

Abstract—In the first of two companion papers, a 54-yr time series for the oyster population in the New Jersey waters of Delaware Bay was analyzed to develop biological relationships necessary to evaluate maximum sustainable yield (MSY) reference points and to consider how multiple stable points affect reference point-based management. The time series encompassed two regime shifts, one circa 1970 that ushered in a 15-yr period of high abundance, and a second in 1985 that ushered in a 20-yr period of low abundance. The intervening and succeeding periods have the attributes of alternate stable states. The biological relationships between abundance, recruitment, and mortality were unusual in four ways. First, the broodstock–recruitment relationship at low abundance may have been driven more by the provision of settlement sites for larvae by the adults than by fecundity. Second, the natural mortality rate was temporally unstable and bore a nonlinear relationship to abundance. Third, combined high abundance and low mortality, though likely requiring favorable environmental conditions, seemed also to be a self-reinforcing phenomenon. As a consequence, the abundance–mortality relationship exhibited both compensatory and depensatory components. Fourth, the geographic distribution of the stock was intertwined with abundance and mortality, such that interrelationships were functions both of spatial organization and inherent population processes.

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Multiple stable reference points in oyster populations: biological relationships for the eastern oyster (*Crassostrea virginica*) in Delaware Bay

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All federal fisheries, and some state fisheries, are managed under biological reference-point guidelines that implement a yearly allocation or quota, often termed TAC (total allowable catch) or TAL (total allowable landing), to constrain fishing mortality (e.g., Wallace et al., 1994). The biological reference-point approach for federal fisheries was mandated by the Magnuson-Stevens Fishery Conservation and Management Act (Anonymous, 1996) which requires management at a biomass that provides maximum sustainable yield, B_{MSY} . Under this system, sophisticated survey, analytical, and modeling procedures are used to identify selected biological reference points, such as the target biomass, B_{MSY} , and carrying capacity, K . Fishing mortality is then set in relation to these goals. As a consequence, much attention has been given to the choice and application of biological reference points in fisheries management (e.g., Sissenwine and Shepherd, 1987; Hilborn, 2002; Imeson et al., 2002; Mangel et al., 2002).

Normally, B_{MSY} is defined in relation to carrying capacity, the biomass present without fishing, where natural mortality balances recruitment (e.g., May et al., 1978; Johnson, 1994;

Mangel and Tier, 1994; Rice, 2001). This stable point is characterized by a population in which most animals are adults, where natural mortality rates are low, and where recruitment is limited by compensatory processes such as resource limitation constraining fecundity. B_{MSY} is most commonly defined as $\frac{K}{2}$, based on the well-known Schaefer model which stipulates the guiding premise that surplus production is highest at $\frac{K}{2}$ (Hilborn and Walters [1992]; see Restrepo et al. [1998] for more details on the federal management system; see NEFSC [1999¹, 2000², 2002³] for examples of implementation of reference-point management).

¹ NEFSC (Northeast Fisheries Science Center). 1999. 29th Northeast regional stock assessment workshop (29th SAW): Stock Assessment Review Committee (SARC) consensus summary of assessments. NMFS NEFSC Ref. Doc. 99-14, 347 p.

² 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 p.

³ 2002. 34th Northeast regional stock assessment workshop (34th SAW): Stock Assessment Review Committee (SARC) consensus summary of assessments. NMFS NEFSC Ref. Doc. 02-06, 346 p.

Some have expressed concerns about managing at B_{MSY} (e.g., Peterman, 1977; Hilborn, 2002; Mangel et al., 2002), but only recently has the possibility been raised that carrying capacity may not be the long-term constant typically assumed under B_{MSY} management. That realization arises ineluctably from the recognition that regime shifts profoundly affect the balance between population and environment (Rothschild, 2000; Collie et al., 2004; Rothschild and Shannon, 2004; Sakuramoto, 2005). Increasingly, fisheries biologists recognize these transitions as an important long-term component of population variation (e.g., Botsford, 1981; Steele and Henderson, 1984; Ware, 2000; Jackson et al., 2001; Choi et al., 2004; Collie et al., 2004; Breitburg and Fulford, 2006). Any change in carrying capacity assuredly changes B_{MSY} .

The acceptance of regime shifts requires an acknowledgement that populations can exist in alternating stable states that are self-reinforcing for protracted periods of time. The record of oyster abundance in Delaware Bay indicates at least two regime shifts (Powell et al., 2008), circa 1970 and circa 1985, with intervening and succeeding intervals having the attributes of alternate stable population states (*sensu* Gray, 1977; Peterson, 1984; Knowlton, 2004). These periods of relative stability are multigenerational and demonstrably not of anthropogenic origin⁴ (see Knowlton, 2004) because fishing mortality rates have been far below natural mortality rates over much of this time. The periods of stability are persistent over a range of climatic conditions (Soniati et al., in press). The association of unique climatic events with each of the regime shifts is consistent with models that emphasize the unique confluence of a set of forcing factors in the initiation of catastrophic events (DeAngelis and Waterhouse, 1987; Deakin, 1990; Hastings, 1991) and supports the observation of Collie et al. (2004) that large-scale changes in the population dynamics of species are commonly characterized by a poor correlation between the response variable and potential forcing factors.

Evaluation of MSY-style reference points requires an understanding of the capacity of a species to expand its biomass over a range of biomasses. In fisheries parlance, this expansion capacity is related to surplus production. Regime shifts change expansion capacity in relation to biomass. Surplus production models are well described (e.g., Sissenwine and Shepherd, 1987; Maunder, 2003), but the influence of range shifts has rarely been considered. In the first of two companion contributions, we develop relationships supporting a surplus production model for a species, the eastern oyster (*Crassostrea virginica*), and a location, Delaware Bay, characterized by distinctive and well described range shifts. We take advantage of a 54-yr time series of oyster abundance, recruitment, and mortality for this analysis.

⁴ We recognize that the introduction of *Haplosporidium nelsoni* (MSX) circa 1957 (Burreson et al., 2000), which subsequently played a critical role in the 1985 regime shift, was likely anthropogenically driven.

Table 1

The bed groups (by location: upbay and downbay) and subgroups (by mortality rate) for the eastern oyster (*Crassostrea virginica*) collected on twenty beds in Delaware Bay, as shown in Figure 1. Mortality rate divides each of the primary groups, themselves being divided by location, a surrogate for up bay-downbay variations in dredge efficiency and fishery area-management regulations.

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

Materials and methods

The survey time series

The New Jersey survey began as a response to overfishing that had reduced stock abundance by the early 1950s. By 2006, this 54-yr record covered a number of unique periods, including the period of time after the onset of MSX, a disease caused by the protozoan *Haplosporidium nelsoni*, circa 1957 (Haskin and Andrews, 1988; Ford, 1997) and the period after the onset of Dermo, a disease caused by the protozoan *Perkinsus marinus*, circa 1990 (Ford, 1996; Cook et al., 1998).

In what follows, we define the population on the twenty primary oyster beds in Delaware Bay (Fig. 1) as the oyster stock in the New Jersey waters of Delaware Bay, but for simplicity we refer to it as the Delaware Bay oyster stock.⁵ The analyses that follow will delineate four bed groups based on the long-term average rates of natural mortality, productivity, and survey catchability (Table 1). Analyses of the Delaware Bay oyster resource

⁵ Oysters are also found on the Delaware side of the bay, although the total bed area is much less than that in the New Jersey waters (Moore, 1911; Maurer et al., 1971; Maurer and Watling, 1973), as well as in many of the river mouths; and an unknown number (but significant during certain periods of history [MacKenzie, 1996; Ford, 1997]) have been present on leased grounds, most of which are situated downbay of Egg Island (see Fig. 1 of Haskin and Ford, 1982). Inadequate survey data exist to include 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-m² basis. However, abundance and recruitment trends typically have been similar on both sides of the bay.

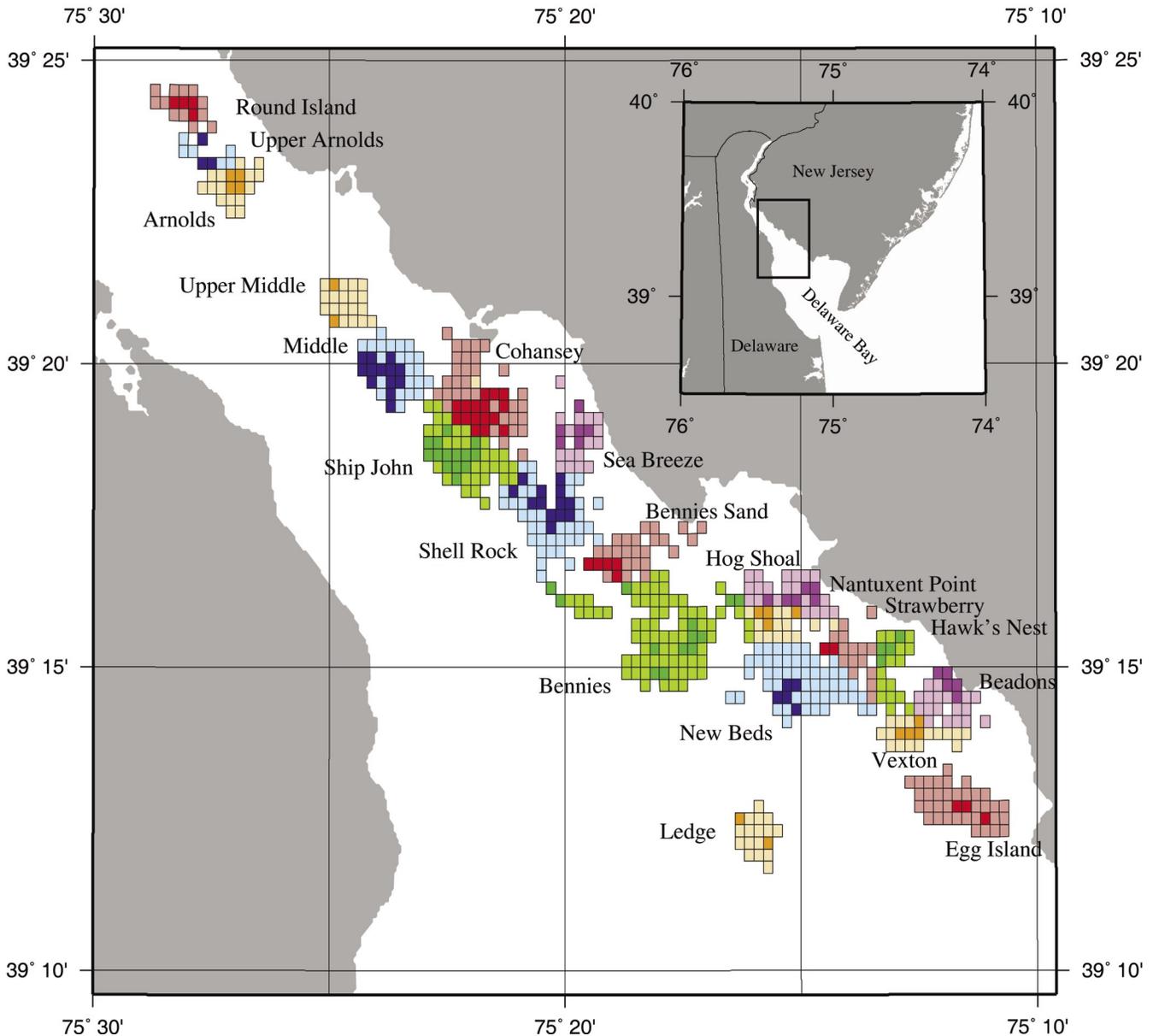


Figure 1

The twenty natural oyster beds of the eastern oyster (*Crassostrea virginica*) in the New Jersey waters of Delaware Bay may be characterized in terms of high-quality (dark shade) and medium-quality (light shade) grids, the term quality referring to a relative differential in long-term average oyster abundance (Powell et al., 2008). The footprints for the Middle bed (upper portion of figure) and the beds downbay from it, excepting New Beds, Egg Island, and Ledge, were updated with data from surveys in 2005 and 2006. The footprints for the remaining beds were based on historical definitions.

of New Jersey routinely reveal a division between an upbay group of eight beds (Round Island, Upper Arnolds, Arnolds, Upper Middle, Middle, Sea Breeze, Cohanse, and Ship John) and a downbay group of twelve beds (Shell Rock, Bennies Sand, Bennies, New Beds, Nantuxent Point, Hog Shoal, Hawk's Nest, Strawberry, Vexton, Beadons, Egg Island, and Ledge) (Fig.1). Salinity, natural mortality rate, and growth rate are higher downbay. Dredge efficiencies are significantly higher

downbay (Powell et al., 2002a, 2007). Both regions can be subdivided by natural mortality rate and productivity. In the upbay group, natural mortality rates and growth rates are significantly lower for the upper three beds, Round Island, Upper Arnolds, and Arnolds, than for the remaining beds. Henceforth these two groups will be termed "the low-mortality" and "medium-mortality" beds, respectively (Table 1). In the downbay group, growth rates and mortality rates are lower for

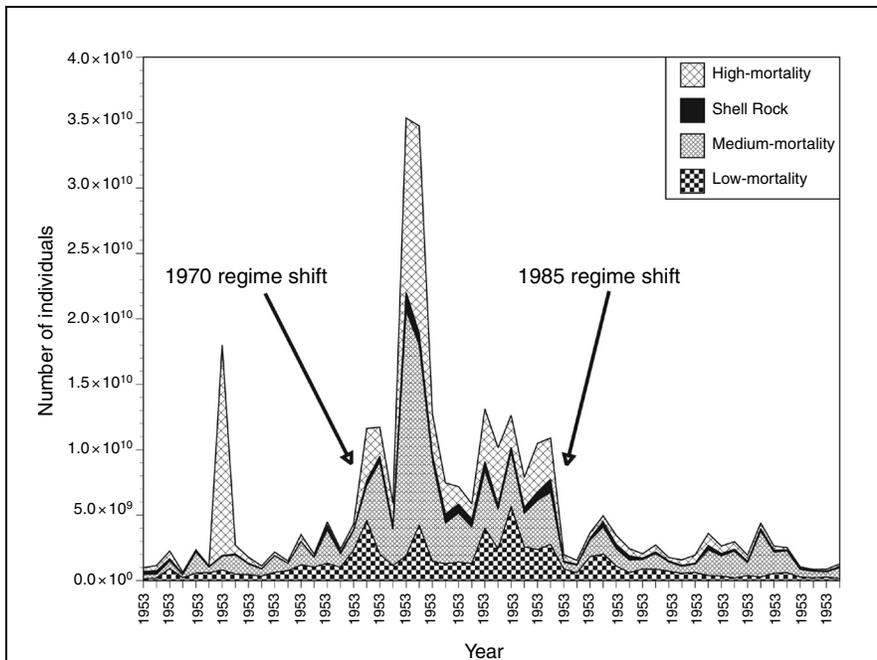


Figure 2

Time series of abundance of the eastern oyster (*Crassostrea virginica*) in Delaware Bay, showing four subgroups defined by location and natural mortality rate. Total oyster abundance for any year is the sum of abundance in the subgroups. Beds in the subgroups are listed in Table 1.

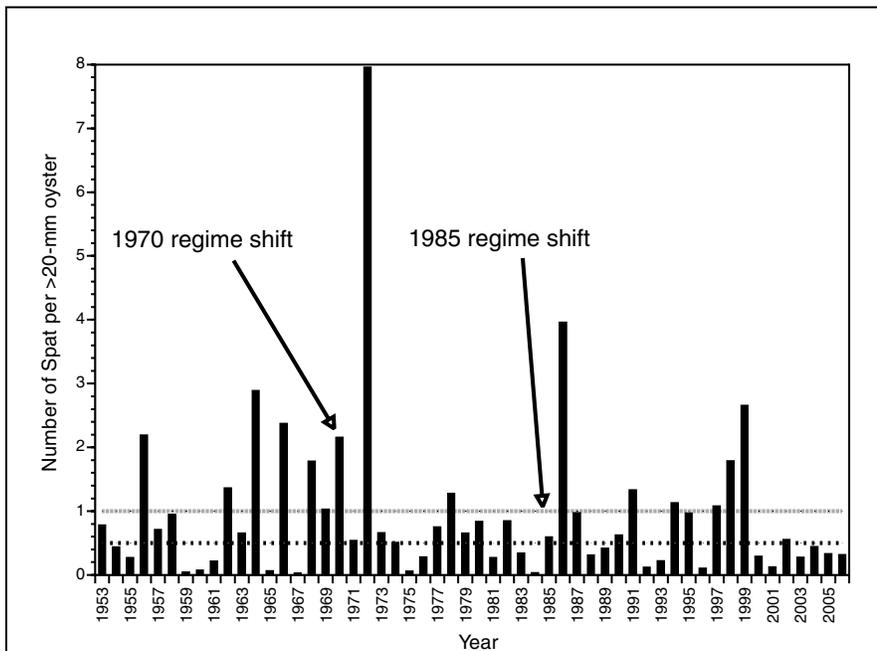


Figure 3

Time series of spat recruitment per >20-mm eastern oyster (*Crassostrea virginica*) in Delaware Bay. Solid and dashed lines mark the 1.0 and 0.5 spat-to-oyster levels, respectively.

Shell Rock, leading to its designation as a medium-mortality bed; the remainder are high-mortality beds (Table 1).

Powell et al. (2008) have described the Delaware Bay time series in detail. The pertinent findings are summarized in the following sections.

Pre-1970 period of low abundance

In the few years before 1957 when survey data were available, the Delaware Bay oyster population was characterized by relatively low abundance (Fig. 2), an unremarkable rate of recruitment (Fig. 3), relatively low natural mortality (Fig. 4), and a spatial distribution in which the fraction of the stock on the medium-mortality beds was relatively low in comparison with the 54-yr median of 0.417 (Fig. 5). The dispersion of the stock was likely maintained by overfishing because the fishery predominantly targeted the medium-mortality beds during this time (Powell et al., 2008). Given that natural mortality rates averaged below 10% during this period, and fishing rates routinely exceeded 10%, we speculate that, had fishing rates been the same as those in later years (typically <7% of the stock), the medium-mortality beds likely would have contributed a larger proportion of the stock, and stock abundance likely would have been higher than that observed.

MSX entered the picture circa 1957. Abundance was unchanged, in part because of implementation of reference point-based management that curtailed overfishing (Fegley et al., 2003; Powell et al., 2008). The early reference point referred to as “the 40% rule” limited removals from individual beds when the volume of live oysters declined below 40% of a bushel haul (Powell et al., 2008). The 40% rule successfully limited harvest from the late 1950s until the 1985 regime shift, after which changes in the fishery imposed by low abundance and Dermo required development of management alternatives and new reference points (Powell et al., 2008). Under the 40% rule,

the highest fishing mortality rate observed after 1958 was about 10% of the stock (Powell et al., 2008). By circa 1960, the effect of an increase in natural mortality, on the order of 5–10% 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 and exceeded 20% in two years (Fig. 4). Mortality substantively increased downbay and by 1960, animals on the high-mortality beds were contributing a disproportionate share of the total mortality of the population (Fig. 6). As a consequence, during the 1960s, individuals on the medium-mortality beds contributed more than their long-term median proportion of the total stock in eight of ten years (Fig. 5). Although the fishery continued to target these beds (Powell et al., 2008), the reduction in total removals minimized the influence of the fishery on the stock.

The 1970 population expansion

In 1970, the oyster population increased by more than a factor of two, and this high level of abundance was maintained for the succeeding 15 years. This was 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, hard clams along the Long Island coast (Krauter et al., 2005; Hofmann et al., 2006), and *Illex* squid off Newfoundland (Dawe et al., 2000). In many of these cases, this abundance was rapidly impacted by overfishing (e.g., Krauter et al., 2008), which artificially limited its duration. A decline in population, however, did not occur for the Delaware Bay oyster stock. However, the general coincidence of abundance in bay and shelf species, both temperate and boreal, bespeaks of a large-scale climatic event that influenced much of the northeast

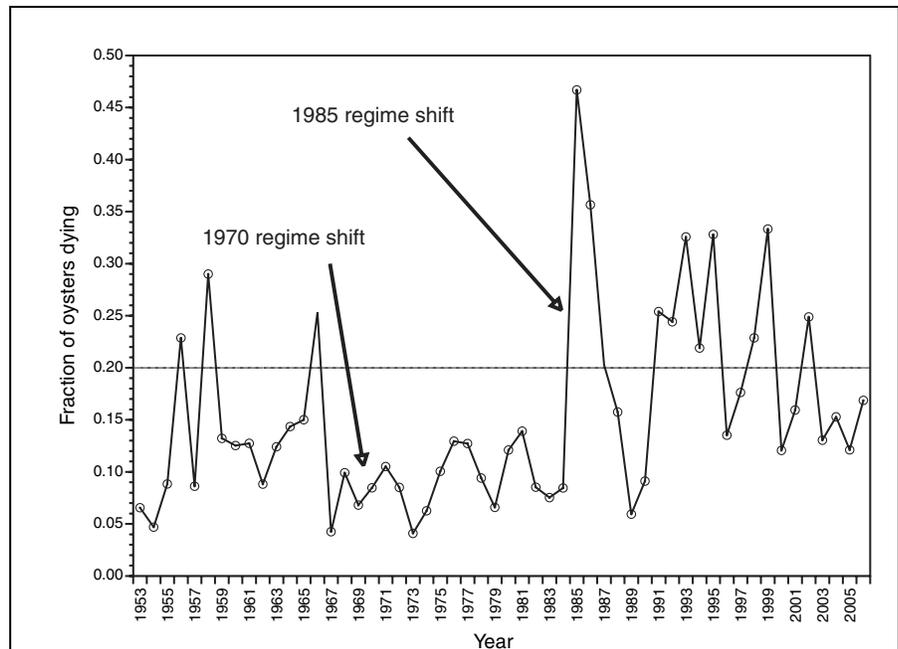


Figure 4

The fraction of eastern oyster (*Crassostrea virginica*) dying each year in the New Jersey waters of Delaware Bay, 1953–2006. Horizontal line marks an arbitrary boundary between mortality in epizootic (above the line) and non-epizootic years.

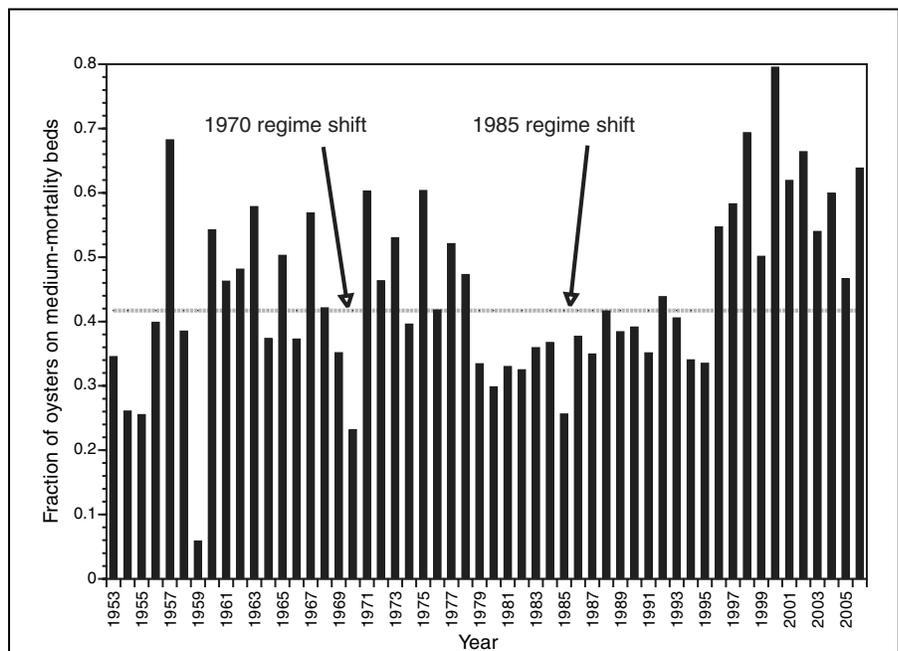
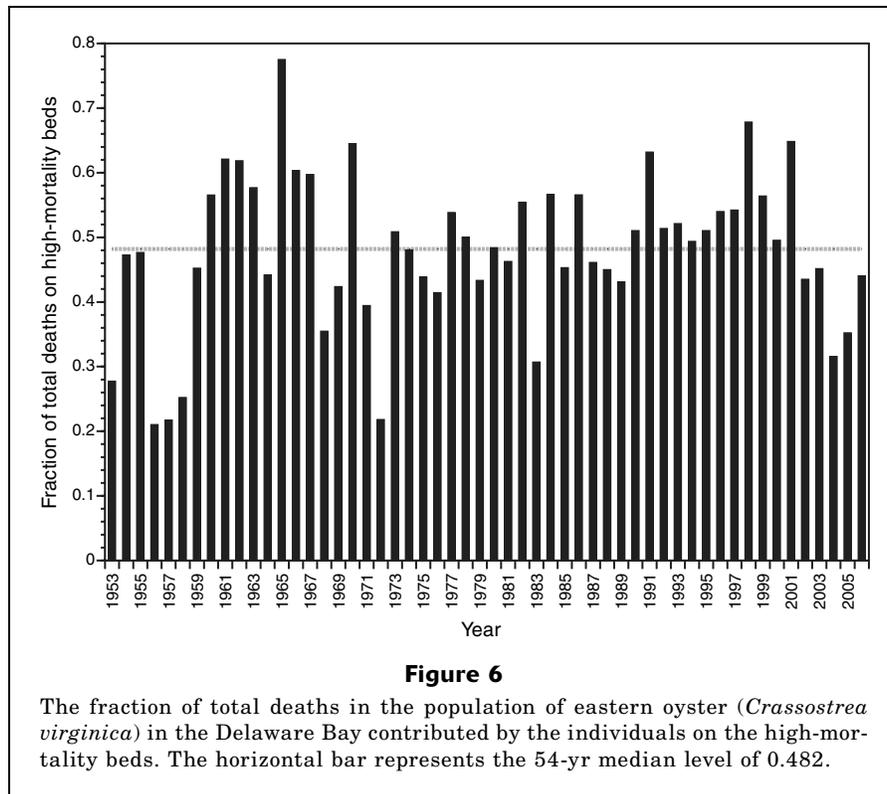


Figure 5

The fraction of the total stock of eastern oyster (*Crassostrea virginica*) in the New Jersey waters of Delaware Bay that was located on the medium-mortality beds, 1953–2006. The horizontal bar represents the 54-yr median of 0.417.



U.S. coastline. Baines and Folland (2007) documented the climatic forcing that certainly provided the basis for the 1970 regime shift, although how climate change in the North Atlantic imposed the conditions for increased productivity on the local scale remains uncertain.

Two noteworthy events preceded population expansion in Delaware Bay. First, 1968–70 were three successive years of relatively high recruitment (Fig. 3). Only one other trio of such years, 1997–99, exists in the time series. Relatively high recruitment in these three years occurred in three of four bay subgroups (medium-mortality, Shell Rock, and high-mortality). No equivalent coincidence of years and bay coverage exists in the time series. Second, beginning in 1967, natural mortality dropped below 10% after the largest MSX epizootic event of the 1960s and remained at or below this level through 1975 (Fig. 4). The coincidence of dramatically lower natural mortality and a triplex of high recruitment years was unique in the time series and certainly provided the proximate conditions for the population expansion of 1970.

The 1970–85 high-abundance interval and its termination

The 1970–85 time period was remarkable for its persistent high level of oyster abundance (Fig. 2). The period was characterized by a lower contribution of animals on the high-mortality beds to total population mortality (Fig. 6) and by natural mortalities that rarely exceeded 13% of the stock annually (Fig. 4). During this

period, the fraction of deaths on the high-mortality beds exceeded the long-term median only six times (Fig. 6). In the first half of the period, the medium-mortality beds contributed proportionately more to the stock, as they had during most of the MSX-dominated decade that preceded this period (Fig. 5). High freshwater inflow contributed to sustainable high abundance by limiting mortality from MSX. A dramatic shift in stock dispersion began in 1979, coincident with the cessation of consistently high freshwater inflows, and led, over a few years, to proportional increases in abundance in the more environmentally sensitive waters of the upbay and downbay margins. An increase in the susceptibility of the population to epizootic disease mortality consequent of the increased abundance downbay evolved from 1985 to 1986 through a coincidence of climatic events into the largest epizootic event in the recorded history of Delaware Bay (Fig. 4). Interestingly, the 1985–86 stock collapse was not obviously associated with any unusual trends in recruitment immediately before or after the collapse (Fig. 3), nor did the distribution of deaths (Fig. 6) or the dispersion of the stock (Fig. 5) change. Abundance declined in all bay regions.

The post-MSX period

The few years immediately following the 1985–86 MSX epizootic event and preceding the onset of Dermo circa 1990 were not unusual in any way, and neither was the first half-decade after Dermo became an important contributor to population mortality. Total abun-

dance remained relatively stable from 1987 through 2001 (Fig. 2). Recruitment was not unusual (Fig. 3). However, natural mortality rose dramatically, from the 10% level immediately after 1986, to often exceed 20–30% throughout the 1990s (Fig. 4). The fraction of deaths contributed by the high-mortality beds did not change markedly over the 1990s, although the fractions of deaths did rise incrementally in 1990 compared to the few preceding years (Fig. 6). The dispersal pattern of the 1980s remained through 1995 (Fig. 5), despite the increased mortality rate on the high-mortality beds.

The response of the stock to Dermo became more apparent in 1996, when the stock began a rapid contraction to its refuge on the medium-mortality beds. This contraction in dispersion occurred at the same time as increased recruitment on these beds (Fig. 5) and counterweighed the accumulating losses of individuals farther downbay (Fig. 6), so that total abundance did not change.

The post-2000 era

Although the time series is still limited in scope, a change in population dynamics is evident around 2000. Beginning in 2000, the recruitment rate declined precipitously and remained low at least through 2006 (Fig. 3). Total abundance declined with continuing high mortality on the high-mortality beds (Fig. 6), but stock consolidation continued, with an increasing proportion of animals on the medium-mortality beds. As a consequence, mortality in the population as a whole declined (Fig. 4). The fraction of total mortality contributed by the high-mortality beds declined to its lowest level since the 1950s and remained low (Fig. 6) because consolidation of the stock upbay limited the number of individuals available to die on the high-mortality beds.

Overview of fishing activities

The analysis that follows makes reference to two distinctive types of fishing on the Delaware Bay oyster beds of New Jersey. From 1953 through 1995, a “bay-season” fishery occurred, in which a portion of the beds was opened, usually for 2–6 weeks in the spring. Oysters were removed *en masse* and transplanted downbay to leased grounds. Based on recent dredge efficiency estimates (Powell et al., 2007), the method for transplanting was relatively nonselective for oyster size; oysters were moved more or less in proportion to their contribution to the size-frequency distribution of the population. In most years, the fishery was limited by the 40% rule. As a consequence, target beds varied during the program from year to year as the relative abundance of the resource varied.

Since 1996, a direct-market fishery has been prosecuted for the most part on beds from Shell Rock downbay (Fig. 1). In this fishery, market-size oysters are taken directly off the beds and marketed immediately or stored for a time on leased grounds before they are marketed. The vast majority of animals removed by this fishery have exceeded 63 mm (Powell et al., 2005).

Model formulations and statistics

Basic population dynamics Quantification of the Delaware Bay time series has been described in Powell et al. (2008). Natural mortality fractions were obtained from box counts under the assumption that

$$N_{oysters_{t-1}} = N_{boxes_t} + N_{live\ oysters_t}, \quad (1)$$

where N = the number of individuals; and
 t = any given year.

Hence

$$\Phi_{bc} = \frac{N_{boxes_t}}{N_{boxes_t} + N_{live\ oysters_t}}, \quad (2)$$

where Φ_{bc} = mortality expressed as the fraction of individuals alive at the end of year t that died during the next year, based on box counts (bc).

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

However, boxes very likely do not adequately measure the mortality of juvenile animals. Juvenile shells are taphonomically more active (Cummins et al., 1986a, 1986b; Powell et al., 1986; Glover and Kidwell, 1993) and thus can be expected to remain intact for a relatively short time. In addition, deaths of smaller animals do not leave intact boxes as often because many deaths are caused by shell-crushing predators (Powell et al., 1994; Alexander and Dietl, 2001; Milke and Kennedy, 2001). Inasmuch as the mortality rate of juvenile animals is likely to be underestimated by box counts, the fraction dying, but not recorded by box counts, Φ_0 , was obtained by difference:

$$\Phi_0 = \frac{(N_t - N_{t-1}) - (R_{t-1} - \Phi_{bc}N_{t-1} - \Phi_f N_{t-1})}{N_{t-1} + R_{t-1}}, \quad (3)$$

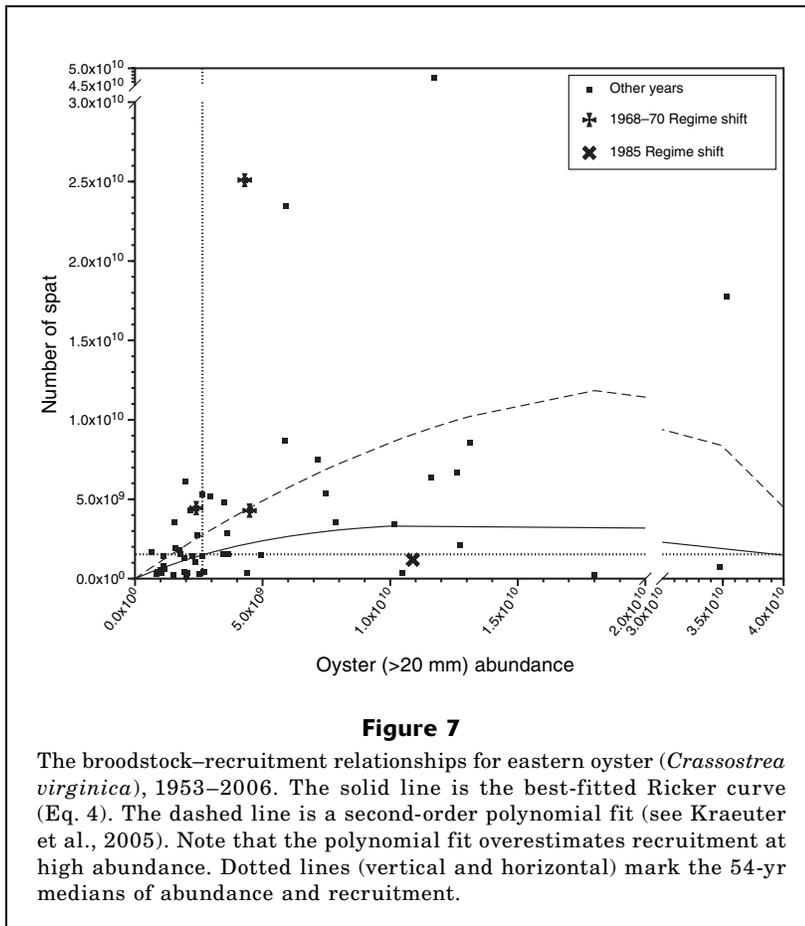
where Φ_f = the fraction taken by the fishery;

R = the number of recruits into the population; and the first parenthetical term on the right-hand side represents the difference in abundance between two consecutive surveys.

Mortality unrecorded by box counts, Φ_0 , varied randomly over the time series, with a 54-yr mean of 0.274 and a 54-yr median of 0.311 (Powell et al., 2008).

Forces modifying abundance: broodstock–recruitment relationship A linear fit to the broodstock and recruitment data returned a regression coefficient of only 0.076 (Fig. 7). The relationship was strongly compensatory. A variety of broodstock–recruitment models might be applied (e.g., May et al., 1978; Hilborn and Walters, 1992; Krauter et al., 2005), given the scatter of data at high abundance and the paucity of extremely high values. We used a relationship that produced declining recruitment at high abundance (overcompensation *sensu* Hancock, 1973; McCann et al., 2003), because shellfish can achieve densities sufficient to limit growth and reproduction (e.g., Fréchette and Bourget, 1985; Fréchette and Lefaivre, 1990; Powell et al., 1995). Application of the simple filtration model of Wilson-Ormond et al. (1997) indicated that present-day abundances, even on the medium-mortality beds, are below such densities, but abundances in the 1970s were very likely high enough and medium-mortality abundances circa 2002 (Fig. 2) may have been high enough to restrict growth. Thus, from Hilborn and Walters (1992):

$$\tilde{R}_t = \tilde{N}_{t-1} e^{-a \left(1 + \frac{\tilde{N}_{t-1}}{\beta} \right)}, \quad (4)$$



where \tilde{R} = the number of spat in millions; and \tilde{N}_{t-1} = oyster abundance in millions.

Fitting this curve to the data for the high- and medium-quality strata (Fig. 1) yields $\alpha = 0.3746$, and $\beta = 5121.9$ (Figs. 7 and 8). We compared the result of Equation 4 to the result of a best-fit linear regression with zero intercept (Fig. 8). The linear relationship is

$$R_t = 0.493 N_{t-1}. \quad (5)$$

Broodstock and box-count mortality Box-count estimates of natural mortality are also related to trends in abundance (Fig. 9). At abundances greater than 4×10^9 , mortality was low. The fraction dying each year averaged 9.6% for these nonepizootic years, defined for convenience as years in which the fraction dying was less than 20%. The nonepizootic death rate was relatively independent of abundance, although the lowest mortalities, less than 6%, occurred at abundances below 6×10^9 .

Of the 14 epizootic years in the 54-yr record, defined in our study as deaths exceeding 20% of the stock, 13 occurred at abundances less than 3×10^9 (Fig. 9). The exception was 1985. Of the 32 years with abundances less than 3×10^9 , 14 were epizootic years. Of these 32, only one had a fractional mortality between 0.15 and 0.20. Accordingly, two divergent outcomes existed over a range of low abundances. In some years, the fraction dying approximated the long-term mean for high-abundance years, about 9.6%. In other years, epizootic mortalities occurred. Epizootic events also occur rarely at very low abundances. Note on Figure 9 that no mortality fraction exceeded 0.17 at abundances below 1.5×10^9 . Thus, a complex relationship exists between abundance and mortality.

We apply an admittedly *ad hoc* empirically derived equation to describe the relationship between box-count mortality and abundance depicted in Figure 9:

$$\Phi_{bc_t} = \omega + \kappa \log_e (\tilde{N}_{t-1} + \rho) - \varphi \tilde{N}_{t-1} + \chi \tilde{N}_{t-1} e^{-\left(\frac{(\tilde{N}_{t-1} - \psi)^2}{2v^2} \right)}, \quad (6)$$

where $\omega = 0.055$;

$\kappa = 0.03$;

$\rho = 1.0$;

$\varphi = 0.0025$

$\chi = 0.1$;

$\psi = 2.2$;

$v = 0.8$; and

\tilde{N} is expressed as billions of animals.

Equation 6 has the unique property of eliciting both depensatory and compensatory trends at low abundance. Sissenwine (1984), Hilborn and Walters (1992), and Peterson et al. (2001) have provided examples of the well-known depensatory process in which increased predatory mortality rate is associated with increased prey population density because of increased prey preference at high prey density. Allen (1979) provided a somewhat unusual case for depensation in oysters determined by substrate availability rather than by disease. Hilborn and Walters (1992) provided an analogous example from human exploitation of declining fish stocks. The present case is unusual, however, because box-count mortality first increases with declining abundance, but this depensatory phase is then followed by compensation in the mortality rate as abundance continues to decline.

Calculation of first passage time

Mean first-passage times were calculated from Redner (2001), according to the methods of Rothschild et al. (2005) and Rothschild and Mullen (1985). Input data were obtained by dividing a two-dimensional data set into quadrants by the medians of the x and y variables (Fig. 10). An example frequency table for the broodstock and recruitment relationship (Table 2) shows the frequency of occurrence of the data from the 54-yr time series in each of the four quadrants, employing the quadrant numbering convention depicted in Figure 10. For instance, years characterized by low abundance and low recruitment, thus falling into quadrant 1, occurred 32% of the time. Table 2 also displays one-year transition probabilities compiled by examining the quadrant location of the x - y datum in successive years. For example, a low-recruitment+low-abundance year falling into quadrant 1, was followed one year later by a high-recruitment+high-abundance year, an occurrence falling into quadrant 4, 18.8% of the time, whereas 50% of the time, the following year was also a low-recruitment+low-abundance year. Thus, given that quadrant 1 is the starting point, the interval of time in which the population finds itself back in quadrant 1 should be a lesser number of years than the time required for the population to shift from quadrant 1 to quadrant 4. Mean first passage times (Table 3) express the number of years likely to elapse before the population with the x - y relationship characteristic of any one quadrant is again described by the relation-

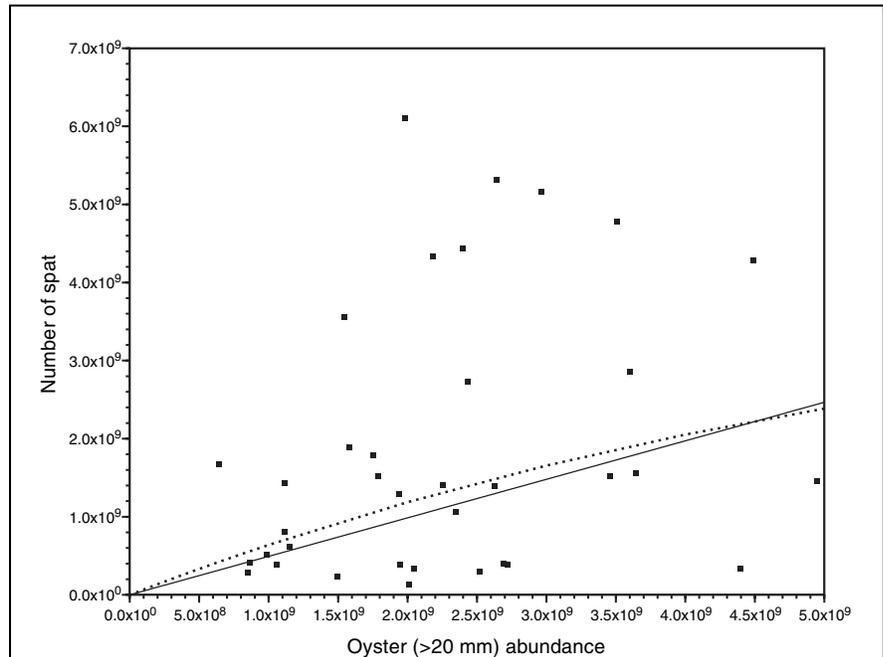


Figure 8

The low-abundance portion of the broodstock–recruitment relationship for the natural oyster beds of eastern oyster (*Crassostrea virginica*) in Delaware Bay, 1953–2006. The dotted line is the best-fitted Ricker curve (Eq. 4), also shown in Figure 7 for the entire data set. The solid line is a linear fit (Eq. 5) with zero intercept. Note that at low abundance, the linear fit travels through the recruitment values slightly below that traversed by the Ricker curve.

ship characteristic of that same quadrant, or obtains the relationship characteristic of one of the three other quadrants.

Results and discussion

Biological relationships that determine population dynamics

Broodstock and recruitment A relationship between broodstock and recruitment is commonly found for shellfish (Hancock, 1973; Peterson and Summerson, 1992; McGarvey et al., 1993; Lipcius and Stockhausen, 2002; Kraeuter et al., 2005), although not in every case has one been observed (Hancock, 1973; Crocos, 1991; Honkoop et al., 1998; Livingston et al., 2000). Such a relationship is commonly assumed for population dynamics models, and the adequacy of these models supports the likely importance of such a relationship in oysters (Mann and Evans, 1998, 2004; Deksheniaks et al., 2000; Powell et al., 2003). However, empirical evidence in oysters is contradictory and not well documented (e.g., Hofstetter, 1983; Mann et al., 1994; Southworth and Mann, 1998; Livingston et al., 2000), and the travails of larval life and at settlement are certainly likely to add considerable uncertainty to the success of any search for such

evidence (Osman et al., 1989; Powell et al., 2002b, 2004; Hofmann et al., 2004).

In Delaware Bay, recruitment rates below 2×10^9 spat are disproportionately associated with abundances of less than 3×10^9 oysters (Fig. 7). The distribution of years in the four quadrants of the broodstock–recruitment diagram was 17, 9, 9, and 18 for quadrants 1, 2, 3, and 4 (as defined in Fig. 10), respectively (Table 2). This distribution was unlikely by chance, given the expectation that one-quarter of the years should fall into each

quadrant: $P \sim 0.10$, $P < 0.10$; $P < 0.10$; $P < 0.10$, for quadrants 1–4, respectively (binomial test: $p = 0.25$, $q = 0.75$). Twice as many high-recruitment events were associated with high abundance than with low abundance, and about twice as many low-recruitment events were associated with low abundance than with high abundance. The 54-yr average recruitment rate, expressed as the number of spat per >20-mm oyster per year, was 0.959. The median was lower, at 0.600. The long-term likelihood of a one-year population-replacement event (i.e. one spat per >20-mm oyster) was 17 in 54, and a recruitment rate half that high occurred in 27 of 54 years (Fig. 3).

Only four massive recruitment events ($>1.7 \times 10^9$ spat) occurred over the 54 years (Fig. 7). The rarity of these occurrences is not unusual (e.g., Loosanoff, 1966; Hofstetter, 1983; Oviatt, 2004; Southworth and Mann, 2004). The events were not predicted by the broodstock–recruitment curve. In most years, however, the broodstock–recruitment relationship was relatively predictive, and the vast majority of recruits sustaining the population over the 54 years accrued from the 50 more-standard recruitment events. Nevertheless, even in average recruitment years, variability about the curve was large, about 4×10^9 spat.

Mean first-passage times calculated from one-year transition probabilities (Table 2) varied from 3 to 8 years (Table 3). Return intervals were about 3 years for a population beginning in quadrant 1 (low recruitment and low abundance) returning to quadrant 1, and for a population beginning in quadrant 4 (high recruitment and high abundance) returning to quadrant 4. The longest return intervals were associated with quadrant 3 (low recruitment and high abundance) as a destination. A population beginning in quadrant 2 or quadrant 3 was somewhat more likely to fall to quadrant 1 than to move to quadrant 4. Thus, overall, populations at low abundance were likely to remain there (quadrant 1) because of low recruitment, whereas populations at high abundance were likely to remain there because of high recruitment. Quadrants 1 and 4 have the characteristics expected of stable states.

The broodstock–recruitment relationship (Fig. 7) indicated that the number of recruits per adult declined at high abundance. Note in particular (Fig. 3) that the number of recruits per adult was not unusually high during the 1970–85 high-abundance period, with the exception of 1972. In fact the number of one-year replacement events (i.e. one spat per adult) was lower for a longer time during this

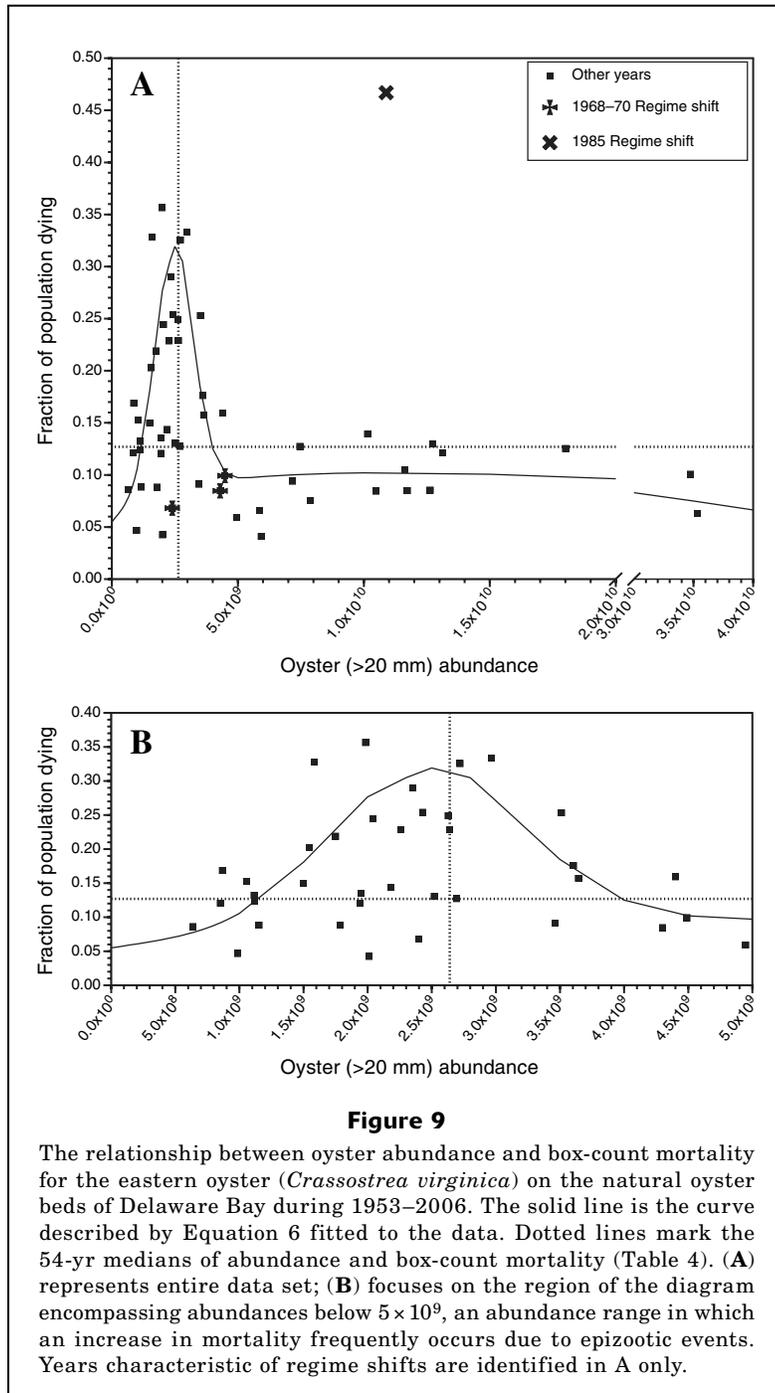


Table 2

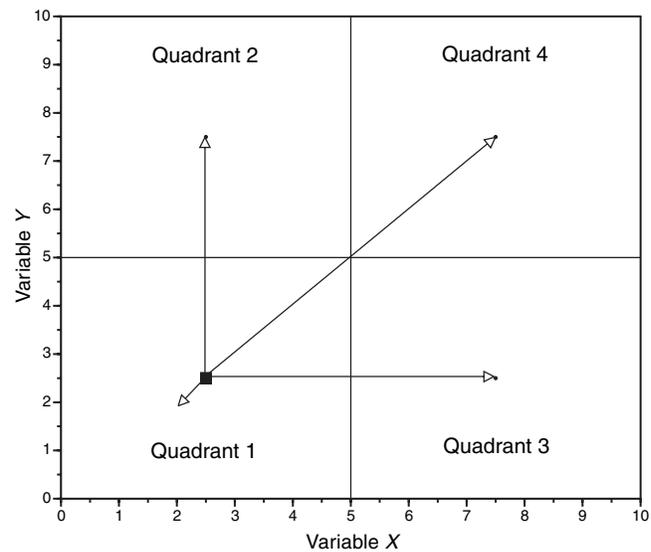
One-year transition probabilities and the frequency of occurrences for the eastern oyster (*Crassostrea virginica*) population in each quadrant over the 54-yr time series were calculated from the Delaware Bay oyster broodstock–recruitment distribution (Fig. 7). Median abundance over 54 years was 2.64×10^9 and median recruitment was 1.53×10^9 . Arrows indicate trajectories between quadrants. Quadrants are defined in Figure 10.

Quadrant	1	2	3	4
1 →	0.500	0.125	0.188	0.188
2 →	0.444	0.222	0.000	0.333
3 →	0.222	0.333	0.333	0.111
4 →	0.111	0.111	0.167	0.611
Frequency of occurrence	0.320	0.170	0.170	0.340
Number of years	17	9	9	18

15-yr period than at any other time before 2000. Thus, high broodstock abundance was not rewarded by equivalently high recruitment. Three mechanisms seem viable. The first is that fecundity declines at high abundance as availability of food becomes limited. Food limitation by high densities of filter feeders is well described (e.g., Peterson and Black, 1987; Rheault and Rice, 1996; Wilson-Ormond et al., 1997). The second is that cannibalism of larvae occurs, but this cause of mortality is of unlikely importance (Andre et al., 1993; Tamburri et al., 2007). The third is that predation rates on juveniles increase at high abundance. Although little evidence of this effect exists (e.g., Whitlatch and Osman, 1994; Powell et al., 1995), a proportional increase in predation on juveniles at high abundance is consistent with optimal foraging theory (Hughes, 1980), under the assumption that oyster predators are optimal foragers (Powell et al., 1995; see also Pyke, 1984; Pierce and Ollason, 1987). All are standard explanations for compensation in the broodstock–recruitment relationship (e.g., Myers and Barrowman, 1996).

The broodstock–recruitment diagram (Fig. 7) indicates that low abundance limited total recruitment in some way. This relationship is clear despite the exclusion from this data series of an unknown number of adults and recruits in State of Delaware waters, along the fringes of the bay, particularly in the river mouths, and on the leased grounds downbay of the high-mortality beds. Moreover, the leased grounds likely retained substantial numbers of adult animals before the mid-1980s, although estimates of abundance are not available. Many fewer were present thereafter because of the demise of the bay-season fishery.⁶ Interestingly, the

⁶ Anecdotal information indicates that numbers were low in the 1960s as well.

**Figure 10**

Mean first passage times for eastern oyster (*Crassostrea virginica*) were calculated by employing an arbitrary quadrant numbering convention. One-year transition probabilities were obtained by examining the position of consecutive x - y data pairs in quadrant space. Four transitions are possible for each starting position, the possibilities for quadrant 1 being depicted. Sixteen total trajectories are possible.

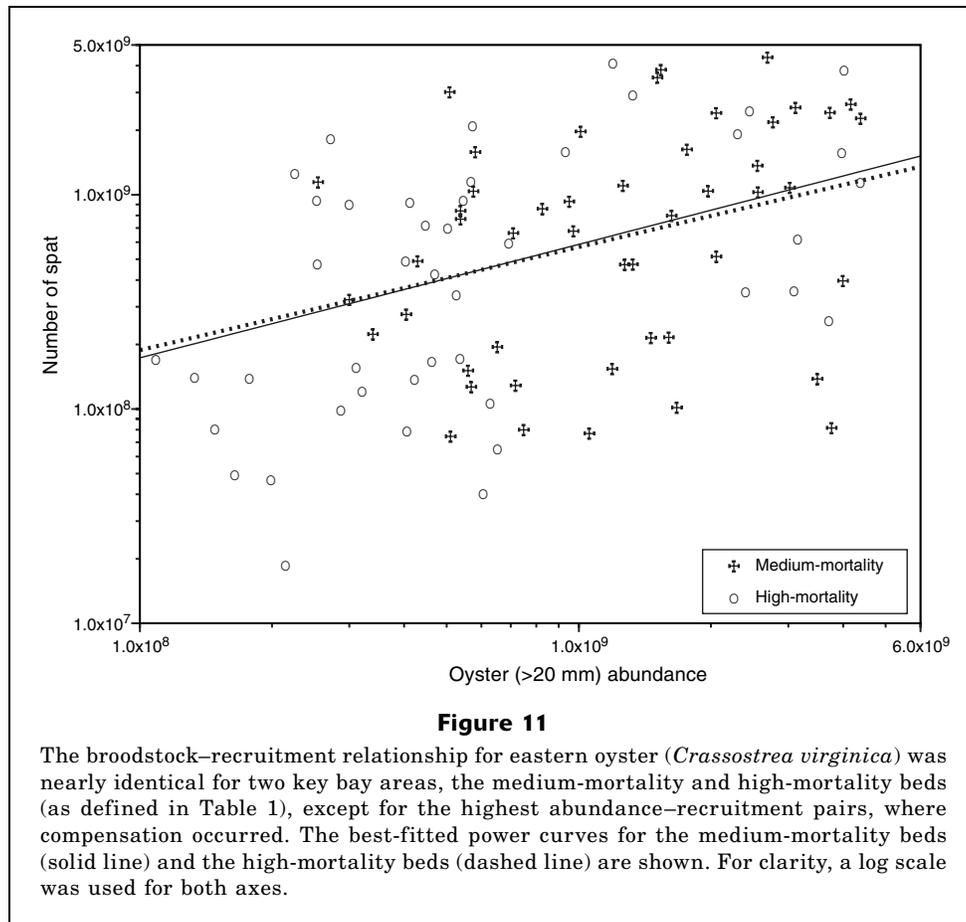
Table 3

Mean first passage times, as well as the distribution of occurrences of the eastern oyster (*Crassostrea virginica*) population in each quadrant, after an infinite number of steps were calculated from the Delaware Bay oyster broodstock–recruitment distribution (Fig. 7). The observed distribution of occurrences is given in Table 2. Arrows indicate trajectories between quadrants. Quadrants are defined in Figure 10.

Quadrant	1	2	3	4
Mean first passage time (yr)				
1 →	3.25	6.06	6.45	5.00
2 →	3.60	5.78	7.82	4.14
3 →	4.20	4.56	5.78	5.24
4 →	5.40	6.26	6.65	2.89
Distribution after an infinite number of steps	0.308	0.173	0.173	0.346

decline in abundance on leased grounds after 1985 does not generate a perceptible change in the broodstock–recruitment relationship.

Oyster larvae tend to set preferentially on live oysters and boxes rather than on cultch (shell clumps, shells,



and shell fragments without attached live oysters or boxes) (Powell et al., 2008); therefore, one possible explanation for the relationship between broodstock and recruitment is that adult abundance increased settlement success by providing a principal source of clean shell. Two avenues of evidence support this idea. First, a recruitment-enhancement program initiated in 2005 strongly indicated that Delaware Bay is not larvae-limited, even at low population abundance levels (unpubl. data, first author). Clean shell planted at the appropriate time consistently sustains a settlement rate 5 to 10 times that for native shell. Second, the relationship between adult numbers and recruitment held for the bay overall, even though the numbers of animals in various regions of the bay varied relatively independently, and independently of numbers for the bay as a whole. The broodstock–recruitment relationship was nearly identical for two key bay areas, the medium-mortality and high-mortality beds (Fig. 11), despite widely and independently varying abundances over the time series (Fig. 5). Different trajectories would have been expected if recruitment rate depended upon a stock-wide abundance with trends divergent from local peregrinations.

Broodstock and mortality Epizootics, here defined as bay-wide disease-induced mortality events affecting

greater than 20% of the stock, occurred in about half of the years since 1989 (Figs. 4 and 9), but with much lower frequency in prior years. Deaths in nonepizootic years affected on average around 10% of the stock. All but one of the epizootics occurred at abundances between 1.5×10^9 and 4×10^9 . The single outlier occurred at just over 10×10^9 animals; this is the 1985 MSX epizootic event that terminated the high-abundance period of the 1970s. The remaining events included the relatively few MSX epizootics of the 1950s and 1960s and the more frequent Dermo epizootics of the 1990s and 2000s. The distribution of data points in the four quadrants based on information in Figure 9 was 9, 17, 17, and 10 in quadrants 1, 2, 3, and 4, respectively (Table 4). This distribution is unlikely to occur by chance, but barely so: $P < 0.10$, $P \sim 0.10$; $P \sim 0.10$; $P > 0.10$, for quadrants 1–4, respectively (binomial test: $p = 0.25$, $q = 0.75$). Note that the use of the median mortality of 0.127 to define high- and low-mortality quadrant groups yields a number of nonepizootic years in the same quadrants as the epizootic years (those with mortalities exceeding 0.20). Thus, the high-mortality quadrants include years when mortalities were not extraordinarily high. Note also that high-abundance years, those with abundance exceeding the median of 2.64×10^9 , include a few epizootic years with abundances near the median. That is, the use of

Table 4

One-year transition probabilities, as well as the frequency of occurrence, of the eastern oyster (*Crassostrea virginica*) population in each quadrant over the 54-yr time series were calculated from the Delaware Bay oyster broodstock–mortality distribution (Fig. 9). Median abundance was 2.64×10^9 and the median mortality fraction was 0.127. Arrows indicate trajectories between quadrants. Quadrants are defined in Figure 10.

Quadrant	1	2	3	4
1 →	0.222	0.444	0.222	0.111
2 →	0.125	0.500	0.063	0.313
3 →	0.059	0.059	0.647	0.233
4 →	0.300	0.400	0.300	0.000
Frequency of occurrence	0.170	0.320	0.320	0.189
Number of years	9	17	17	10

medians allocates most, but not all, epizootic years in the abundance range of 1.5×10^9 to 3×10^9 to a single quadrant.

Nevertheless, even with this ambiguity, high-mortality events were more likely with low abundance and some transitions were more likely to occur than others. Mean first-passage times were particularly long for transitions to quadrant 1 (low-mortality+low-abundance), always exceeding 6 years (Table 5). Mean first-passage times were also long for most transitions to quadrant 3, the low-mortality+high-abundance quadrant, with the exception of those with quadrant 3 as the initial state. By contrast, the population was likely to return to quadrant 2 (high-mortality+low-abundance) from most quadrants in about 3–4 years (Table 5). This return interval is an expression of the relative frequency of Dermo epizootics. Interestingly, the tendency to return to quadrant 2 (high-mortality+low-abundance) was distinctly less from quadrant 3 (low-mortality and high abundance) than from other quadrants. High-mortality events were unlikely to occur when abundance was high. The distribution of first-passage times again supports the presence of multiple stable states for the Delaware Bay oyster population.

The distribution of mortality with abundance is not constant, nor does it display a simple density dependency. Epizootics occurred less often at high abundance and near lowest abundance. Decreased mortality at low abundance was not unexpected for a population exposed to a disease that generates epizootic conditions (Gill, 1928; Ackerman et al., 1984; Kermack and McKendrick, 1991). Normally, transmission rates of disease decline with decreased host density because contact rates decrease (Black, 1966; Andreassen and Pugliese, 1995; Godfray and Briggs, 1995; Heesterbeek and Roberts, 1995) and this leads to lower rates of mortality. This decline in transmission rates is true for nearly all diseases but does not seem to be the case for MSX

Table 5

Mean first passage times as well as the distribution of occurrences of the eastern oyster (*Crassostrea virginica*) population in each quadrant after an infinite number of steps were calculated from the Delaware Bay oyster broodstock–mortality distribution (Fig. 9). The observed distribution of occurrences is given in Table 4. Arrows indicate trajectories between quadrants. Quadrants are defined in Figure 10.

Quadrant	1	2	3	4
Mean first passage time (yr)				
1 →	6.54	3.55	6.14	4.59
2 →	6.87	3.03	7.09	3.67
3 →	8.10	6.00	3.11	4.21
4 →	6.18	3.88	5.68	5.11
Distribution after infinite steps	0.153	0.339	0.321	0.196

or Dermo, which are characterized by inherently high transmission rates over a wide range of abundance (Hofmann et al., 1995; Powell et al., 1996, 1999). In the Delaware Bay oyster stock, the declining frequency of epizootics at low abundance originates in the dynamics of stock dispersion. A contraction of the stock away from areas of highest disease mortality normally is associated with low abundance. Thus, epizootics are most likely to occur in a narrow window of abundance as the stock expands from its habitat of refuge on the medium-mortality beds, thereby leaving a greater proportion of the stock once again on the medium-mortality beds. This stock contraction, consequently, mitigates against a recurrence of the high-mortality event. Depensation in the mortality rate as abundance declines is, of course, an extinction scenario, were it to continue. The countervailing compensatory process of stock contraction is the dominant protective action against local extinction, rather than a decline in host density that reduces disease transmission rates.

What is unusual is the low probability of epizootics at high abundance. Mortality rates are often assumed to be invariant over a wide abundance range for marine species (e.g., Paloheimo, 1980; Hoenig, 1983; Vetter, 1987; Clark, 1999) and, contrariwise, increased mortality at high abundance is expected of most populations exposed to epizootic disease (e.g., Anderson and Gordon, 1982; Andreassen and Pugliese, 1995; Godfray and Briggs, 1995; Jaenike, 1998). Neither expectation conforms to what has been observed. Thus, one of the interesting quandaries is the maintenance of population abundance near the higher carrying capacity of the population during the 1970s–1985 high-abundance period. Some portion of this was caused by reference point-based management, which controlled fishing mortality to values normally below 5% of the stock (Powell et al., 2008). Some portion was due to higher than

average freshwater inflows for much of the 1970s, which limited the influence of MSX. However, the fact that high abundance continued for at least five years after freshwater inflows subsided to more normal conditions circa 1979, and the depensation in the abundance–mortality relationship, would indicate that high abundance may reduce the probability of epizootics. This possibility has been treated theoretically by Powell et al. (1996), who showed that simulated oyster populations undergoing significant increases in abundance were very unlikely to also generate Dermo epizootics. Simulations indicate that the oyster population can expand more rapidly than Dermo can expand and intensify, when the number of recruits is high (Fig. 7). Alternatively, or perhaps as an abetting process, the number of infective elements in the water column may be reduced below the level needed to generate an infective dose because of the volume of water filtered by the population at high abundance. An infective dose is hypothesized for MSX (Ford et al., 1999; Powell et al., 1999), and some evidence supports dose-dependency in Dermo (Bushek et al., 1997). However, insufficient information on the interaction of disease with oyster populations at high abundance is available to definitively decipher the relationship between parasite and host at high abundance because oyster populations at high abundance are now rare or nonexistent for study.

Interpretation and application of the compensatory and depensatory portions of the mortality curve described by Equation 6 (Fig. 9) come with a number of important caveats. 1) The probability of occurrence of an epizootic has increased since 1990 with the replacement of MSX by Dermo as the primary disease that produces mortality. An increase in frequency may be expected because of the greater tolerance of the parasite for low salinity (e.g., Ford, 1985; Powell et al., 1996; Ford et al., 1999; Ragone Calvo et al., 2001). Thus the ambit of oyster population dynamics may be more restricted by Dermo than by MSX. 2) The time series contains no high-abundance years since the replacement of MSX by Dermo circa 1990. Whether a return to high abundance is precluded by Dermo is unknown, but the difference in transmission dynamics between the two parasites (e.g., Ford and Tripp, 1996) and the expanded environmental range of Dermo in comparison to MSX would indicate that this may be the case. 3) Environmental conditions have not been constant over the 54 years, and environmental change significantly influences the chief agents of increased mortality, MSX and Dermo, as well as the autocorrelational dynamics of the epizootic process (e.g., Soniat et al., 1998). The mortality curve integrates environmental and biological dynamics. 4) The rise in winter temperature since the 1970s, that accelerated after 1990 (Scavia et al., 2002; Nixon et al., 2004), may have modified the interaction of disease with oyster population dynamics (e.g., Ford, 1996; Cook et al., 1998, see also Hofmann et al., 1995; Powell et al., 1996), decreasing the applicability of the pre-1990 portion of the time series. 5) As abundance declines, a greater proportion of the oyster population is found on

Table 6

One-year transition probabilities, as well as the frequency of occurrences of the eastern oyster (*Crassostrea virginica*) population in each quadrant over the 54-yr time series were calculated from the Delaware Bay oyster recruitment–mortality distribution (Fig. 12). Median recruitment was 1.53×10^9 and the median mortality fraction was 0.127. Arrows indicate trajectories between quadrants. Quadrants are defined in Figure 10.

Quadrant	1	2	3	4
1 →	0.308	0.385	0.077	0.231
2 →	0.231	0.385	0.077	0.308
3 →	0.143	0.071	0.714	0.071
4 →	0.231	0.231	0.154	0.385
Frequency of occurrence	0.241	0.259	0.259	0.241
Number of years	13	14	14	13

the medium-mortality beds (Powell et al., 2008). As a consequence, the probability of an epizootic begins to decline at abundances somewhere above 1×10^9 animals. Insufficient data are available to determine the trajectory for extrapolating this curve to lower abundances; therefore considerable uncertainty exists regarding the implementation of the abundance–mortality curve for abundances below 0.8×10^9 .

Mortality and recruitment Both MSX and Dermo reduce the energy budget of a host (e.g., Hofmann et al., 1995; Ford et al., 1999) and, as a consequence, may reduce fecundity. Some empirical evidence exists that disease reduces the fecundity of individual oysters (Mackin, 1953; Barber et al., 1988; Ford and Figueras, 1988; Barber, 1996; Paynter, 1996; Dittman et al., 2001). One expectation is that fecundity may drop during epizootic years. No overall pattern is found between recruitment and box-count mortality in Delaware Bay (Ford and Figueras, 1988); however, the four massive settlement events with spat numbers above 1.5×10^{10} occurred during years when box-count mortality was very low, quadrant 3, (Fig. 12). Whether this coincidence is an independent outcome of two processes responding to common environmental and population forces, or whether it documents a causative connection, cannot yet be determined.

Data points in the recruitment and box-count mortality distribution fell into quadrants 1–4 with a frequency of 13, 14, 14, and 13 years, respectively (Table 6). Such a distribution is expected by chance. Cases of high recruitment occur equally often with low and high mortality. Despite the seeming randomness of the relationship, mean first-passage times are far from equivalent across all transitions (Table 7). The high-recruitment+low-mortality state is reached from the other three quadrants about three times less frequently

than is any other population state. Once there, the population is much more likely to remain there than move to any of the other three quadrants. High recruitment with low mortality is a relatively stable state.

Unrecorded mortality Box-count mortality is generally a measure of mortality of larger animals. Presumably, much of the mortality unrecorded by box counts is associated with predation in the first year of life and, therefore, likely would not show a discernible relationship with recruitment. Estimates of survival to one year of age indicate that mortality rates are at least a factor of three to five above the population average for older animals (Powell et al., 2009), confirming that much of the unrecorded mortality is juvenile mortality. The assumption that juvenile mortality rate varies randomly with respect to other indices of population dynamics is supported by comparisons with abundance, recruitment, and box-count mortality (Figs. 13–15).

Influence of regime shifts on biological relationships

Both the broodstock abundance–recruitment (Fig. 7) and abundance–mortality (Fig. 9) curves have outlying points. These are more common in the former than in the latter. Arguably, data for years when regime shifts occur should not be used in defining such relationships because the purpose of such relationships is to understand and model the typical population dynamics of the stock. Stock dynamics during regime shifts are atypical.

The abundance–mortality relationship (Fig. 9A) shows only a single outlying point. This outlier (X), the only case of epizootic mortality at stock abundances greater than 5×10^9 , marks the regime shift year of 1985, when stock abundance reverted to the low-abundance state after more than a decade of high abundance. The 1968–70 period, during which time conditions supported a dramatic population expansion, did not leave an indelible imprint. All three years were characterized by low mortality, but many other such years displayed similar abundance levels.

In contrast, the abundance–recruitment scatterplot (Fig. 7) contains four clear high-recruitment outliers. In this case, the 1985 regime shift is not unusual. Other low-recruitment years show high abundance. The 1968–70 period contains one of the four outliers (Fig. 7) and the years 1972–74 contain the other three. The inference drawn from Figure 2 is that these four outliers are of two types. One outlier is the previously mentioned outlier that occurred during the 1968–70 period and represents the unusual event that dramati-

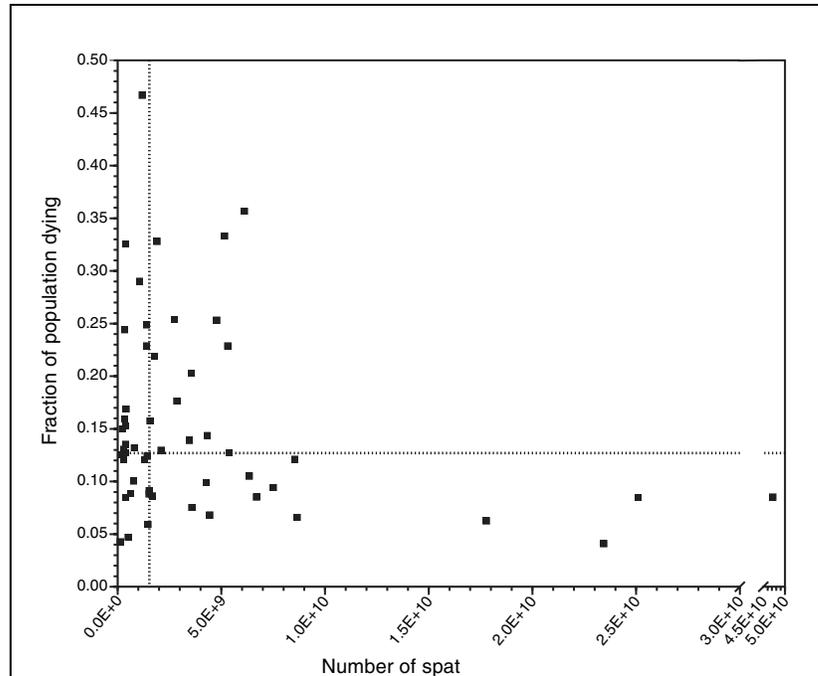


Figure 12

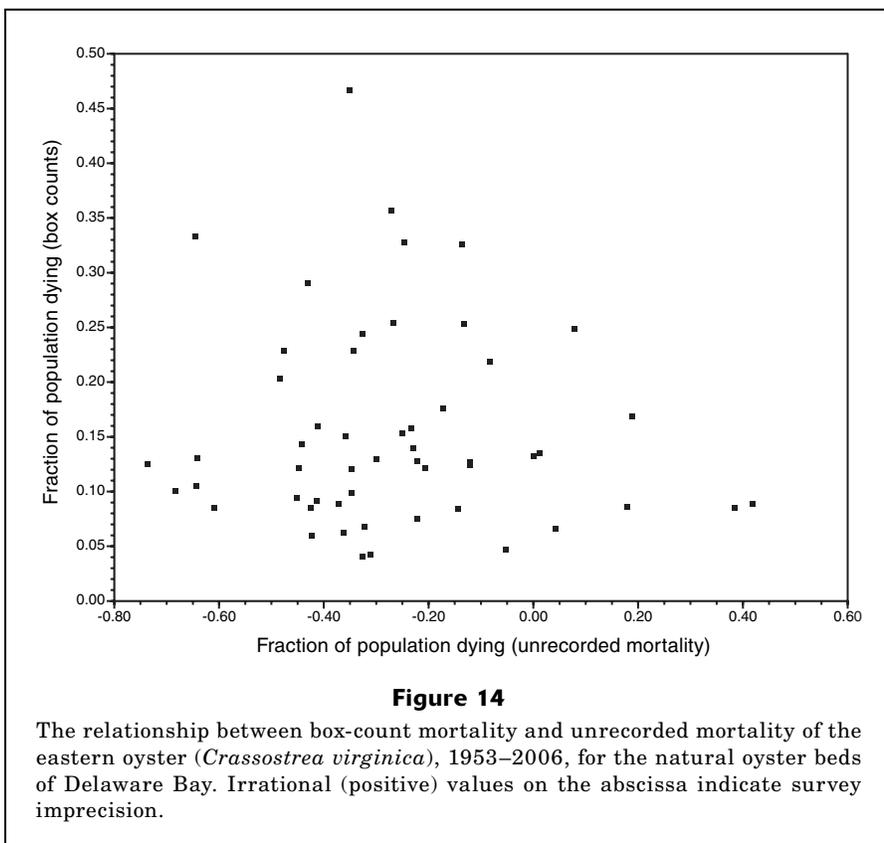
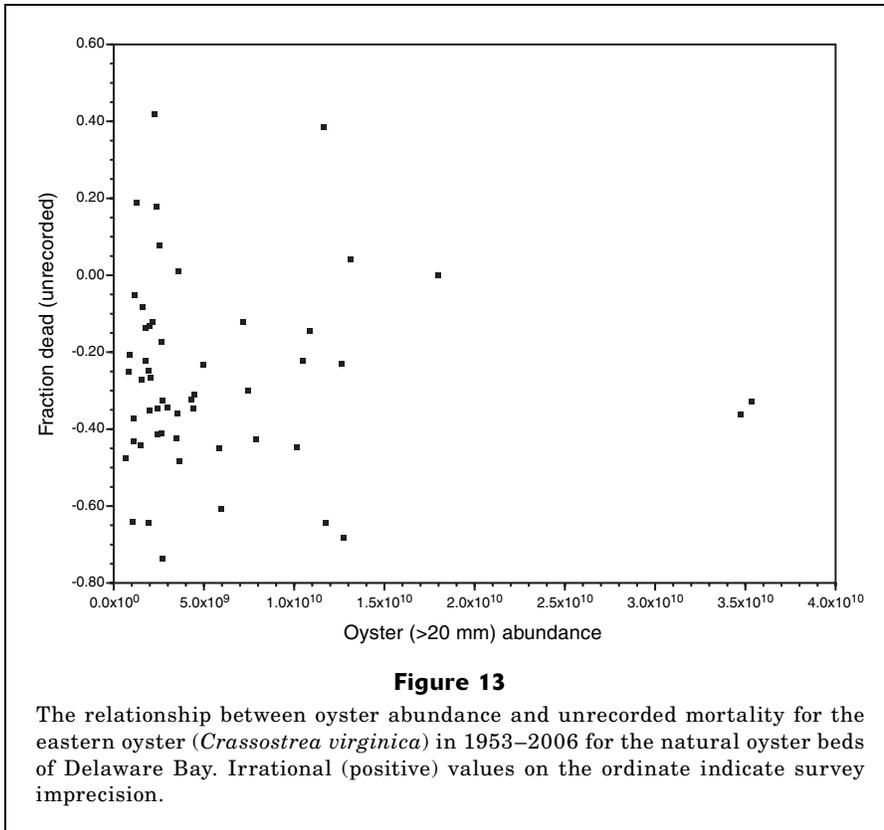
The relationship between box-count mortality and recruitment for the eastern oyster (*Crassostrea virginica*) in 1953–2006 for the natural oyster beds of Delaware Bay. Dotted lines indicate the 54-yr medians of box-count mortality and recruitment.

Table 7

Mean first passage times and the distribution of occurrence of the eastern oyster (*Crassostrea virginica*) population in each quadrant after an infinite number of steps were calculated from the Delaware Bay oyster recruitment–mortality distribution (Fig. 12). The observed distribution of occurrences is given in Table 6.)) Arrows indicate trajectories between quadrants. Quadrants are defined in Figure 10.

Quadrant	1	2	3	4
Mean first passage time (yr)				
1 →	4.45	3.72	9.97	4.52
2 →	4.83	3.79	9.91	4.17
3 →	5.94	6.52	3.78	6.80
4 →	4.92	4.65	9.08	4.05
Distribution of occurrence after infinite steps	0.225	0.264	0.264	0.247

cally impacted the stock. The other three are associated with an unusual transit of abundance above carrying capacity (Powell et al., 2008, 2009) and represent events that had no long-term consequences for the stock, except to maintain abundance near the carrying capacity



originally established circa 1970. In this scenario, these years were not unique. Nevertheless, for both cases, the performance of the stock was not representative of the dynamics defined by the remaining 50 years of observation. As a consequence, a mathematical relationship weighting these four observations overly much (e.g., the polynomial fit in Fig. 7) would not appropriately parameterize a model of the stock either in its high-abundance or low-abundance state.

The influence of spatial relationships on population dynamics

The relationships between broodstock, recruitment, and mortality expressed by Equations 4 and 6 and by Figures 7 and 9 attempt to portray the time series of observations in terms of the ambit of the stock's population dynamics. In fact, in one sense, this misrepresents the true range of the species' population dynamics at any particular time because the ambit of the stock in one regime differs from that of the other. First-passage times support this conclusion, as does a closer look at the distribution of abundance, recruitment, and mortality for the four bay regions over the full time series (Powell et al., 2008).

Consider first the broodstock abundance–recruitment relationship (Fig. 7). We identify two sets of points characteristic of times when the stock was relatively consolidated within its distributional range (Fig. 16). In these periods, a large proportion of the stock was found on the medium-mortality beds (Fig. 5). Such an occurrence was characteristic of the stock in both low- and high-abundance regimes and for extended periods of time, including most years between 1960 and 1963 (low-abundance regime), the 1970–77 period (high-abundance regime), and the 1997–2006 period (low-abundance regime). The 1970s occurrences all fall in quadrant 4 (high abundance+high

recruitment) (Fig. 16). Whereas other years also fall in this quadrant, when the stock is consolidated at high abundance, the likelihood that recruitment will be above the median of all years is extraordinarily high. When the stock is dispersed, the likelihood is not as great, but still, in most years, the population's performance falls into quadrant 4. Thus, stock dispersion has little influence on the outcome of recruitment events during the high-abundance regime.

In contrast, occurrences when relatively more of the stock was found on the medium-mortality beds during the low-abundance regime fall disproportionately into quadrant 1 (low abundance+low recruitment) (Fig. 16). Eight of fourteen occurrences in these years fall into this quadrant, a value significantly greater than expected by an even distribution of points among the four quadrants ($P < 0.005$), and 10 of 14 display low recruitment (quadrants 1 and 3), a value significantly greater than expected by an even split ($P \sim 0.05$). Thus, when the stock is consolidated within its range, and in its low-abundance regime, a high-recruitment event is unlikely. During the late 1980s and early 1990s, the stock was at relatively low abundance, but more distributed among bed regions (Fig. 5). These years are more evenly distributed among the four quadrants (Fig. 16). In particular, three occur in quadrant 3, accounting for a high percentage of all such events, and five fall above the long-term median for recruitment. Thus, although a dispersed stock can result in low recruitment during the low-abundance regime, the chance of a high-recruitment event is much improved.

One inference from these data is that high recruitment events are the result of spawning by oysters down-bay of the medium-mortality region, in waters of higher salinity. This inference is supported by the tendency for the high-mortality beds to recruit more consistently (Powell et al., 2008). The fact that quadrants 1 and 4 are primarily represented by years when a consolidated stock distribution was present indicates that spawning potential differs between the two regimes. Perhaps it is no coincidence that the 1970 stock expansion was preceded by a tendency for the stock to expand at low abundance, thereby increasing the probability of a high recruitment event at low abundance. And perhaps it is no surprise that the decrease in recruitment during the first years of the 2000s (Powell et al., 2008) was preceded by a consolidation of the stock beginning in

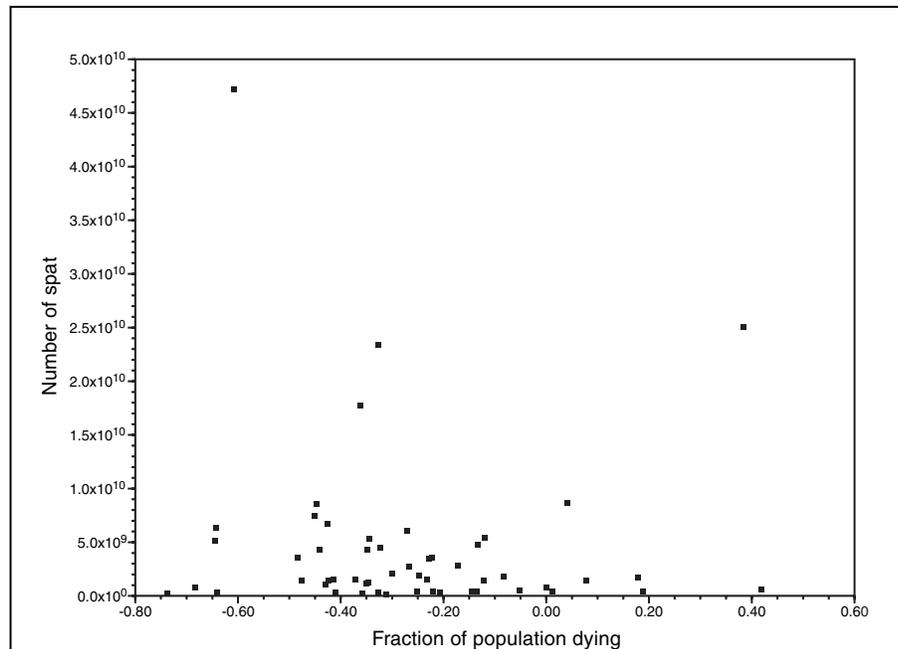
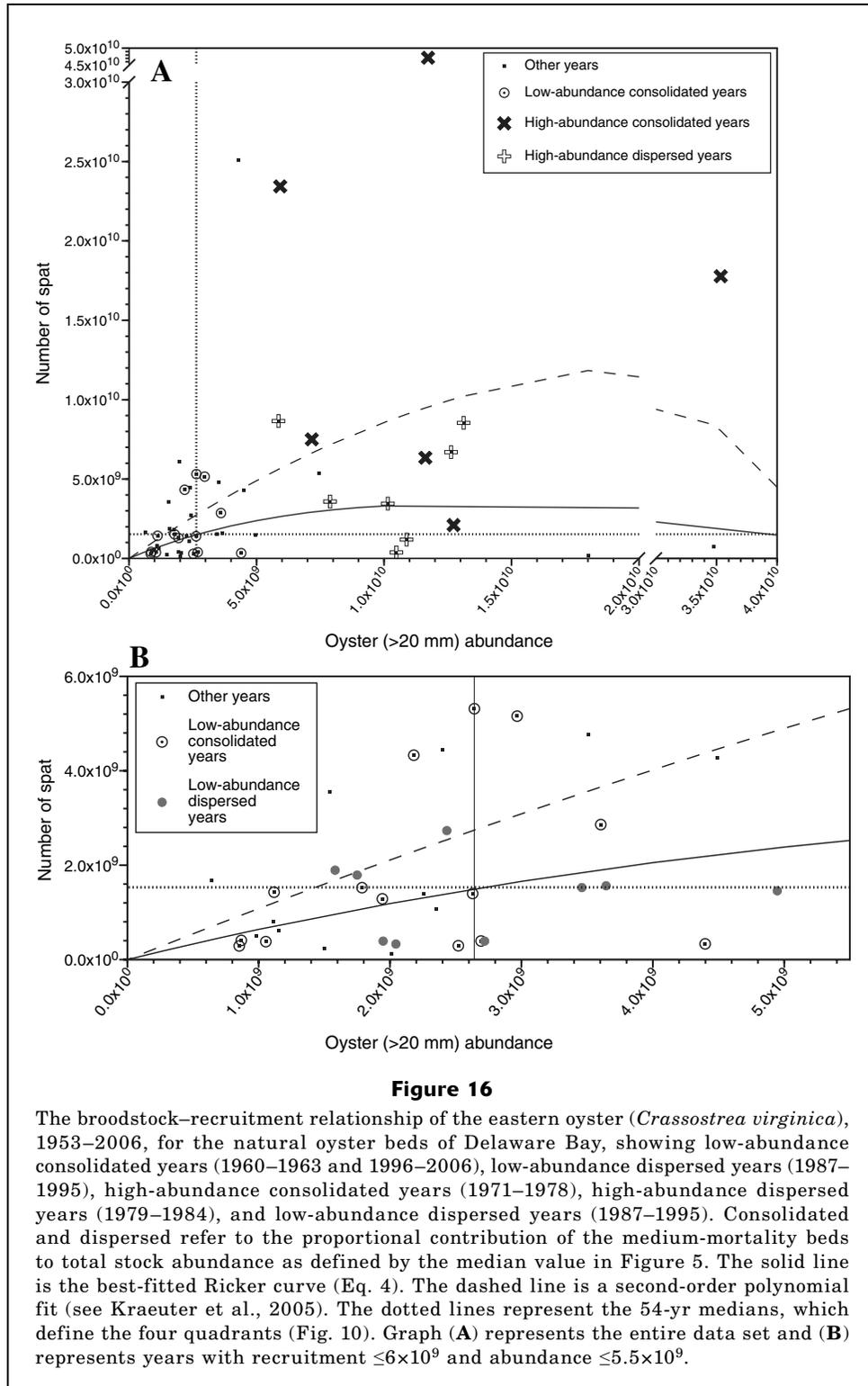


Figure 15

The relationship between unrecorded mortality and recruitment in 1953–2006 for the natural oyster beds of Delaware Bay. Irrational (positive) values on the abscissa indicate survey imprecision.

1996, which reduced the probability of a high-recruitment event. All of these observations would imply that a high recruitment is primarily driven by increased spawning potential on higher-salinity beds. Thus, the broodstock–recruitment relationship (Fig. 7) fails to emphasize a substantive impact from stock dispersion. The range in recruitment at a given abundance, blithely inferred to represent stochastic variation about a mean, in actuality includes a large influence from stock distribution that cannot be readily represented by a simple mathematical relationship between observed recruitment and stock size. This dispersion imprint is a dominant contributor to the dynamics of a population at low abundance, but not at high abundance, when compensatory processes begin to become important, and helps explain why the 1970 regime shift was an unlikely event.

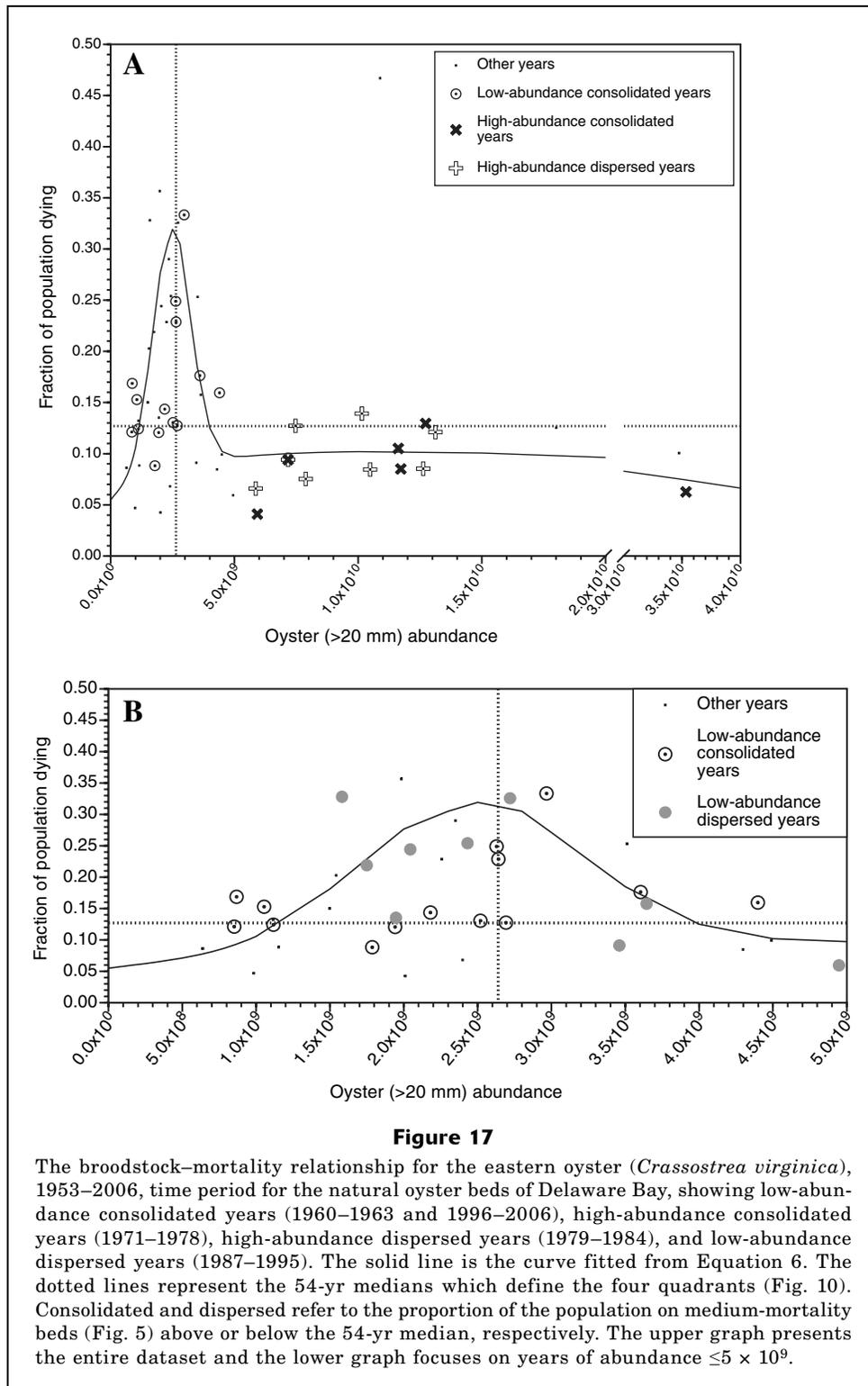
The influence of geographic dispersion is also observed in the abundance–mortality diagram (Fig. 9). Not surprisingly, the high-abundance regime is associated with low mortality, regardless of the degree of consolidation of the stock (Fig. 17). This association conforms with the relationships observed for the broodstock–recruitment relationship (Fig. 16). By contrast, the years characterized by consolidated and dispersed stock during the low-abundance regime are divergent, and again this divergence is similar to our conclusion drawn from the broodstock–recruitment relationship. The mortality rate should be lower when more oysters are found on the medium-mortality beds, and this



is the case. Epizootic mortalities (>0.20 in Fig. 17) occurred in four of eight years when the stock was dispersed, but only in three of fourteen years when consolidated. The second proportion differs significantly from the first ($P < 0.025$). Epizootics are an

important mechanism leading to stock consolidation, and a consolidated stock is resistant to further epizootic challenge.

If one considers the relationships of recruitment and mortality to broodstock abundance, the high-



abundance regime is noteworthy for low mortality and high recruitment, regardless of stock dispersion. However, during low-abundance intervals, the consolidated stock is in a relatively stable state and characterized by low mortality and low recruitment.

The dispersed state is moderately less stable, characterized by higher mortality and higher recruitment. The interesting coincidence of similar trends in mortality and recruitment in both instances is noteworthy.

Conclusions

The oyster population in Delaware Bay exhibits population dynamics that are not normally described in commercial species. One reason is the presence of multiple distinct, dynamically stable states delimited by temporally rapid regime shifts. Such dynamics are becoming more widely appreciated in fished species as a whole; therefore these unique dynamics may be more apparent than real. Oyster populations display four unusual biological relationships, however, that impute greater peculiarity to their population dynamics. First, it seems likely that the broodstock–recruitment relationship, at least at low abundance, is driven more by the provision of settlement sites for larvae by the adults than by fecundity. Second, the natural mortality rate is temporally unstable and bears a nonlinear relationship with abundance (Fig. 9). This nonlinearity is driven by MSX and Dermo, both acting similarly despite the multifarious differences in their life histories, and by the environmental gradient of the habitable areas, which provide habitats of refuge from disease during epizootics. Third, high abundance and low mortality, though likely requiring favorable environmental conditions, also seem to be self-reinforcing, although the specific underpinning dynamics remain unclear. As a consequence, an increased probability of high mortality occurs over a relatively small range of total abundances. The mortality relationship exhibits both compensatory and depensatory components. Fourth, the geographic distribution of the stock is intertwined with the variables of abundance, recruitment, and mortality, such that biological relationships are functions both of spatial organization and inherent population processes. As a consequence of the imprint of geographic distribution on population dynamics, epizootic-level mortalities normally occur only when the animal has expanded its population beyond the refuge sufficiently that a significant fraction of the population is exposed to higher mortality. Consolidation limits mortality. What is equally interesting is the parallel influence on recruitment such that the consolidated stock has a lower recruitment potential, while also minimizing epizootic mortality.

One is often dismayed by the dispersion of data in plots of the relationships of broodstock to recruitment and abundance to mortality. This dispersion is normally ascribed to stochastic processes, and stochasticity is certainly a causal element. However, both governing regime and geographic distribution of the stock influence the dispersion of these data. Of note is the influence of stock dispersion, where the ambit of the population when the stock is in a contracted state is dissimilar from the ambit when the stock is in a dispersed state. This dynamic imposes a wider range in stock performance for a given stock abundance than would be observed for either distributional state alone. At least for oysters, a substantive component of apparent stochasticity observed in the relationships of

recruitment and mortality to abundance originates not from simple year-to-year variation in stock performance, but from different distributions for the stock dictated by modifications in the geographic distribution of the stock, and these distributional states tend to be self-reinforcing, as evidenced by similar changes in both recruitment and mortality over half-decadal or longer intervals of time.

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