaro, M., W.-C. Wang & W. Gong. 2006. Model and observational analysis of the northeast U.S. regional climate and its relationship to the PNA and NAO patterns during early winter. *Month. Weath. Rev.* 134:3479–3505.
- Osman, R. W., R. B. Whitlatch & R. N. Zajac. 1989. Effects of resident species on recruitment into a community: Larval settlement versus post-settlement mortality in the oyster *Crassostrea virginica*. *Mar. Ecol. Prog. Ser.* 54:61–73.
- Oviatt, C. A. 2004. The changing ecology of temperate coastal waters during a warming trend. *Estuaries* 27:895–904.
- Paraso, M. C., S. E. Ford, E. N. Powell, E. E. Hofmann & J. M. Klinck. 1999. Modeling the MSX parasite in Eastern oyster (*Crassostrea virginica*) populations. II. Salinity effects. *J. Shellfish Res.* 18:501–516.
- Parvinen, K. 2002. Evolutionary branching of dispersal strategies in structured metapopulations. *J. Math. Biol.* 45:106–124.
- Patterson, K. R. 1996. Modelling the impact of disease-induced mortality in an exploited population: The outbreak of the fungal parasite *Ichthyophonus hoferi* in the North Sea herring (*Clupea harengus*). *Can. J. Fish. Aquat. Sci.* 53:2870–2887.
- Peterson, C. H. 1984. Does a rigorous criterion for environmental identity preclude the existence of multiple stable points? *Am. Nat.* 124:127–133.
- Peterson, C. H. & R. Black. 1993. Experimental tests of the advantages and disadvantages of high density for two coexisting cockles in a southern ocean lagoon. *J. Anim. Ecol.* 62:614–633.
- Powell, E. N., K. A. Ashton-Alcox, S. E. Banta & A. J. Bonner. 2001. Impact of repeated dredging on a Delaware Bay oyster reef. *J. Shellfish Res.* 20:961–975.
- Powell, E. N. & K. A. Ashton-Alcox. 2004. A comparison between a suction dredge and a traditional oyster dredge in the transplantation of oysters in Delaware Bay. *J. Shellfish Res.* 23:803–823.
- Powell, E. N., K. A. Ashton-Alcox, J. A. Dobarro, M. Cummings & S. E. Banta. 2002a. The inherent efficiency of oyster dredges in survey mode. *J. Shellfish Res.* 21:691–695.
- Powell, E. N., K. A. Ashton-Alcox & J. N. Kraeuter. 2007. Reevaluation of eastern oyster dredge efficiency in survey mode: Application in stock assessment. *N. Am. J. Fish. Manage.* 27:492–511.
- Powell, E. N., H. Cummins, R. J. Stanton, Jr. & G. Staff. 1984. Estimation of the size of molluscan larval settlement using the death assemblage. *Estuar. Coastal Shelf Sci.* 18:367–384.
- Powell, E. N., J. D. Gauthier, E. A. Wilson, A. Nelson, R. R. Fay & J. M. Brooks. 1992. Oyster disease and climate change. Are yearly changes in *Perkinsus marinus* parasitism in oysters (*Crassostrea virginica*) controlled by climatic cycles in the Gulf of Mexico? *P.S.Z.N.I.: Mar. Ecol.* 13:243–270.
- Powell, E. N., J. J. Gendek & K. A. Ashton-Alcox. 2005. Fisherman choice and incidental catch: Size frequency of oyster landings in the New Jersey oyster fishery. *J. Shellfish Res.* 24:469–476.
- Powell, E. N. & J. M. Klinck. 2007. Is oyster shell a sustainable estuarine resource? *J. Shellfish Res.* 26:181–194.
- Powell, E. N., J. M. Klinck & E. E. Hofmann. 1996. Modeling diseased oyster populations. II. Triggering mechanisms for *Perkinsus marinus* epizootics. *J. Shellfish Res.* 15:141–165.
- Powell, E. N., J. M. Klinck, E. E. Hofmann & S. Ford. 1997. Varying the timing of oyster transplant: Implications for management from simulation studies. *Fish. Oceanogr.* 6:213–237.
- Powell, E. N., J. M. Klinck, E. E. Hofmann & S. M. Ray. 1994. Modeling oyster populations. IV: Rates of mortality, population crashes and management. *Fish. Bull. (Wash. D. C.)* 92:347–373.
- Powell, E. N., J. N. Kraeuter & K. A. Ashton-Alcox. 2006. How long does oyster shell last on an oyster reef? *Estuar. Coast. Shelf Sci.* 69:531–542.
- Powell, E. N., K. M. Parsons-Hubbard, W. R. Callender, G. M. Staff, G. T. Rowe, C. E. Brett, S. E. Walker, A. Raymond, D. D. Carlson, S. White & E. A. Heise. 2002b. Taphonomy on the continental shelf and slope: Two-year trends—Gulf of Mexico and Bahamas. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 184:1–35.
- Powell, E. N., J. Song, M. S. Ellis & E. A. Wilson-Ormond. 1995. The status and long-term trends of oyster reefs in Galveston Bay, Texas. *J. Shellfish Res.* 14:439–457.
- Powell, E. N., R. J. Stanton, Jr., D. Davies & A. Logan. 1986. Effect of a large larval settlement and catastrophic mortality on the ecologic record of the community in the death assemblage. *Estuar. Coastal Shelf Sci.* 23:513–525.
- Reeve, J. D. & W. W. Murdoch. 1985. Aggregation by parasitoids in the successful control of the California red scale: A test of theory. *J. Anim. Ecol.* 54:797–816.
- Reverdin, G., D. Cayan & Y. Kushnir. 1997. Decadal variability of hydrography in the upper northern North Atlantic in 1948–1990. *J. Geophys. Res.-Oceans* 102:8505–8531.
- Rice, J. 2001. Implications of variability on many time scales for scientific advice on sustainable management of living marine resources. *Prog. Oceanogr.* 49:189–209.
- Richardson, A. J. & D. S. Schoeman. 2004. Climate impact on plankton ecosystems in the northeast Atlantic. *Science (Wash. DC)* 305:160–163.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board. Can.* 191:1–382.
- Ritchie, T. P. & R. W. Menzel. 1969. Influence of light on larval settlement of American oysters. *Proc. Natl. Shellfish. Assoc.* 59:116–120.
- Rothschild, B. J., J. S. Ault, P. Gouletquer & H. Héral. 1994. Decline of the Chesapeake Bay oyster population: A century of habitat destruction and overfishing. *Mar. Ecol. Prog. Ser.* 111:29–39.
- Rothschild, B. J. & L. J. Shannon. 2004. Regime shifts and fishery management. *Prog. Oceanogr.* 60:397–402.
- Smith, G. F., D. G. Bruce, E. B. Roach, A. Hansen, R. I. E. Newell & A. M. McManus. 2005. Assessment of recent habitat conditions of eastern oyster *Crassostrea virginica* bars in mesohaline Chesapeake Bay. *N. Am. J. Fish. Manage.* 25:1569–1590.
- Smith, G. F., K. N. Greenhawk, D. G. Bruce, E. B. Roach & S. J. Jordan. 2001. A digital presentation of the Maryland oyster habitat and associated bottom types in the Chesapeake Bay (1974–1983). *J. Shellfish Res.* 20:197–206.

- Soniat, T. M., B. C. Broadhurst, III & E. L. Haywood, III. 1991. Alternatives to clam shell as cultch for oysters and the use of gypsum for the production of cultchless oysters. *J. Shellfish Res.* 10:405–410.
- Soniat, T. M., E. E. Hofmann, J. M. Klinck & E. N. Powell. The El-Niño Southern Oscillation and the North Atlantic Oscillation differentially modulate the oyster parasites, *Perkinsus marinus* and *Haplosporidium nelsoni*. *Int. J. Earth Sci.* (in press).
- Soniat, T. M., J. M. Klinck, E. N. Powell & E. E. Hofmann. 2006. Understanding the success and failure of oyster populations: Climatic cycles and *Perkinsus marinus*. *J. Shellfish Res.* 25:83–93.
- Stauber, L. A. 1943. Ecological studies on the oyster drill, *Urosalpinx cinerea*, in Delaware Bay, with notes on the associated drill, *Eupleura caudata* and with practical consideration of control methods. Bivalve, New Jersey: Oyster Research Laboratory, New Jersey Agricultural Experiment Station. 180 pp.
- Stearns, S. C. 1981. On measuring fluctuating environments: Predictability, constancy, and contingency. *Ecology* 62:185–199.
- Steele, J. H. & E. W. Henderson. 1984. Modeling long-term fluctuations in fish stocks. *Science (Wash. DC)* 224:985–987.
- Sutton, R. T. & D. L. R. Hodson. 2003. Influence of the ocean on North Atlantic climate variability 1871–1999. *J. Clim.* 16:3296–3313.
- Svensson, C. J., S. R. Jenkins, S. J. Hawkins & P. Åberg. 2005. Population resistance to climate change: Modelling the effects of low recruitment in open populations. *Oecologia* 142:117–126.
- Taylor, W. P. 1934. Significance of extreme or intermittent conditions in distribution of species and management of natural resources, with a restatement of Liebig's law of minimum. *Ecology* 15:374–379.
- Valero, J. L., J. M. Orensanz, A. M. Parma, D. Armstrong & R. Hilborn. 2004. Geoduck (*Panopea abrupta*) recruitment in the Pacific Northwest: Long-term changes in relation to climate. *Cal. Coop. Ocean. Fish.* 45:80–86.
- Warburton, F. E. 1958. Control of the boring sponge on oyster beds. *Fish. Res. Bd. Can. Prog. Rep. Atl. Coast Stns.* 69:7–11.
- Ware, D. M. 2000. Aquatic ecosystems: Properties and models. In: P. J. Harrison & T. R. Parsons, editors. Fisheries oceanography: An integrative approach to fisheries ecology and management. Oxford: Blackwell Science. pp. 163–194.
- Weinberg, J. R., T. G. Dahlgren & K. M. Halanych. 2002. Influence of rising sea temperature on commercial bivalve species of the U.S. Atlantic coast. *Am. Fish. Soc. Symp.* 32:131–140.
- Woods, H., W. J. Hargis, Jr., C. H. Hershner & P. Mason. 2005. Disappearance of the natural emergent 3-dimensional oyster reef system of the James River, Virginia, 1871–1948. *J. Shellfish Res.* 24:139–142.
- Young, T. P. 1994. Natural die-offs of large mammals: Implications for conservation. *Conserv. Biol.* 8:410–418.
- Zuschin, M. & R. J. Stanton, Jr. 2001. Experimental measurement of shell strength and its taphonomic interpretation. *Palaios* 16:161–170.
- Zuur, A. F. & G. J. Pierce. 2004. Common trends in northeast Atlantic squid time series. *J. Sea Res.* 52:57–72.