

Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing

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ABSTRACT: The oyster population in the Maryland portion of Chesapeake Bay, USA, has declined by more than 50-fold since the early part of this century. The paper presents evidence that the mechanical destruction of habitat and stock overfishing have been important factors in the decline, even though it is commonly thought that 'water quality' and, more recently, oyster diseases are critical. Quantitative analyses show that the long-term decline of oysters largely results from habitat loss associated with intense fishing pressure early in this century, and stock overfishing from early in the century through recent times. Furthermore, the major ecological effects on Chesapeake Bay occurred well before World War II, before industrialization and the reported prevalence of disease. To effect the recovery of the ailing Chesapeake Bay oyster stock, a 4-point management strategy is proposed.

KEY WORDS: Oysters · Population dynamics · Overfishing

INTRODUCTION

Eastern oyster *Crassostrea virginica* landings from Chesapeake Bay, USA, are at historically low levels. The catch peaked in Maryland at 615 000 t in 1884; it has declined to about 12 000 t in 1992 (Fig. 1).

The decline has been attributed to 'reduced water quality', diseases, and fishing (Haven et al. 1981, Kennedy & Breisch 1981, 1983, Héral et al. 1990). However, the decline in oyster landings began well prior to recently identified water quality problems and/or significant disease outbreaks, as shown in Fig. 1. Heinle et al. (1980) said that 'nutrients in effluent delivered into the Bay have increased significantly since 1950', and others have concluded that the Bay's 'water quality' and living resources have deteriorated as a result of pollution (EPA 1983). Oyster diseases (i.e. the protozoan parasites *Minchinia nelsoni*

'MSX' and *Perkinsus marinus* 'Dermo'), were not reported until the 1950s to 1960s in Chesapeake Bay (Mackin et al. 1950, Wood & Andrews 1962, Andrews & Wood 1967, Sinderman 1970). Much of the decline is likely associated with fishing practices. As the oyster fishery developed, the physical integrity of the oyster bars was damaged by oyster-fishing gear. Hand tongs were the principal oyster-fishing gear from the mid-17th century to 1865. Hand tongs probably had a minor effect on oyster bar structure. Because hand-tong oystering can cover only a limited area per oyster fisherman per day and can only operate at depths no greater than 6 m, the areal extent and intensity of hand tonging is relatively limited. In addition, tongs have a relatively small effect on the reef substrate because of their limited mobility and because they are operated by hand, are relatively small, and are mechanically inefficient.

The record of increasingly destructive procedures begins with large oyster dredges which were legalized in 1865 (Stevenson 1894). The dredges were dragged over large areas of oyster bottom each day, and as they were dragged over the bottom they removed and dis-

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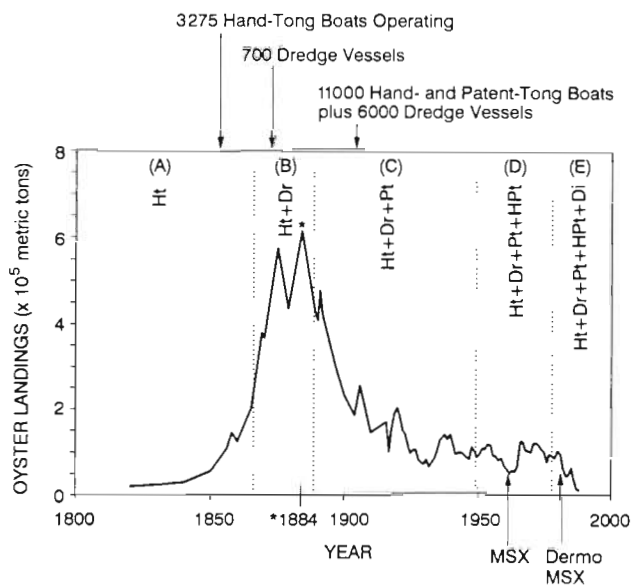


Fig. 1. Time series of Maryland, USA, oyster landings (source: Maryland Department of Natural Resources). Panel segments show corresponding evolution of oyster fishing gears: (A) use of hand tongs (Ht); (B) introduction of dredges (Dr) (*note production peak in 1884); (C) introduction of patent tongs (Pt) which corresponds with the beginning of the catch decline; (D) introduction of the hydraulic patent tong (HPt) in 1950 and date when disease was first recorded; (E) the addition of diver harvesting (Di) in 1980

associated components of the bar. In addition the dredges could be operated in deeper waters than the hand tongs. The use of these dredges began to degrade the physical integrity of centuries-old oyster shell accretions, the so-called oyster bars (Ingersoll 1881, Winslow 1881a, b, DeAlteris 1988). By the late 1870s, 700 dredge vessels had contributed to increasing both the absolute intensity of fishing and its areal extent. In 1887, introduction of hand-operated patent tongs enabled the capture of oysters in deeper waters, extending the range and fishing efficiency of the fleet to previously unfished deep-water bars. Attempts to constrain total fishing effort by restricting the use of dredge gear to sail-powered vessels only were evidently of limited effectiveness; the number of large sail-powered craft had increased to greater than 1000 vessels by 1890 (U.S. Commission of Fisheries 1901). The notion, even at the turn of the century, that fishing was intense and that the decline in catch reflected a decline in abundance was reinforced by the observation in 1900 that the dredges practically exhausted the bars before the end of the fishing season (Grave 1907). By 1950, hydraulic-powered patent tongs were introduced. These are the most 'destructive' to the bar substrate because of their capability to penetrate and disassociate bar structure. This capability arises from their weight and hydraulic power. Hydraulic-powered

patent tongs operate much like an industrial crane; with each 'bite' a patent tong will remove a section of the bar amounting to 0.25 m³. There are about 580 hydraulic patent tong boats operating in Maryland waters now.

This paper shows that 100 yr of increasingly intensive and mechanized fishing has contributed to leveling the profile of the oyster bars in Chesapeake Bay. As a result these formerly productive areas are covered with silt so that they are not now capable of producing oysters, and those remaining unsilted areas are considerably less productive than in the past. In fact, 'fishing down' of the oyster stock and destruction of oyster habitat by fishing may have been more important factors causing the decline of the oyster than either water quality or disease, particularly inasmuch as degraded habitat and susceptibility to parasitism may be correlated.

METHODS

Oyster habitat. Oyster bar destruction was assessed by comparing data on the areal extent of oyster habitat ca 1907, ca 1980, and ca 1990.

From 1907 to 1912, 111 600 ha or 25% of the Maryland portion of the Chesapeake Bay bottom was identified as natural oyster-bar habitat (Yates 1913) (Fig. 2). Yates carefully defined the 'shelled-areas' constituting natural oyster bars by using a sophisticated system of triangulation and sounding chains. Samples were taken inside bar boundaries by hand tongs to increase the resolution of shelled-area estimation (Grave 1907, Yates 1913).

From 1974 to 1982 the Maryland Department of Natural Resources (MDNR) surveyed sediment composition of the bay bottom with hydroacoustics (MDNR 1982). Acoustic results were calibrated by 'ground truthing' with bottom-sediment grabs to specifically assess shelled areas. Bottom sediments were broken into 5 categories: (1) shelled, (2) sand and shelled, (3) sand, (4) mud, and (5) sandy mud. For our comparisons, we conservatively classified the MDNR-reported shelled and sand-and-shelled areas as natural oyster bars.

From 1989 to 1990, 24 oyster bars, surveyed originally by Yates in the early part of the century, were sampled by the University of Maryland's Chesapeake Biological Laboratory (CBL) using hydraulic patent tongs (Rothschild et al. 1990). Sample allocation for the CBL survey was determined by superimposing a rectangular lattice grid composed of unit cells over each bar defined by Yates' maps. Each unit cell had dimensions 146 m east-west and 183 m north-south (2.7 ha). Patent tong samples of 1.41 m² were taken

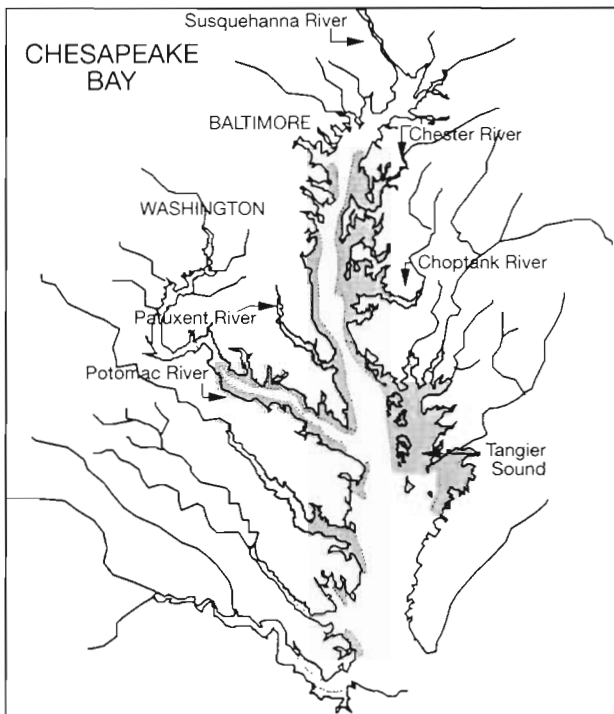


Fig. 2. Chesapeake Bay with shaded area showing the turn of the century historical range of oyster bars according to Yates (1913)

at each grid lattice point to determine bottom type composition and oyster density. 'Shelled bottom' was defined as a sample that contained more than 0.5 l volume of oyster shell.

Although the Yates, MDNR, and CBL surveys varied slightly in methodology, their results provide a basis for comparison. We compared oyster bar habitat for the 3 surveys by superimposing the gridded lattice over the charts produced from the early and recent surveys. This allowed us to calculate the period-specific natural oyster bar area for the early 1900s, 1980s, and 1990s. Two least-squares regression relationships of the average remaining shelled area for various-size oyster bars were estimated for surveys conducted at 2 time periods: (1) Yates (ca 1907) and MDNR (ca 1980), and (2) MDNR (ca 1980) and CBL (ca 1990).

Stock assessment. We employed stock assessment methods for evaluating oyster: (1) yield per recruit, and (2) average density ca 1890 and ca 1990.

In order to determine the effect of fishing on the oyster stock, yield per recruit and spawning stock biomass isopleths (Beverton & Holt 1957) were calculated based on estimates of (1) growth, (2) weight and length (largest dimension of shell length), (3) length and age at first sexual maturity, (4) natural mortality, (5) fishing mortality, and (6) the minimum length of oysters taken by the fishing gear.

Oyster growth at age was represented by the von Bertalanffy growth curve

$$L_t = L_\infty (1 - e^{-K(t-t_0)}),$$

where L_t is length at age t , L_∞ is average maximum length, K is the growth model coefficient, and t_0 is age zero. L_∞ was estimated on the basis of known sizes of 'large' oysters. The growth-model coefficient K was computed using a reasonable estimate of L_∞ by solving simultaneous equations between 2 constrained points corresponding to an age zero t_0 at which the length L_0 is zero and some age t_λ at which the length L_λ is defined, yielding

$$K = \frac{1}{t_\lambda - t_0} \ln \left(\frac{L_\infty - L_0}{L_\infty - L_\lambda} \right)$$

Weight (W_t , in g) at a given length (L_t , in mm) was obtained using the allometric weight-length model $W_t = \alpha L_t^\beta$, from a representative sample of 598 oysters collected during our field work. Weight is defined as the shell and body mass combined, and length is the longest shell dimension. Conversion of the length-at-age growth curve to weight-at-age according to a von Bertalanffy model was accomplished by inserting L_∞ for L_t in the weight-length relationship $W_\infty = \alpha L_\infty^\beta$ and expanding to some estimated power β . Biomass-at-age was computed as the product of the numbers-at-age times their average weight-at-age, then this quantity was summed over all ages to calculate population biomass B .

Length and age at first sexual maturity (t_m) were determined from the field studies of Galtsoff (1964) and Rothschild et al. (1990).

The natural mortality rate was determined from our own field observations (Rothschild et al. 1990, 1991) and the literature.

Total instantaneous mortality rates at the turn of the century and at present were determined using the length-based method of Ault & Ehrhardt (1991), Ehrhardt & Ault (1992). The method requires estimates of growth parameters L_∞ and K ; the minimum size of capture; the maximum selection size; and the average length in the catch for each time period computed from the minimum size of capture to the maximum selection size. Total instantaneous fishing mortality was determined by subtracting natural mortality from estimates of total instantaneous mortality.

The calculations above permit the computation of yield per recruit and spawning stock biomass isopleths (Beverton & Holt 1957). Yield in weight (Y_w) was assumed proportional to average population biomass (\bar{B}) as $Y_w = F\bar{B}$ across the range of exploitable sizes (ages), where fishing mortality rate F is the proportionality constant. At each given F , the yield per recruit in weight is obtained by integrating age-specific yield

per recruit in weight over the range of exploitable ages. Spawning-stock biomass at a given fishing mortality rate was computed by integrating the age-specific biomass from the age at first maturity to the oldest age represented in the stock. These values were then expressed as the numerator of the spawning stock biomass ratio whose denominator is the spawning stock biomass at zero exploitation.

Yield in weight per unit-habitable-area was calculated by dividing the catch total biomass by the estimated total oyster bar acreage. Estimates for yield per unit-habitable-area made for the turn of the century and recent times were compared with results from our assessment surveys (Rothschild et al. 1990, 1991).

RESULTS AND DISCUSSION

Decline in oyster habitat

Our analysis shows that oyster bar acreage declined by more than 50% from 1907 to 1982 (Fig. 3). The estimated linear regression relationships for the Yates(x)–MDNR(y) and MDNR(x)–CBL(y) acreages were $y = -32.4 + 0.45x$ (df = 662) and $y = 28.4 + 0.64x$ (df = 23), respectively. Correlation coefficients for each regression line were significant, $r = 0.83$ ($p < 0.05$) and $r = 0.91$ ($p < 0.05$), respectively. Slope coefficients approximate the average shelled area remaining at the time of the latest survey.

A particular example is shown in Fig. 4 where the shelled area estimates made successively by Yates (1913), MDNR (1982), and Rothschild et al. (1990) for Lighthouse Bar in the Choptank River are shown graphically. The 292.3 ha of shelled area originally reported by Yates (1913) declined to 199.6 ha of shell and sand-shell at the time of the MDNR survey (Fig. 4a); only 139.3 ha remained on CBL assessment (Fig. 4b), an overall decline of about 52%. In general, decline of shelled areas was associated with concomitant increased acreage of mud and sand bottoms.

Estimated areas from the CBL survey appeared smaller than MDNR area estimates, particularly on large oyster bars (i.e. >162 ha) (Fig. 3). However, overall shelled-area distribution was roughly similar (Fig. 4).

Decline in oyster habitat, estimated at about 50%, is probably conservative because our baseline comparisons used Yates' data collected post-1907, after the largest decline of oyster catches. However, the downward trend in substantial habitat loss is confirmed by other recent studies. Seliger & Boggs (1988a) report reductions of 74, 86, and 95% in oyster bar habitat in Broad Creek, Tred Avon, and Chester River, respectively.

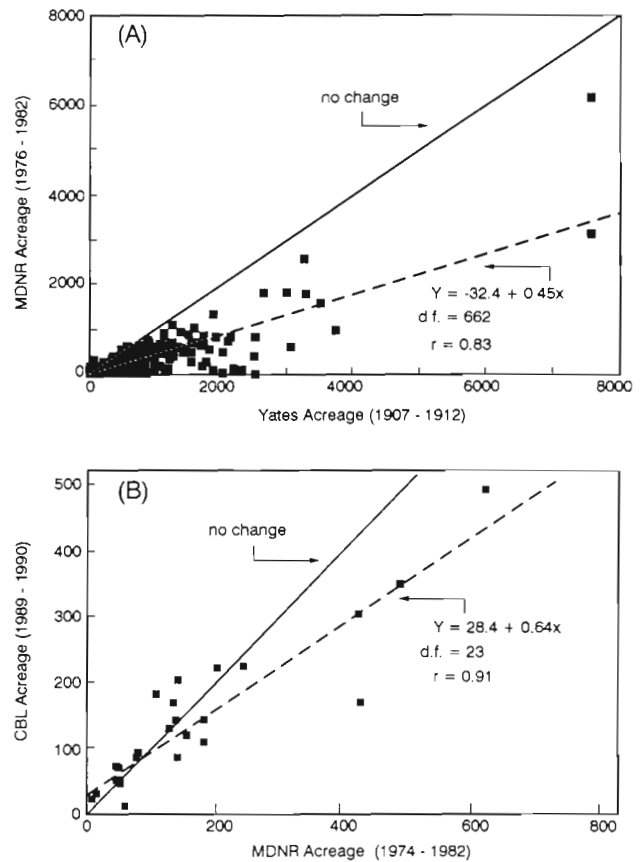


Fig. 3. Relationships of the extant shelled areas from various-size oyster bars estimated during surveys conducted at 2 time periods: (A) Yates (ca 1907) (Yates 1913) and Maryland Department of Natural Resources (ca 1980) (MDNR 1982); and (B) MDNR (ca 1980) and Chesapeake Biological Laboratory (ca 1990) (Rothschild et al. 1990). The slope estimates the average remaining shelled area habitat at the last survey. In both panels the solid 45° line represents no change in habitat area between surveys

In addition to the substantial decline in substrate area upon which young oysters can grow, the 'quality' of existing bars must have also been affected. The reduced profile of oyster bars modifies the water flow near the oyster and presumably increases the deposition of silt on the bar. In general, mature well-developed oyster bars with a high profile are associated with relatively intense current flows (i.e. 2 to 4 $l\ d^{-1}\ g^{-1}$ oyster tissue) (Lam & Wang 1990), which provide conditions favorable for increased growth and survivorship (Peterson & Black 1987, Frechete et al. 1989). Relatively intense flow evidently mitigates the negative effects of siltation and biodeposition, and increases consumption rates (Lund 1957, Haven & Morales-Alamo 1970, Keck et al. 1973, Bahr 1976, Peterson & Black 1987, Seliger & Boggs 1988a, Frechete et al. 1989, Lam & Wang 1990).

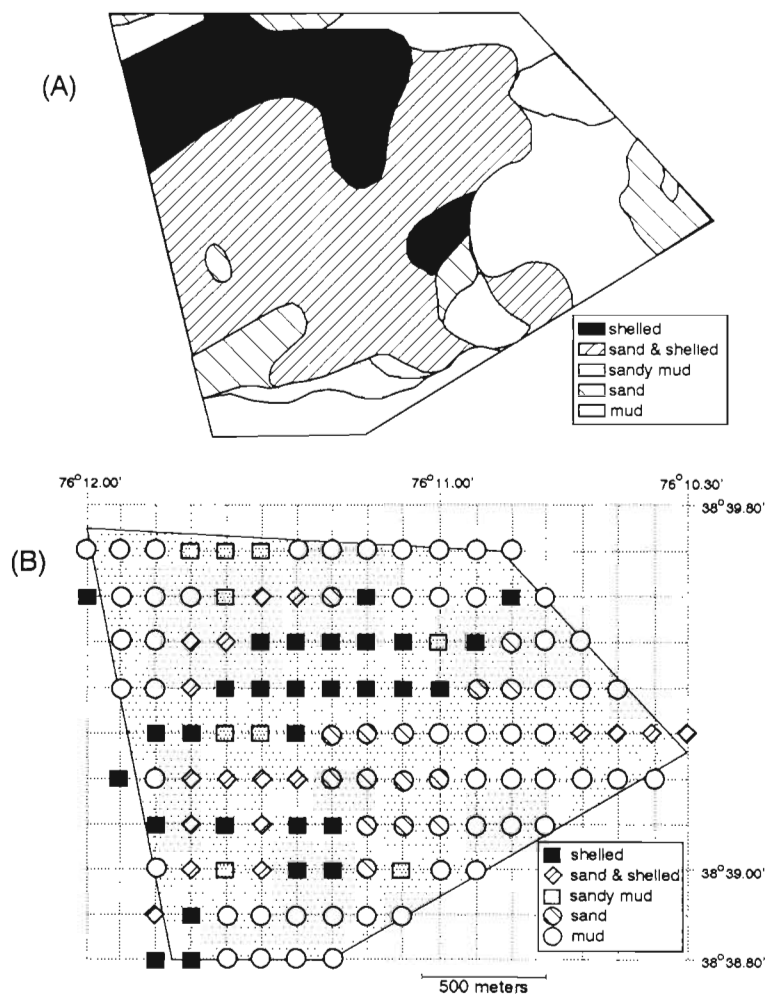


Fig. 4. Comparison of oyster bar boundaries for Lighthouse Bar in Choptank River, Maryland, USA, defined by: (A) Yates (1913) and Maryland Department of Natural Resources (MDNR 1982), and (B) Yates (1913) and Chesapeake Biological Laboratory (Rothschild et al. 1990) surveys. In (A) and (B) the polygon perimeter represents shelled area defined by Yates (1913). Legends define the bottom composition of the polygon interior as defined by MDNR (1982) (A) and CBL (Rothschild et al. 1990) (B)

It is reasonable to think that a flattening of bar profile affects the dynamics of sedimentation on and around the bar. Extant bar habitat in Chesapeake Bay is characterized by lowered vertical profile (DeAlteris 1988, Seliger & Boggs 1988a). Oyster habitat is subjected to much siltation (Schubel 1972, Mackenzie 1983, 1989, Seliger & Boggs 1988a), which probably reduces the nutritional value of ingested food relative to the metabolic cost of suspension feeding via the production of pseudofaeces. MacKenzie (1983) reported that productive oyster bars mitigate the effects of siltation. In undisturbed habitat, increased oyster growth rates to some degree compensate for increased sedimentation rates which allow vertical growth of oyster bars (DeAlteris 1988). Much of the silt and sediments

noxious to oysters comes from several origins: (1) from point sources external to the bars, (2) from oyster faeces, and (3) pseudofaeces (Loosanoff & Tommers 1948, Lund 1957, Bahr 1976, Winter 1978, Héral et al. 1983). Sediments reduce oyster gill function and metabolic efficiency by increasing pseudofaeces production. Oysters exposed to sediments have decreased growth and reproductive efficiency, while mortality and disease susceptibility increase (Héral et al. 1983). Siltation also reduces the quality and quantity of suitable habitat for 'spat' (recruiting juvenile oysters) settlement (Keck et al. 1973, Bahr 1976, Mackenzie 1983, 1989).

In addition to the destruction of deeper-water bars, those bars that were in shallow water were also evidently destroyed by fishing and development. When European explorers first visited Chesapeake Bay (ca 1600) they found extensive bars exposed at low tide and in shallow waters (Kennedy & Breisch 1983, Kent 1988, Kennedy 1989); bars with these characteristics are virtually nonexistent today.

As evidence that the complex of bar destruction, possible siltational effects on nutrition, fishing, and disease has affected the habitat, we compare the yield per habitable acre, which is proportional to the biomass per habitable area, in 1884 and 1991. For example in 1884 the yield was $615 \times 10^3 \text{ t} = 615 \times 10^9 \text{ g}$ total weight of oysters. The habitable area was 279 000 acres = $1.116 \times 10^9 \text{ m}^2$. Thus the yield per habitable area in 1884 was $615 \times 10^9 / 1.116 \times 10^9 \approx 550 \text{ g m}^{-2}$. In 1991

the yield was $12.3 \times 10^3 \text{ t} = 12.3 \times 10^9 \text{ g}$. If we take the reduction in habitable area to be ca 50%, then the yield per habitable area is $12.3 \times 10^9 / 0.558 \times 10^9 \approx 22 \text{ g m}^{-2}$. Therefore the yield per habitable area in 1991 is roughly 4% of that in 1884, a reduction of 96%. Similar calculations using the estimated densities from our survey of 26 bars reflected about the same conclusions with respect to the decline in abundance per habitable area.

Stock assessment

To our knowledge, no previous stock assessment has been conducted on the eastern oyster. Here we apply well-established stock assessment techniques (e.g.

Beverton & Holt 1957) to analyze oyster population dynamics. To determine the effect of fishing on the oyster stock, yield per recruit and spawning stock biomass isopleths were calculated based on estimates of (1) growth, (2) weight and length, (3) length and age at first sexual maturity, (4) natural mortality, (5) fishing mortality, and (6) the minimum length of oysters taken by the fishing gear.

The estimation of the parameters associated with size, growth, mortality and reproduction is somewhat problematic in the sense that there are, suprisingly, no in-depth studies of these parameters in the literature. Virtually no growth or mortality data exist on oysters larger than 85 mm. Accordingly, we have been forced to inspect the various reported values and use our judgement to present what we believe to be the best available impression of oyster stock dynamics. We did not conduct a sensitivity analysis because the quality of the data and the potential for interactions among the variables would have made the interpretation of that analysis difficult. We are confident of having used the best available estimates of important parameters and consider this novel application of stock assessment techniques to be justified by the new insights it brings to the implications for alternative management actions in the oyster fishery.

Oyster growth was estimated by considering our field observations and those of a number of authors throughout Chesapeake Bay (Table 1). In all of these studies, growth per unit time for various size classes of small (< 100 mm) oysters was estimated by maintaining oysters in containers over time (it is not known how the use of various types of containers affects growth rate). Archeological digs on Indian midden sites around Chesapeake Bay have uncovered shells greater than 200 mm long (Kent 1988). Also, fisheries studies in the late 1800s reported living oysters as large as 230 mm in

maximum length (Goode 1884). Webster (1953) found living oysters as large as 165 mm. In our own field work we observed oysters as large as 185 mm in several different Chesapeake Bay tributaries. It appears from our examination of 16 000 oysters that 150 mm in length is a reasonable estimate of the average maximum length L_{∞} of an oyster. Our observations and those available in the literature suggest that an oyster 85 mm in shell length is about 3 yr old (Table 1). Thus, the coefficient K of the von Bertalanffy growth model was estimated as $K = \frac{1}{3} \ln[150/(150 - 85)] = 0.28$. This results in the growth curve $L_t = 150(1 - e^{-0.28t})$. Weight (W_t , in g) at a given length (L_t , in mm) was obtained using the nonlinear model $W_t = \alpha L_t^{\beta}$, where $\alpha = 3.94 \times 10^{-4}$ and $\beta = 2.80$ (df = 596, $r = 0.95$, $p < 0.05$).

Extensive studies on *Crassostrea virginica* show the size at first sexual maturity to be 31 mm or about 1 yr of age (Galtsoff 1964, Rothschild et al. 1990). While the fecundity for a 31 mm oyster may be relatively small per capita compared to large gravid females, the actual number of oysters in the population at the smaller size is substantially greater.

The eastern oyster is a 'weakly' protandric hermaphrodite, i.e. some older males become females (Galtsoff 1964, Kennedy 1983). Consonant with this life-history characteristic, Kennedy (1983) noted that the proportion of females increased directly with size. In general, high levels of fishing mortality will modify the 'natural' sex ratio of protandric hermaphrodites such as eastern oysters. This is because in an unexploited population of protandric hermaphrodites, the larger individuals will tend to be female. Thus, as fishing mortality increases, the average length of populations decreases, and the percentage of females decreases. In other words, as fishing intensity increases, the production of eggs per adult biomass decreases faster than in a non-hermaphroditic population. Kennedy (1983) noted

declining proportions of females on most oyster bars for central Chesapeake Bay between 1960 and 1978. He suggested that the decline was due to an unspecified 'environmental stressor'. Increased fishing mortality is a likely alternative explanation for the change in sex ratio.

Our own field observations and a literature review of the estimated rate of natural mortality for oysters suggest that the instantaneous coefficient is about 0.15 yr^{-1} (Table 2). This estimate of natural mortality applies to disease-free oysters. Under severe epizootic conditions (i.e. by Dermo and MSX), the coefficient may reach 0.5 yr^{-1} (McHugh &

Table 1. Records of mean lengths-at-age and maximum observed size of eastern oysters from various sources

Source	Age (yr)					Maximum size (mm)
	1	2	3	4	5	
Goode (1884)						230
Beaven (1950)	57	74	83			
Beaven (1953)	40	60	80			
Butler (1953)	25	58	68			
Webster (1953)						165
McHugh & Andrews (1955)	20	65	95	100	110	120
Shaw (1966a, b)	23	48	65			
Shaw & Merrill (1966)	30	75	87			
Abbe (1987)	30	70	85	105		
Kent (1988)	25	50	75	100		160
Kennedy (1989)	32		75			
Krantz (pers. comm.)						200
Rothschild et al. (1990)	40	65	85	92		185

Table 2. Estimates of natural mortality rate (M), total mortality rate (Z), and survivorship (S) at age from various sources. HDP: high disease prevalence

Source	Age (yr)	M (yr)	Z (yr)	S (%)
Beaven (1950)	0+	0.446		64
	2	0.139		87
	3	0.198		82
McHugh & Andrews (1955)	3	1.386		25(HDP)
Shaw (1966a)	2	0.151		86
	3	0.357		56
Shaw (1966b)	2	0.020		98
Abbe (1987)	3	0.105		90
	3	0.051		95
Rothschild et al. (1990)	3	0.160		85
This paper, ca 1890	2.1+	0.150	2.40	9
This paper, ca 1990	2.6+	0.150	1.45	23

Andrews 1955, G. Krantz, Oxford Laboratory, pers. comm.). It is well known that as the instantaneous rate of natural mortality rate increases, both the average yield per recruit and the optimal minimum size of first capture decrease (cf. Beverton & Holt 1957).

The pathogens 'Dermo' and 'MSX' were first described in 1907 and 1914, respectively (Mackin et al. 1950, Wood & Andrews 1962). However, Dermo was not identified in *Crassostrea virginica* until 1949 (Mackin et al. 1950), and MSX was first recognized in moribund and dead Chesapeake Bay oysters in 1959 (Wood & Andrews 1962, Sindermann 1970). Andrews & Hewatt (1957) speculated that Dermo may have been present in Chesapeake Bay prior to initial detection in 1949; how-

ever, Andrews & Hewatt (1957) presented no quantitative evidence to support their contention. Andrews & Wood (1967) made similar unsupported conjectures for MSX. In fact, there is scant information to warrant the assumption that disease was prevalent in Chesapeake Bay at the turn of the century.

Most epizootic studies for eastern oysters have been qualitative and do not provide sufficient quantitative estimates of the population fractions affected by disease. Such information would allow assessment of disease impacts on the oyster stock.

Data from stock assessment studies reported by Brooks (1905) conducted in 1882–1883 in Maryland were used to determine the average length of oysters in the catch at the turn of the century. The contemporary rates were established using our extensive survey data. The minimum size of capture was regulated as 64 mm in 1890 and 76 mm in 1990. Using our growth curve, the maximum selection size was set at a size that corresponded to an age of 15 yr.

In 1890 the mean length of oysters in the catch was 73 mm. The size at first capture was 64 mm (or 2.1 yr). The total instantaneous mortality rate was therefore 2.4. The instantaneous rate of fishing mortality is estimated at 2.25. In our 1990 survey the mean length of oysters in the catch was 88 mm and the size of first capture 76 mm (2.6 yr). Total instantaneous mortality is therefore 1.45 and the fishing mortality is 1.3. So fishing mortality in recent years, although very high, is substantially lower than it was at the turn of the century.

The calculations above permit the computation of yield per recruit and spawning stock biomass isopleths (Fig. 5). These results show that early in the century

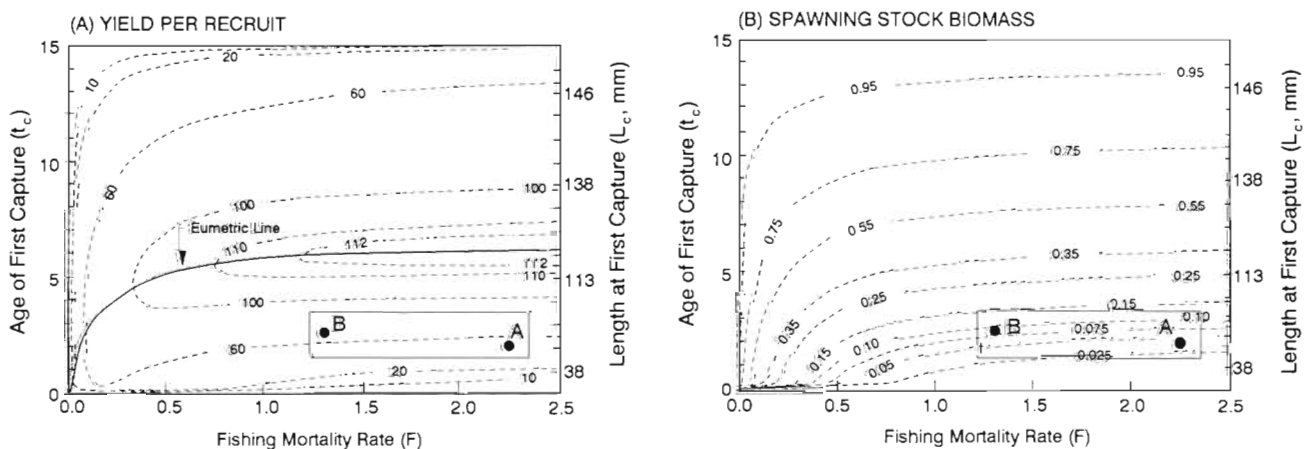


Fig. 5. (A) Yield per recruit and (B) spawning stock biomass isopleths expressed as functions of fishing mortality rate F and age of first capture t_c for the Chesapeake Bay, USA, oyster stock. Spawning-stock biomass is expressed as a fraction of the unexploited stock (i.e. fishing mortality rate equals zero). Point A shows roughly the 1900 position of the fishery, and B shows roughly the 1990 position. The rectangular area shows the range of the fishery over the last century. Parameters for generation of the isopleths were: natural mortality rate (M) = 0.15, average maximum weight (W_m) = 488.5 g, growth model coefficient (K) = 0.28 yr⁻¹, age at first maturity (t_m) = 0.92 yr. The eumetric line characterizes the age at first capture maximizing the yield per recruit for a given F .

and in 1990 high fishing mortality and the relatively low size at first capture suggest substantial overfishing. Fishing mortality, particularly on smaller oysters, has been sufficiently intense to reduce the yield per recruit and spawning stock biomass to less than optimum levels. The sex ratio in the fished population has probably changed to a preponderance of males.

Therefore, 2 independent lines of evidence support the conclusion that both oyster abundance and spawning stock biomass per recruited oyster have declined substantially since the late 1800s. First, comparison of oyster yield per unit area shows that the average density of oysters is presently about 4% of that estimated in 1884. Second, comparison of the average spawning stock biomass per recruit (SSBR) shows that with a 'disease-free' natural mortality rate of 0.15 the SSBR is about 8.4% of the unexploited state. On the other hand, if disease has actually increased the natural mortality rate to 0.5, then the current SSBR is about 2.2% of the unexploited level. The effects of fishing have evidently reduced the spawning efficiency per unit biomass of the oyster population. The areal extent of oyster bars and the oyster biomass per unit area have been substantially reduced. A decrease in fishing mortality by 50% would only increase yield per recruit by 16% and the spawning stock biomass by 75%. On the other hand, an increase in the size of first capture to 122 mm would result in roughly double the yield per recruit and quintuple the spawning stock biomass.

Management implications

Total oyster habitat in the Maryland portion of Chesapeake Bay is probably 50% or less of what it was a century ago due to mechanical destruction of the bars. The remaining habitat is evidently of substantially poorer quality on average (MacKenzie 1983, 1989, Seliger & Boggs 1988a); the biomass per unit habitat is about 1% of that at the turn of the century. There was once shell or other substrate where oysters could grow, these areas are now covered with silt and are suboptimal substrate for adults or recruits, which impedes potential recovery. It may be that the susceptibility to disease is correlated with a reduction of oyster bar profile. In addition, the population-dynamic structure of the population has probably changed substantially.

It is not known whether these factors have been exacerbated by diminished water quality and other environmental degradation (Heinle et al. 1980, EPA 1983, Seliger & Boggs 1988b), even though considerable concern is voiced regarding Chesapeake Bay water quality and the effects of diseases on oysters. The effects of fishing manifested through modification

of oyster bars probably have had a much greater influence on the long-term decline of the oyster. Furthermore, it is evident that such large changes in bar structure understandably affect other populations that support other food chains.

The effects of a diminished oyster population abundance certainly must have changed the 'ecology' of Chesapeake Bay, and these effects must have become evident at the time of the maximum stock decline (i.e. 1884 to 1910). Effects at that time must have included the oyster's reduced capacity to filter the water column (Newell 1988), presumably resulting in increased quantities of dead phytoplankton, which when settled to the bottom, contributing to increased bacterial abundance and anoxic water conditions (Kemp & Boynton 1984), a situation which had begun well before World War II (Newcombe & Horne 1938).

In addition to modification of habitat it appears that the oysters have been subject to stock overfishing. Stock overfishing occurs when size-specific fishing mortality produces less than maximum yield per recruit. In fact, there was stock overfishing before the turn of the century (cf. Fig. 5). Prior to 1890 small oysters (<6.35 cm) were taken from Chesapeake Bay in large quantities to supply the oyster seed fishery for northern coastal states where oyster bars were already exhausted by overfishing (Ingersoll 1881, Winslow 1881a, b). In response to general concern with declining oyster catches in Chesapeake Bay, a 6.35 cm minimum size was imposed in 1890 to conserve the resource. However, catches still continued to decline and the minimum size was raised again to 7.62 cm in 1927. Catches continued to decline post-1927 but the 7.62 cm size limit remains in effect today.

Recent management has moved small oysters from productive to less-productive areas. This management technique is in itself localized stock overfishing and may be overall deleterious, particularly if there is a high mortality of transferred oysters, or if they are contaminated with disease.

Stock overfishing may very well be causally related to recruitment overfishing, as they may influence one another (Rothschild 1986). Recruitment overfishing occurs when spawning stock biomass produces less than average maximum recruitment. Presently the fishery is operating on a stock that is less than 10% of the unexploited spawning stock biomass on a yield per recruit basis, and probably less than 5% when the loss of habitat is also included. Though increased fishing intensity will increase the number of oysters caught (that is above the present low levels), average weight in the population will steadily decrease, and so, ultimately, will the total weight of the catch. In this regard an increase in spawning stock biomass would compensate to some extent for the reduction in bar area. This

can be accomplished by an increase in the minimum size of oysters taken. It is interesting to observe that a substantial reduction in fishing mortality would not increase the oyster equilibrium yield per recruit; rather, more substantial gains would accrue from an increase in the size of capture, facts of considerable economic significance to the management of the public fishery. Potential increases in yield per recruit alone on specific bars will not be sufficient to recover the substantial loss of catch. While increased yield per recruit will produce modest catch increases, only significant increases in recruitment on existing habitat and/or increasing the base habitat area would allow catches to approach historical levels.

To effect the recovery of the eastern oyster stock in Chesapeake Bay and to revitalize Maryland's oyster fishery we propose a 4-point strategy involving: (1) fishery management, (2) repletion, (3) habitat replacement, and (4) broodstock sanctuaries.

The fishery management strategy should include the implementation of a scientifically regulated and managed fishery to control size-specific fishing mortality, taking into account, of course, the fact that in some circumstances spat settle on larger oysters, which can be monitored using sampling theoretic techniques (Rothschild et al. 1990, 1991, Chai 1992).

The repletion strategy – placing shell on existing substrate – should be modernized to effect habitat replacement, increase the growth and survivorship of oysters, and to buoy the catches of commercial watermen. Repletion consists of 2 components: (1) mining 'fossil' oyster shell and then deploying the shell into specific areas to improve spat recruitment, and (2) transplanting recruited spat into areas of improved growth and survivorship. While the State of Maryland has been operating a shell repletion program since about 1960, it has not resulted in any change in the decline in landings and we have shown that it could be improved considerably by using operations research and system analysis techniques to optimize shell allocation and oyster production (Rothschild et al. 1990, 1991).

A habitat replacement strategy – building new substrate – should be implemented to create additional suitable oyster habitat for the recruitment of spat, and the growth and survivorship of new recruits. The lack of suitable oyster habitat is the principal impediment to any substantial long-term oyster population recovery. As it takes decades to create an oyster bar naturally, engineering replacement habitat with artificial structures in optimum growth and survival areas seems to represent a viable alternative.

A broodstock sanctuary strategy would include the designation of 'no-fishing' restrictions in specific areas of engineered replacement habitat and those natural

areas of the Bay where the production of larvae and spat settlement are known to be high. The broodstock sanctuary aspect can reinforce and amplify the positive attributes of the fishery management, repletion, and habitat replacement strategies.

Some of these management measures to restore bars de novo may not be cost-effective in the short run, but more targeted repletion combined with scientifically regulated and managed fishing is likely to at least partially restore the bars, important habitat for oysters, and other commercial and recreational species, such as blue crabs and striped bass.

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