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IS OYSTER SHELL A SUSTAINABLE ESTUARINE RESOURCE?

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ABSTRACT The decline of the eastern oyster (*Crassostrea virginica*) as an estuarine resource is well documented for many estuaries on the United States east coast. This decline is often associated with a decline in the shell resource and ultimately the disappearance of the shell bed. We develop a model that expressly and conjointly evaluates oyster abundance and surficial shell quantity and examine whether stability in the stock and the habitat can be simultaneously achieved. Simulations suggest that a steady-state shell content exists for any set of recruitment and natural mortality rates and that the amount of shell present at steady state varies over a wide range as recruitment and natural mortality vary. Shell mass is maximized at a natural mortality rate near the rate observed in unfished populations unimpacted by disease. A species dependent on the maintenance of hard substrate for survival, as is the oyster, might have a life span adapted to maximize the accretion of carbonate; thereby sustaining the substrate on which it depends. Relatively small changes in the recruitment rate produce large changes in abundance and consequently shell mass and the scale of variation dwarfs that of natural mortality or fishing. Only variations in the rate of shell loss or the average size of animals at death produce equivalent excursions in shell mass. In comparison, the ambit of natural mortality imposed by the disease process fortuitously occurs in a range that restrains the change in carbonate mass, probably because increased mortality reduces abundance but also increases the death rate, thus adding more shell. Simulations covering a range of fishing rates indicate that no fishing rate exists that is likely to be sustainable of the shell resource over the long term. Fishing will always abet the taphonomic and depositional processes conspiring to debilitate the oyster bed. Successful management of the oyster shell resource is obstructed by the simple fact that no additional mortality, whether imposed by disease or through fishing, can occur that will not result in habitat loss at some rate. The shell resource is maximized when the population is at predisease natural mortality rates and unfished. Thus, if fishing is to be permitted or if disease has increased persistently the natural mortality rate, the only recourse of the manager is the perpetual addition of shell in compensation to the loss or the acceptance of the degradation of the shell bed.

KEY WORDS: oyster, shell, structure, oyster reef, taphonomy, disease, natural mortality, shell carbonate, resource management

INTRODUCTION

The influence of shell in structuring the benthic habitats of bays and estuaries is an emerging management issue (Abbe 1988, Gottlieb & Schweighofer 1996, Lenihan & Peterson 1998, Gutiérrez et al. 2003, Breitbart et al. 2000, Brumbaugh et al. 2006). Shell adds complexity to the muddy bottom, thereby increasing species diversity (Larsen 1985, Coen et al. 1999, Harding & Mann 2000, Harding & Mann 2001, Mann 2000, Gutiérrez et al. 2003), arguably increasing secondary production although this is not well documented, enhancing recruitment and survival of shellfish species (Haven & Whitcomb 1983, Abbe 1988, Kraeuter et al. 2003b, Bushek et al. 2004, Green et al. 2004, Soniat & Burton 2005), and, when present in significant amounts, adding bathymetric complexity to the ecosystem (Haven & Whitcomb 1983, DeAlteris 1988, Grizzle 1990, Powell et al. 1995a, Allen et al. 2005). In most temperate zone estuaries of the east and Gulf coasts of the United States, the most important shell resource is oyster shell and this shell normally contributes significant bathymetric complexity in the form of oyster reefs, variously also termed beds, bars, or rocks (e.g., Haven & Whitcomb 1983, Powell et al. 1995a, McCormick-Ray 2005, Woods et al. 2005). Oyster habitat varies from vertically distinct, consolidated structures to shell-rich muddy bottoms little differentiated in relief from their surrounds (Whitcomb & Haven 1987, Grizzle 1990, Powell et al. 1995a, Allen et al. 2005). Regardless, the habitat is a unique shell-rich component of the estuarine ecosystem.

The decline of the eastern oyster (*Crassostrea virginica*) as an estuarine resource is well documented for many estuaries on the

east coast (Hargis & Haven 1994, Rothschild et al. 1994, Woods et al. 2005). Though not always documented, this decline is often associated with a decline in the shell resource and ultimately the disappearance of the shell bed (Marshall 1954, Woods et al. 2005, Bergquist et al. 2006). Historically, the decline in the shell resource has been attributed to fishing, in this case the removal of or redistribution of shell by dredges (e.g., Marshall 1954, Woods et al. 2005). In some cases, clear documentation of the removal of shell by dredges is available (Masch & Espey 1967, May 1971, Powell et al. 1995a); however, these reports are consistently associated with the purposeful removal of shell rather than fishing. Fishing is inferred as an agent primarily by association. Documented declines in reef area are often those areas open to commercial harvesting. Sedimentation is also identified as an agent responsible for the decline in surficial shell content. Oyster beds with low relief are susceptible to sedimentation (DeAlteris 1989, Lenihan 1999, Smith et al. 2001). In this case, however, the shell is not lost *per se*, but its role in ecosystem function ceases.

Neither of these explanations for shell loss considers the role of shell production as an important component of the benthic shell cycle. Contrariwise, recent evidence emphasizes the role of shell production and taphonomic processes degrading shell (Powell et al. 2006). These processes operate regardless of fishing and abet the burial of shelly bottom through depositional processes. Taphonomic degradation is sufficient to produce substantive changes in shell content over decadal time periods, when the abundance of living oysters is low. The data suggest that the ultimate progenitor of the destruction of oyster habitat is population decline, by overfishing (Hargis & Haven 1988, Rothschild et al. 1994, Jordan et al. 2002) or disease

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(Andrews 1968, Andrews 1988, Krantz & Jordan 1996, Cook et al. 1998), leading to a decrease in the carbonate input necessary to counterweigh the perpetual resistless loss of shell through taphonomic degradation and leading ultimately to an increasing susceptibility of the shell bed to burial resulting in permanent habitat loss.

The decline in eastern oyster populations, the concern that some portion of the decline originates from overfishing, and the likelihood that disease has reduced the sustainable yield of oyster populations has led to increased rigor in the management of oyster fisheries. The States of New Jersey and Delaware have led in this effort, because both states have adopted biological reference points directed at stabilizing population abundance and have instituted recruitment enhancement programs through shell planting (e.g., Bushek et al. 2004, Abbe 1988, Bowling 1992, Soniat et al. 1991, Soniat & Burton 2005) to expand oyster abundance. In the case of New Jersey, a fisheries model is used to directly evaluate the allowable harvest under the restrictions of disease mortality such that the population abundance has a $\leq 25\%$ probability of decline (Klinck et al. 2001, HSRL 2006). In other words, population expansion is anticipated to occur in three of four years.

These more sophisticated approaches continue to fail to resolve goals for maintaining the oyster bed, however. That is, the population can be stabilized whereas the oyster shell ultimately necessary for long-term sustainability declines. That scenario has existed in Delaware Bay since 2000 (Powell et al. 2006). Management has, as yet, not quantified abundance goals that can produce sustainable populations and also sustainable shell resources. Arguably, the management goal should include an abundance or biomass reference point and a substrate reference point leading to simultaneous fulfillment of the two conditions:

$$\frac{dN}{dt} = 0 \quad (1)$$

and

$$\frac{dS}{dt} = 0 \quad (2)$$

where N is the abundance of oysters, S is the quantity of surficial shell, and t is time. That is, neither the stock nor the shell resource should decline over time. Eq. (1) is implemented in New Jersey (HSRL, 2006) and is the basis for the federal management of fisheries at maximum sustainable yield (Anonymous 1996, Applegate et al. 1998, Restrepo et al. 1998). In this contribution, we develop a management model that expressly and conjointly evaluates oyster abundance and shell quantity. We seek cases where Eqs. (1) and (2) are simultaneously achieved and discuss implications for the development of biological reference points for the management of exploited oyster populations.

MATERIALS AND METHODS

Basic Model Structure

The model is parameterized using information from Delaware Bay (HSRL 2006, Powell et al. 2006). Oysters in Delaware Bay typically attain sizes of 70–80 mm, with maximum size nearing 120 mm. Animals of 70–80 mm are about three years

old, except in the upper reaches of the bay where low salinity and low food supply reduce growth rate. Population dynamics is controlled to a significant extent by adult mortality caused by Dermo disease (Ford 1996, Dittman et al. 2001, HSRL 2006), except in the upbay low-salinity reach. MSX disease is not a primary mortality source, as it is in geographically neighboring regions (Sunila et al. 1999, Ford et al. 1999; Burreson et al. 2000, Volety et al. 2000). The oyster fishery since 1996 has removed less than 1.5% of the stock by abundance and 3% of the stock by biomass in nearly all years (HSRL 2006). As a consequence, the population is dominantly controlled by natural processes of recruitment and mortality and has been since the onset of Dermo disease circa 1990.

The biological model defining the living population is defined as:

$$\frac{dN}{dt} = -(\eta + m(t) + f(t))N + r(N) \quad (3)$$

where m is the natural mortality rate (yr^{-1}), f is the fishing mortality rate (yr^{-1}), r is the recruitment rate, and N is expressed on a per-m^2 basis. Unless explicitly expressed otherwise, f is assumed to be zero and not carried forward in subsequent mathematical expressions. Although a constant natural mortality rate is often assumed in fisheries models (Paloheimo 1980, Vetter 1987, Clark 1999), the temporal vagaries of the disease process as influenced by changes in climate require that m be allowed to vary between years in some cases. We will consider both the case of invariant m and temporally variable m in subsequent simulations. The natural mortality rate m is normally estimated from box counts (Soniat et al. 1989, Christmas et al. 1997, Ford et al. 2006). In Delaware Bay, box-count mortality underestimates the total mortality in the population (HSRL 2006). Much of this underestimation is believed to be associated with juveniles. This underestimate, subsequently included implicitly, is shown explicitly in Eq. (3) as an additional mortality rate η . Thus, total mortality Z can be expressed as $Z = f(\eta, m, f)$.

Because the goal of this exercise is to examine conditions under which the oyster population and the shell substrate are stable, N in Eq. (3) is defined to be the adult component of the population. For simplicity, we focus on animals averaging 70 mm in most simulations. Animals 60–80 mm in size contribute the bulk of the living shell carbonate in the oyster population downestuary of the lowest salinity reach in Delaware Bay and the bulk of the carbonate added to the oyster bed upon death in these downbay reaches. Taphonomic processes degrade small shells more rapidly than large shells (Powell et al. 1986, Cummins et al. 1986, Glover & Kidwell 1993), and, although documentation for oysters remains illusory, a deviation from this general trend would be unexpected. Animals >80 mm are relatively rare. Thus 70 mm is a representative size at death for adult Delaware Bay oysters. Consequently, except where noted, the mortality and recruitment terms as invoked by Eq. (3) focus on the 60–80-mm size class and the recruitment rate r in Eq. (3) pertains to the addition of 70-mm animals into the population.

The shell resource is modeled as described by Powell et al. (2006):

$$\frac{dS}{dt} = (b(t) - l)S \quad (4)$$

where b (yr^{-1}) is the rate of shell addition as estimated from box counts (Powell et al. 2006), l (yr^{-1}) is the rate of shell loss, and

S is expressed on a per- m^2 basis. Powell et al. (2006) provide values of l for Delaware Bay oyster beds. To estimate b , we recognize that shell is added to the oyster bed through the death of living individuals. Accordingly, the equality:

$$\gamma m(t) N = b(t) S \quad (5)$$

must hold. γ in Eq. (5) is a conversion from numbers to shell weight and is based on information shown in Figure 1 that yields the relationship

$$SW = 0.00041 \times L^{2.70} \quad (6)$$

where SW is shell weight in grams and L is oyster length (anterior-posterior dimension) in mm. For a 70-mm individual, $\gamma = 39.3 \text{ g individual}^{-1}$.

To evaluate Eq. (3), we use the broodstock-recruitment relationship of HSRL (2006):

$$r'(N') = N' e^{\alpha \left(1 - \frac{N'}{\beta'}\right)} \quad (7)$$

where $\alpha = -0.1706$ and $\beta' = -3.822 \times 10^9$ individuals, and the prime (') designates values based on the entire population summed over the entire bay rather than the ≥ 70 -mm size fraction on a per- m^2 basis. Recruits into the ≥ 70 -mm size fraction are estimated by rescaling Eq. (7) assuming that the large size fraction contributes about 13% to population abundance. Estimates for Delaware Bay in 2005 place this fraction at 26% (HSRL 2006); however, this high ratio represents a period of unusually low recruitment. Values for 1999, just after a period of high recruitment, indicate that large animals contributed about 4% to population abundance at that time. Thus 13% is a representative intermediate value. In Delaware Bay, animals ≥ 70 mm are ≥ 3 y in age except in the lower salinity reaches where 4–5 y are required to grow to this size. True recruits are debited by three years of natural mortality as a consequence, such that the number of 70-mm recruits is estimated as

$$r(N) = \omega e^{-(2m+\eta)} r'(N') \quad (8)$$

where ω is a conversion factor returning the whole-bay recruitment estimate of Eq. (7) to a per- m^2 basis.

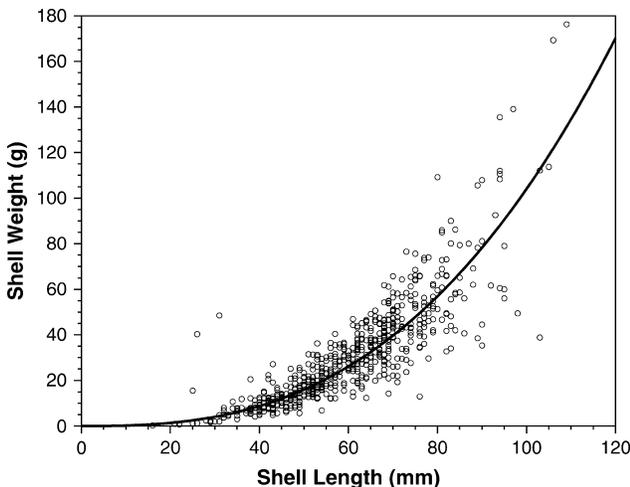


Figure 1. The relationship between shell weight and shell length (anterior-posterior dimension) for oysters from Delaware Bay.

Steady State

Redefining shell generation rate b in terms of animal mortality gives the following two equations to solve:

$$\frac{dS}{dt} = \gamma m(t) N - lS \quad (9)$$

and

$$\frac{dN}{dt} = -m(t) N + r(N) \quad (10)$$

for an unfished population.

The steady state solution is obtained by letting mortality rate be constant (m_0) and setting the time derivative to zero. The resulting algebraic equations are easily solved for the steady state values as:

$$S_s = \frac{\gamma m_0 N_s}{l} \quad (11)$$

and

$$N_s = \beta \left(1 - \frac{\log_e m_0}{\alpha}\right). \quad (12)$$

Evidence suggests that the natural mortality rate for oysters before the advent of Dermo and MSX disease was about 10% per year, based on box counts, with rates varying from 0.05–0.15 y^{-1} (Bushek 2007). Dermo epizootics raise the mortality rate to levels of 0.2–0.4 y^{-1} for periods of one to two years. Simulations will focus on box-count mortality rates of 0.05–0.50 y^{-1} . Shell loss rates vary by oyster bed, being highest at moderate salinities and lowest at the up-estuary and down-estuary extremes of the oyster's range (Powell et al., 2006). An average across the salinity gradient yields $l = 0.18 \text{ y}^{-1}$ with a range of 0.05–0.37 y^{-1} . Simulations will focus on this range of shell loss rates.

Quasi-Steady State with Time-Dependent Mortality

Evidence supports the formulation of epizootic episodes of mortality using a sinusoidal waveform. Both Dermo and MSX are influenced by salinity. For Dermo, the influence of climatic cycles is well described (Powell et al. 1992, Kim & Powell 1998, Soniat et al. 2006). In Delaware Bay, disease epizootics tend to be of two to three years in duration with maximal mortality rates of the order of 30% of the adult population yearly (Bushek 2007). A quasi-steady state solution is obtained with cyclical time-dependent mortality by using the time-dependent mortality in the steady state formulae as

$$S_q = \frac{\gamma m(t) N_s}{l} \quad (13)$$

and

$$N_q = \beta \left(1 - \frac{\log_e m(t)}{\alpha}\right). \quad (14)$$

Time-dependent mortality is imposed by allowing m to vary sinusoidally with an amplitude of:

$$m = m_0 \pm 0.5 m_1 \quad (15)$$

where $m_1 - m_0$ is the amplitude of the mortality range.

The quasi-steady solution is valid under the assumption that the rate of change of mortality, $m(t)$, is slower than the time

required for the model to achieve equilibrium. Mortality is assumed to vary over time scales of 4 y, but a few years to a decade are required for the model to come to equilibrium, as is presented in the next section. So, these quasi-steady solutions are only approximately valid. Nevertheless, they provide general information about the slow variation of the equilibrium solutions.

Time-Dependent Model

Eqs. (13) and (14) do not reproduce true time-dependent behavior, but do permit evaluation of the potential range of excursion of shell content and population abundance given cyclical changes in mortality rate. A comparison with the results of a time-dependent calculation permits identification of the sensitivity of shell to the influence of rapid changes in population dynamics relative to its potential. The time-dependent model invoking Eqs. (3) and (4) was solved using a Runge-Kutta numerical solver.

RESULTS

Steady State Base Case

A simulation was conducted with an average shell loss rate of $l = 0.18 \text{ y}^{-1}$, under the proviso that shell-contributing animals averaged 70-mm in size with a carbonate mass of 39.3 g, and that animals of this size comprised 13% of the total population. Figure 2 shows the abundance and shell mass at steady state for each increment of mortality rate from $<0.05\text{--}0.50 \text{ y}^{-1}$. The number of animals declines steadily with increasing rates of natural mortality at steady state. The decline is nearly linear with the population approaching extinction at mortality rates much above 0.3 y^{-1} (Fig. 2B). The shell mass produced traces out a nonlinear relationship with mortality and abundance because increased mortality initially increases the rate of shell addition, while also reducing population abundance. The interaction results in a shell mass that declines with increasing rate as the mortality rate increases (Fig. 2A). As a consequence, shell mass trends towards an asymptote at high abundance (Fig. 2C).

Note that the x -axis on this and subsequent figures is the box-count mortality rate. This mortality rate underestimates the true mortality rate Z of the population. An additional mortality rate, η in Eq. (3), is implicit in the x -axis values, such that the value $m = 0$ implies $Z = \eta$. In Figure 3, we extend the mortality rate axis to lower total mortality rates, assuming that the mortality rate derived from box counts underestimates the true natural mortality rate to some degree. Shell mass reaches a maximal value for box-count mortality rates near $0.05\text{--}0.10 \text{ y}^{-1}$ (Fig. 3A). The decline in shell content at lower mortality rates is belied by the coincident higher numerical abundance (Fig. 3B). More animals exist, but the realization of fewer deaths reduces shell input relative to shell loss. A plot of abundance *versus* shell mass (Fig. 3C) shows this relationship clearly. Shell content rises as abundance declines from high to moderate levels because natural mortality increases until the increase in carbonate input becomes limited by the lower abundance reducing the total number of deaths. Thus oyster beds may be mortality limited when low natural mortality rates and concomitant long life spans permit high abundance and limit shell addition rate, but abundance limited when short life spans co-occur with high rates of natural mortality.

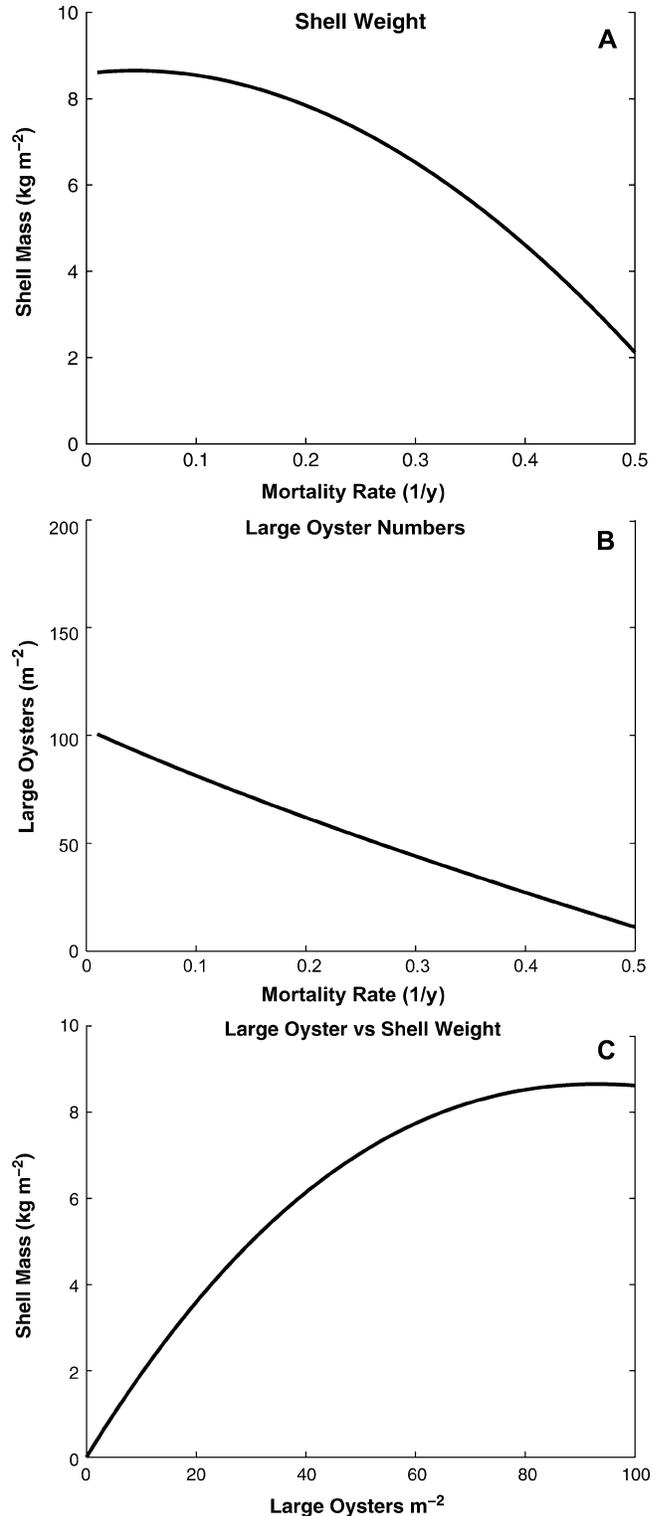


Figure 2. The relationships between shell mass, the abundance of large animals, and the rate of natural mortality for an average shell loss rate $l = 0.18 \text{ y}^{-1}$, a representative ratio of large-to-total animals of 0.13, and an average carbonate mass for a large animal of 39.3 g, equivalent to an animal 70 mm in length.

The maximal shell mass just exceeds 8 kg m^{-2} . A crude estimate of surficial shell mass, available to an oyster dredge, on Delaware Bay oyster beds, yields 6.2 kg m^{-2} . This estimate is

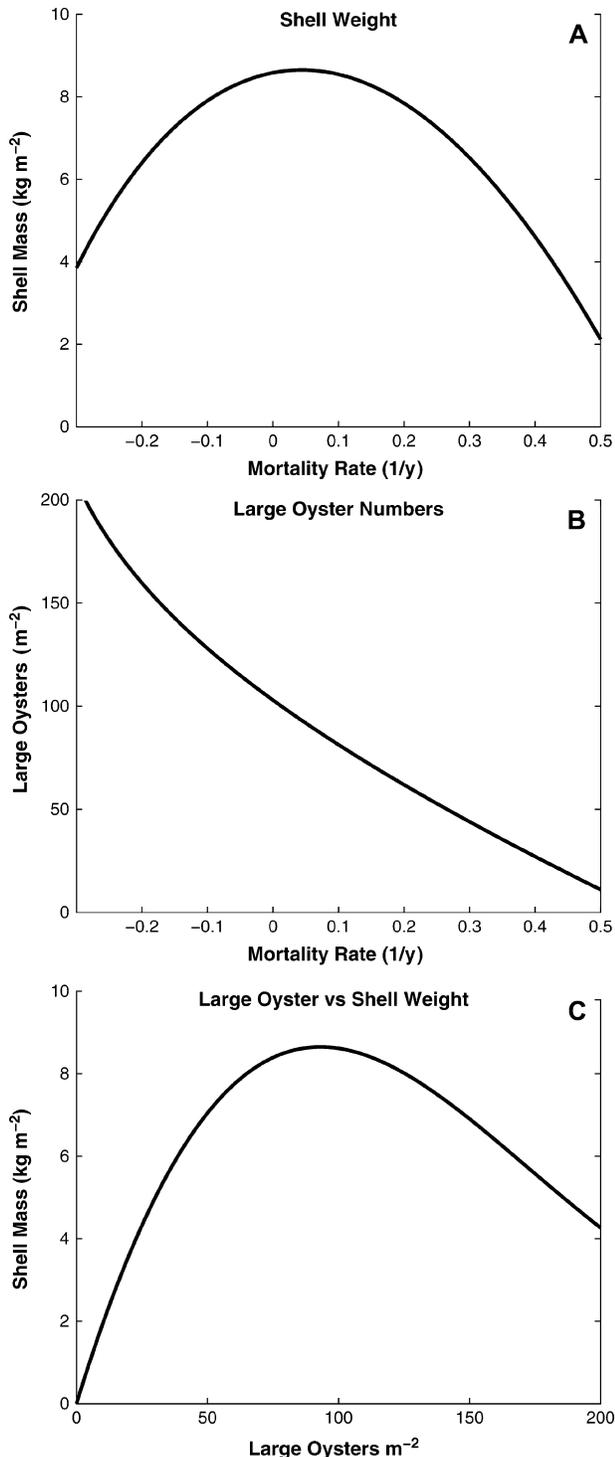


Figure 3. The relationships between shell mass, the abundance of large animals, and the rate of natural mortality for an average shell loss rate $l = 0.18$, a representative ratio of large-to-total animals of 0.13, and an average carbonate mass for a large animal of 39.3 g, equivalent to an animal 70 mm in length. The negative mortality rates cover a range of potential mortalities if the factor $[\eta$ in Eq. (3)] correcting for the underestimate of mortality by box counts is overestimated.

obtained from a measured average of 4.6 L m⁻² shell, the density of oyster shell of 2.2 g ml⁻¹, and the assumption that a measure of dry shell volume is about 59% shell and 41% dead space

caused by the open packing of oyster shell clumps. This measure was obtained from samples taken on Delaware Bay oyster beds. Thus, the model returns a surficial shell mass comparable to that observed on Delaware Bay oyster beds.

Influence of Shell Loss Rate and Animal Size at Death

Simulations were run covering the range of measured shell loss rates. An increase in shell loss rate by about a factor of two, to 0.37 y⁻¹, reduces steady-state shell content by about half over the base case (Fig. 4A). Reducing measured shell loss rate by about a factor of 3, to 0.05 y⁻¹, increases shell mass by about a factor of 4 (Fig. 4B). Population abundances remain unchanged in these simulations. Thus, varying shell loss rate by a factor of about 6 changes shell mass by about the same factor. The stability of the shell resource is significantly influenced by the rate at which the taphonomic processes proceed on the oyster bed.

Oysters grow to a smaller characteristic adult size at lower salinity in Delaware Bay. At the uppermost reaches, animals rarely exceed about 50 mm. Such an animal has a carbonate mass of about 15.8 g. A simulation of this case shows that populations of equivalent density, but lower characteristic adult size, will accrue far less carbonate mass (Fig. 5A). The converse occurs with larger animals as might have dominated populations prior to the advent of disease, as might be characteristic of habitats with high food supply, or which might live at higher latitudes where proportionately more of the annual energy budget is invested in growth rather than reproduction (Hofmann et al. 1992). A simulation with the average size at death equivalent to 90 mm, animals with carbonate masses of 77.5 g, shows a factor of 4 increase in carbonate mass in comparison with the case for 50-mm animals (Fig. 5B). Thus, the size reached by the average adult individual significantly influences the rate of carbonate addition and particularly so if differential sizes are reached under similar rates of natural mortality.

Fishing

Fishing removes animals and carbonate, the latter because the shell does not accrete to the carbonate mass of the bed. In Delaware Bay, fishing rates above about 7% of stock abundance are believed to be unsustainable, based on analysis of a 53-y record of stock abundance and fishery catch (HSRL 2006). Estimates available in recent years indicate that the targeted removal of large animals by the fishery (Powell et al. 2005) translates into a removal ratio of about two between abundance and biomass. That is, the removal of 5% of the stock by abundance is equivalent to a removal of about 10% of the market-size stock, equivalent to an $f = 0.105$ for 70-mm animals.

Figure 6 shows the influence of a range of fishing mortality rates at a natural mortality rate of 0.1 y⁻¹. The abundance of 70-mm animals declines with increasing mortality along approximately the same trajectory regardless of whether the source of mortality is natural or a product of fishing (Fig. 6B versus 2B). The trajectories traced out by the accumulated shell diverge markedly in comparison (Fig. 6A versus 2A). For natural mortality, the shell mass remains fairly stable over a range of low mortality rates before declining at an accelerating rate as mortality rate continues to rise. For fishing, shell mass declines rapidly with the imposition of fishing, but the rate of decline of shell mass decreases with increasing fishing pressure. Thus, a box-count mortality of 0.1 y⁻¹ does not much impact

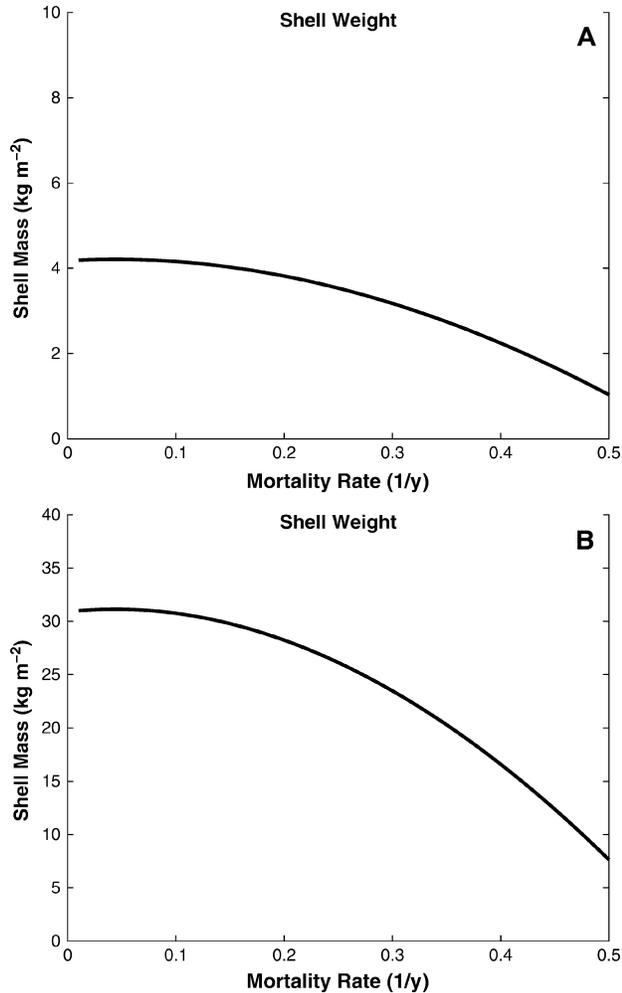


Figure 4. The relationships between shell mass and the rate of natural mortality for shell loss rates of (A) 0.37 y^{-1} and (B) 0.05 y^{-1} for a population with a representative ratio of large-to-total animals of 0.13, and an average carbonate mass for a large animal of 39.3 g, equivalent to an animal 70 mm in length. An example of an intermediate shell loss rate, 0.18 y^{-1} , is shown in Figure 1. Note the different y-axis scales between figures.

shell mass. In contrast, a fishing mortality rate of 10% results in a distinct decline in shell mass. A rise of natural mortality rate to 0.3 y^{-1} results in a moderate reduction in shell mass. A fishing mortality rate of 0.3 y^{-1} in contrast results in a distinct decline in shell mass. The differential trajectories originate from the fact that an increase in natural mortality rate, as long as rates remain relatively low, increases the number of shells added to the bed relative to the decrease in abundance. This occurs because a drop in abundance when abundance is relatively high also tends to increase recruitment and the number of animals passing through the population initially increases. For fishing, on the other hand, although the influence on recruitment is similar, the increase in the number of deaths does not increase the rate of addition of shell.

Recruitment Rate

Shell loss rates vary geographically, but appear to be relatively stable year to year in any one location (Powell et al.

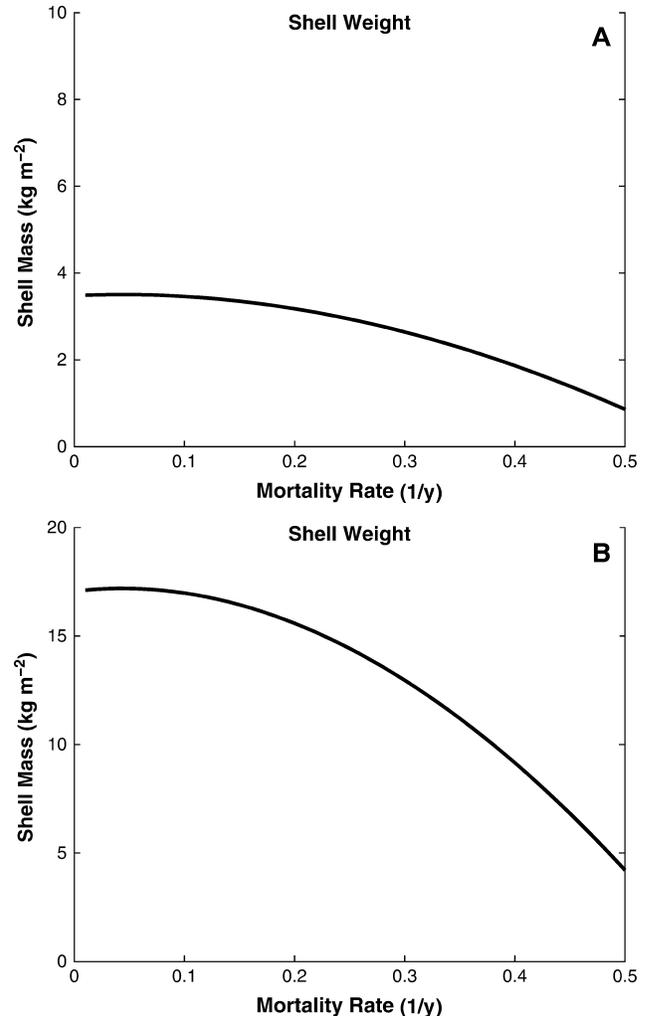


Figure 5. The relationships between shell mass and the rate of natural mortality for a population with adult animals averaging (A) 50 mm in length with an estimated carbonate mass of 15.8 g and (B) 90 mm with an estimated carbonate mass of 77.5 g, with a representative ratio of large-to-total animals of 0.13, and a shell loss rate of $l = 0.18 \text{ y}^{-1}$. The relationship for a 70-mm animal is shown in Figure 2. Note the different y-axis scales between figures.

2006), although the data supporting this conclusion is admittedly still rather sparse. Recruitment rates vary over a wide range yearly, with periods of low recruitment often of extended duration (Loosanoff 1966, Austin et al. 1996, HSRL 2006). An increase in recruitment rate relative to broodstock abundance of 10% results in a large excursion of abundance and shell mass, both more than doubling (Fig. 7A,B) in comparison with the norm (Fig. 2A,B). A 25% reduction in recruitment rate relative to broodstock abundance produces a much lower population abundance and a significant decline in shell mass (Fig. 7C,D). Note that shell mass, in this case, declines from about 8 kg m^{-2} in the case of a recruitment rate anticipated from the broodstock-recruitment relation described by Eq. (7) (Fig. 2A) to just under 3 kg m^{-2} (Fig. 7C). The differential between these two simulations is equivalent to a difference in the number of recruits per adult of 0.64 in the low recruitment case and 0.92 in the high recruitment case when population abundance is low [$\frac{N}{P} \ll 1$ in Eq. (7)]. In Delaware Bay, yearly

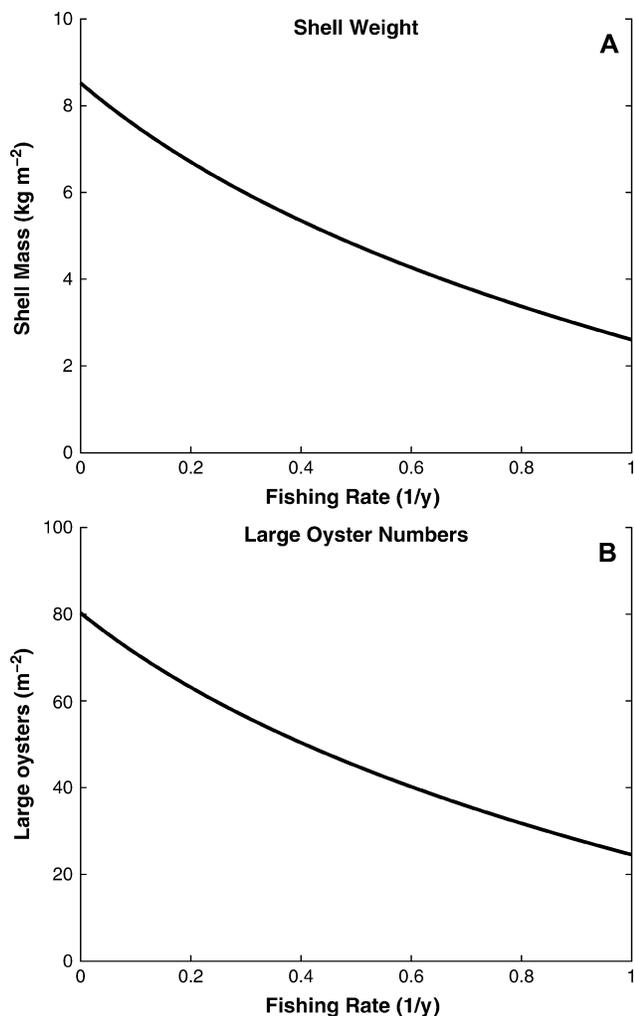


Figure 6. The relationships between shell mass, population abundance, and the rate of fishing mortality for fished populations with adult animals averaging 70 mm in length with an estimated carbonate mass of 39.3 g, with a representative ratio of large-to-total animals of 0.13, a natural mortality rate of 0.1 y^{-1} , and a shell loss rate of $l = 0.18 \text{ y}^{-1}$. Note the different y-axis scales between figures.

variations have ranged from <0.25 to >1.50 recruits per adult over the 53-y time series of record (HSRL 2006), a much wider range. Thus, relatively small changes in the recruitment rate produce large changes in abundance and consequently shell mass and the scale of variation dwarfs that of natural mortality or fishing.

Time-Dependency of Shell Response

In Figure 8, we compare the results of a quasi-steady state simulation of varying mortality with a 4-y periodicity typical of Dermo disease (Fig. 8A,B) to a time-dependent calculation of the same epizootiology (Fig. 8C,D). Abundances vary from about 55–70 individuals m^{-2} as natural mortality oscillates between 0.1 and 0.3 y^{-1} . The range is about the same in both simulations (Figs. 8A,C). The quasi-steady state calculation shows that shell mass might be anticipated to vary from about 6.5–8.5 kg m^{-2} by this means (Fig. 8B). However, the time-dependent simulation shows a realized variation of $<0.5 \text{ kg m}^{-2}$ (Fig. 8D). The much reduced variability in shell mass in

comparison with that anticipated by comparing the steady-state shell mass over the same mortality range, as shown by the quasi-steady state calculation, shows that shell mass responds relatively slowly to short-term vagaries in natural mortality rate. The same would be true in response to changes in recruitment rate or the average size at death. That is, significant changes in shell content require persistent changes in population dynamics over a period of years. The origin of this effect can be found in (1) the relatively long shell half-lives compared with the capacity of natural populations to expand and contract (Powell et al. 2006) and (2) the similarity of the rates of shell loss and gain in comparison with the volume of shell on the bed. In the present simulation, the yearly input of shell carbonate is about 1.1 kg m^{-2} with excursions above and below this value of less than 1 kg . The yearly loss of shell is about 1.2 kg m^{-2} . Thus, only a small increment in shell can occur when mortality rates are low and only a small decrement in shell can occur when mortality rates are high over a two-year segment of the 4-y cycle, when the shell resource is varying around 8 kg m^{-2} . Of course, a larger shell loss rate would result in a larger response, as would a longer cycle period.

DISCUSSION

Caveats

Oyster beds contain a layer of loose shell on the surface below which may exist a quantity of consolidated shell that contributes the bulk of the geological mass. Our simulations address the fate of the loose layer of surficial shell that caps the reef proper. This shell accretes through mortality of the living animals and is lost through taphonomic processes. To the extent that accretion exceeds loss, some of this shell will slowly be incorporated into the consolidated mass. Conversely, to the extent that the surficial shell is inadequate to protect the consolidated mass from the vicissitudes of taphonomy, this older shell may be remobilized into the surficial layer. The interaction between the surficial shell and the consolidated mass is not well understood, although theoretical models of shell bed formation have been formulated (Kidwell 1986, Powell 1992) and is not a component of the shell budgets simulated herein. Thus, we do not attempt to simulate accretion or loss of the carbonate mass itself. This study focuses only on the fate of unconsolidated surficial shell in what Davies et al. (1989) termed the taphonomically-active zone (TAZ). The interaction between the surficial and consolidated shell, however, remains a significant uncertainty in evaluating the fate of the oyster shell resource. Many simulations discussed herein estimate steady-state surficial shell masses insufficient to protect the underlying consolidated shell mass and can be expected to expose this older shell to taphonomic attack. The steady state appellation is a misnomer in this case, as loss of underlying shell will continue apace.

The simulations have focused on adult animals averaging 70 mm in size. The relationship of shell weight to shell length is highly nonlinear, so that an increment in shell length to 95 mm doubles the shell mass added per death. Thus, variations in natural mortality and growth, by varying the size at death, may substantively modify the relationship between abundance and shell mass. That oyster populations at one time contained substantive numbers of old animals of large size is suggested

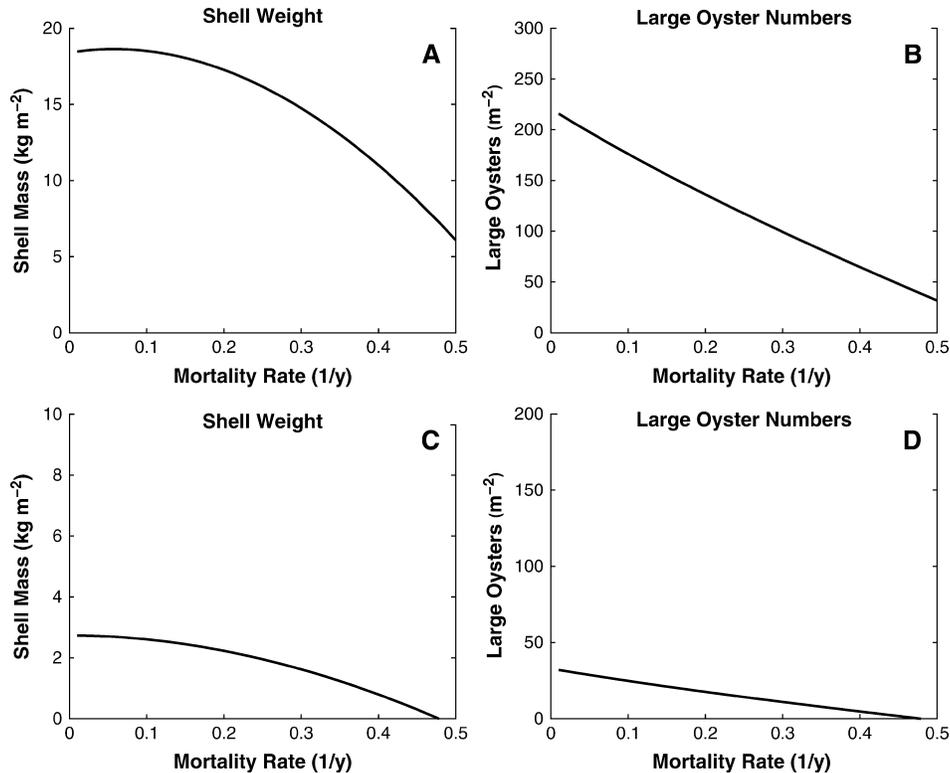


Figure 7. The relationships between shell mass, population abundance, and the rate of natural mortality for populations of differing recruitment rate with adult animals averaging 70 mm in length, with an estimated carbonate mass of 39.3 g, with a representative ratio of large-to-total animals of 0.13, and a shell loss rate of $l = 0.18 \text{ y}^{-1}$. Simulated populations were exposed to a recruitment rate equivalent to (A,B) 0.92 recruits per adult at low abundance and (C,D) 0.64 recruits per adult at low abundance. Figure 2 shows an intermediate case of 0.84 recruits per adult. Note the different y-axis scales between figures.

by early surveys (Moore 1907, Moore 1911). This dynamic interaction is beyond the scope of the simple model developed herein and represents a limitation on inferences drawn from it.

The simulations we have conducted are premised on the fact that sufficient shell is always available for recruitment. Oyster larvae respond to a variety of cues (Hidu & Haskin 1971, Bushek 1988, Osman et al. 1989, Fitt & Coon 1992), but the single biggest influence on recruitment, namely the tendency for newly planted shell to attract substantially increased settlement, remains largely unexplained. That larval settlement can exceed 1,000 spat per bushel of clean cultch is well documented anecdotally, although perhaps not in the scientific literature. In contrast, long-term average recruitment rates in Delaware Bay are about 83 spat per bushel (HSRL 2006). Thus, adequate shell for recruitment would appear to be present over a wide range of shell mass. Nevertheless, consideration of the results of the model investigated herein must be undertaken with the caveat that the influence of shell mass on recruitment is not included and largely unknown.

Shell Resource Dynamics

Bearing these three caveats in mind, the simulations shown in Figures 2–8 can provide insight into the dynamics of the shell resource and its management. The simulations suggest that a steady-state shell content exists for any set of recruitment and natural mortality rates and that the amount of shell present at

steady state varies over a wide range because recruitment and natural mortality vary. However, this apparent stability belies the fact that low surficial shell contents almost certainly result in mobilization and loss of the underlying shell mass over time and consequently enhanced susceptibility to burial. Presume, for example, that the thickness of any oyster shell is on the order of 6 mm. Covering 1 m² this thick requires $6 \times 10^3 \text{ cc}$. Oyster shell is composed of calcite, with a density of 2.71 g cc^{-1} . However, oyster shell density is generally lower than pure calcite because of the number of boring endobionts and the protein matrix (Price et al. 1976) contributes to shell volume in disproportion to weight. An estimate of oyster shell density from shells obtained from Delaware Bay oyster beds yields a value of 2.2 g cc^{-1} . These values are comparable to values for oyster shell fragments obtained by Yoon et al. (2004). Using that value, $6 \times 10^3 \text{ cc}$ is equivalent to 13.2 kg of shell. Coverage this thin is unlikely to be sufficient to accrete vertically to any significant extent. Certain simulations yield a steady-state carbonate mass $\geq 20 \text{ kg m}^{-2}$. The shell addition rate that permits permanent accretion to form bathymetric highs is unknown, but once shell reaches a thickness of greater than single-shell coverage, some apparent carbonate loss is likely caused by accretion into the consolidated geological mass rather than taphonomic degradation. In the majority of simulations depicted in Figures 2–8, however, surficial shell content rarely exceeds 10 kg m^{-2} , and so oyster beds should not accrete vertically to any significant extent over a wide range of

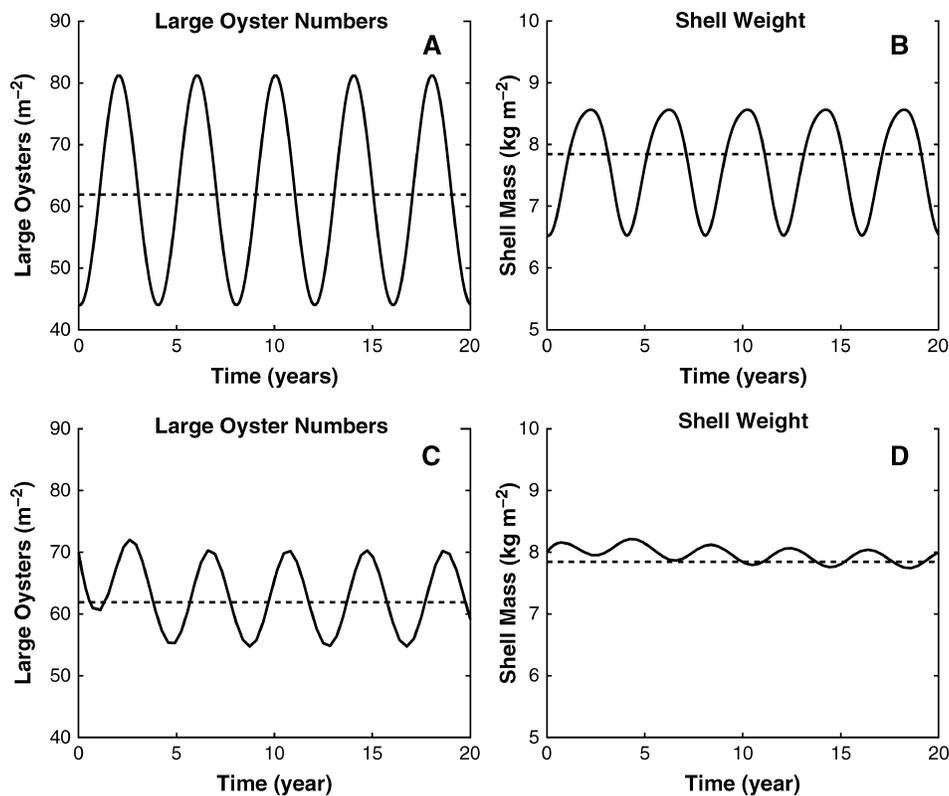


Figure 8. The relationships between shell mass, the abundance of large animals, and the rate of natural mortality for an average shell loss rate $l = 0.18$, a representative ratio of large-to-total animals of 0.13, an average carbonate mass for a large animal of 39.3 g, equivalent to an animal 70 mm in length, and a 4-y periodic variation in natural mortality rate from 0.1–0.3 y^{-1} . (A,B) The results of a quasi-steady state calculation in which the shell mass at any given time approximates the shell mass anticipated to be present under equivalent but persistent conditions. (C,D) The results of a time-dependent simulation showing the dampening effect of the time scale of taphonomic loss on the shell budget under conditions of large short-term variations in the living community producing shell.

population dynamics and taphonomic rates observed today. Powell et al. (1995a) could not identify significant changes in vertical relief over many years in a survey of Galveston Bay oyster reefs, a result consistent with these simulations, and with other surveys of equivalent type.

This latter inference is also supported by an interesting confluence. Evidence from the evaluation of long-term time series of stock abundance, recruitment, and mortality in Delaware Bay leads to the inference that average nondisease mortality rates from box counts are on the order of 0.10 y^{-1} (HSRL 2006, Bushek 2007). This mortality rate is probably the mortality rate that existed in un-fished oyster populations prior to the advent of MSX and Dermo disease. This low mortality rate is consistent with that expected as well from an animal of relatively long life span (Hoenig 1983). Galtsoff (1964) maintained *Crassostrea virginica* for 9 y, so oysters likely can live for a decade or longer, considerably beyond the conservative estimates provided by Comfort (1957) and Custer and Doms (1990) but consistent with estimates for fossil crassostreid species (Kirby, 2000) and recent estimates reported in Berrigan et al. (1991). Interestingly, a simulation of an oyster population characterized by average recruitment and shell loss rates suggests that shell mass is maximized at a natural mortality rate of this order (Fig. 2). A species dependent on the maintenance of hard substrate for survival, as is the oyster, might be adapted to maximize the accretion of carbonate;

thereby maximizing the likelihood of sustaining substrate and habitat on which the future of the population depends. Oysters are the only taxon living today (nonoyster fossil analogues include rudists—Sanders 1999) that make their own substrate but do not protect that substrate, at least partially, with living tissue, as do corals; thus requiring their own deaths to sustain their descendents. Our simulations strongly indicate a confluence of adult mortality rate and maximal shell mass, suggesting such an adaptation. Although longevity is a component of the evolutionary theory associated with the concepts of r and k selection (Stearns 1976) and may be proportional to species adult size in some taxa (Powell & Stanton 1996), and although longevity is considered as a component of the response to parasitism (e.g., Minchella 1985, Kirchner & Roy 1999), the evolution of longevity in bivalves is not well understood. In oysters, however, it is certainly reasonable to presume that the need to maintain substrate might modulate the life span, because any tendency towards a life span beyond that which would maximize shell mass would be limited by the resulting reduction in habitat quality.

Natural Processes Varying Shell Mass

The oyster diseases MSX and Dermo have seriously depressed population abundances. An increase in natural mortality rate from 0.1 y^{-1} to an epizootic level of 0.3 y^{-1} , typical of

epizootic conditions for Dermo disease (HSRL 2006), produces the anticipated strong reduction in population abundance. A decline in shell mass is concomitant, but not of the same order. Shell mass declines more slowly initially as mortality rate exceeds 0.1 y^{-1} , but then accelerates as mortality rate continues to increase. Thus, the ambit of natural mortality imposed by the disease process fortuitously occurs in a range that seemingly restrains the change in carbonate mass. The reason is likely the fact that increased mortality reduces the abundance of the population providing shell, but also increases the death rate of that reduced population, thus adding proportionately more shell, and these offsetting effects, up to a point, damp the response of the shell resource to abundance decline. Thus the oyster bed is, to some extent, resilient to the influence of the disease process. In fact, shell content of oyster beds may be mortality limited at very low natural mortality rates where long life spans limit shell addition rate. Such a condition is as undesirable for the oyster as conditions which result in short life spans and high rates of natural mortality, in which the number of deaths, now limited by abundance, limits the rate of shell addition.

The resiliency of shell mass to variations in the natural mortality rate remains as long as recruitment is adequate. Variations in recruitment, persistent over time, generate strong responses in shell mass. Maintenance of an adequate recruitment rate is the single most profound response to the needs of the population and also the shell resource, because an increase in recruitment can substantively offset a larger increase in natural mortality. Thus, relatively small changes in the recruitment rate produce large changes in abundance and consequently shell mass, and the scale of variation dwarfs that of natural mortality or fishing. Only variations in the shell loss rate or the average size at death produce equivalent excursions in shell mass.

Low salinity does not always result in the stunting of the adults in the population (e.g., Soniat et al. 1998), but scope for growth may decline at low salinity as the cost of maintenance increases (Hofmann et al. 1992, Hofmann et al. 1994, Soniat et al. 1998). In Delaware Bay, food supply also declines with declining salinity (Powell et al. 1997) and this, in combination with the increased energy costs of maintenance, restricts adult size. Such a restriction severely reduces shell input and, as a consequence, an average loss rate would produce a lowered shell mass. Luckily, taphonomic loss rates may be lowest at the salinity extremes (Powell et al. 2006) and, at low salinity, the effect would substantively offset the lower shell input rates resulting from lower characteristic adult size. Though as yet unexplored, lower shell loss rates at low salinity may be a key to the survival of oyster beds at the extreme salinity reaches of the animal's range. On the other hand, the tendency, albeit anecdotal, for low-salinity beds to succumb preferentially to depositional processes may be as much because of the lower rates of shell addition as to the influence of increased sedimentation near the riverine suspended sediment source.

Factors influencing growth rate independent of age modulate shell content when age-dependent mortality holds sway. An increase in the average size at death from 70–90 mm doubles shell mass. Thus, food supply, a key ingredient determining growth (Powell et al. 1995b, Wilson-Ormond et al. 1997, Hyun et al. 2001), is a critical environmental variable maintaining the shell bed.

Variations in the shell resource are both muted in amplitude and delayed in response in comparison with changes in population abundance. One consequence of this is to view the shell resource as a static, conservative property of the ecosystem. However, the very properties that confer a limited response to relatively large scale, but short-term, changes in population dynamics guarantee a relatively long-term recovery from persistent changes that eventually result in substantive changes in shell mass. Thus, management of the shell resources must minimize the incremental deterioration of shell content that ultimately will produce reductions in shell coverage taking decadal periods for recovery. Fishing is one good example.

Fishing

Fishing is a unique activity in that the mortality of the population is increased without concomitantly increasing the shell addition rate. As a consequence, fishing has two profound effects. First, abundance is reduced. Second, a reduction in shell mass is enabled because the shell removed by the fishery is shell not available to support the demands of taphonomy. It is unlikely that fishing directly reduces shell content on the bed substantially unless the activity involves the removal of spatting shell for grow-out on leased grounds, because most oysters going to market are culled of attached shell (Powell et al. 2005). The transplant of spatting shell, a time-honored approach to exploitation of the resource, once widespread (e.g., Fegley et al. 1994, Powell et al. 1997, Kraeuter et al. 2003a), has fallen into disfavor in some areas of the east coast influenced by disease, because mortality rates are too high to sustain the minimal recovery of approximately 1 bushel of marketable oysters per bushel of spatting shell transplanted (Menzel 1950a, Menzel 1950b, Owen 1953, Gunter 1955). Regardless, this approach removes a disproportionate volume of shell, despite the lower efficiency of capture of shell in comparison with oysters (Powell et al. in press, Powell et al. 2002, Powell & Ashton-Alcox 2004) and should be eschewed, unless the bed can be retained in shell balance with the removal. This latter, from the simulations herein, is an unlikely outcome.

The direct-market fishery, the direct removal of market-size animals from an oyster bed for sale, removes little surficial shell, but direct marketing nevertheless imposes a reduction in shell content, albeit indirectly, because marketed animals fail to die naturally and thereby fail to add shell to the bed. This reduction is most profound at low fishing rates, with shell content declining proportionately less as fishing mortality increases. Fishing can be a relatively benign activity if the fishing rate is much lower than the natural mortality rate: $f \ll m$. Under this condition, natural processes dominate the fate of the shell resource because most of the animals destined to die naturally achieve that goal; but this requires $f \ll 0.1 \text{ y}^{-1}$, a fishing mortality rate rarely countenanced. In contrast, fishing mortality rates at the scale estimated, for example, for the Chesapeake Bay by Jordan et al. (2002) and Rothschild et al. (1994) impose a significant cost to the shell budget. Regardless, simulations covering a range of fishing rates indicate that no fishing rate exists that is ultimately sustainable of the shell resource over the long term. Any fishing rate will abet the taphonomic and depositional processes conspiring to debilitate the oyster bed habitat. Thus, fishing in the absence of shell replenishment is certain, over time, to degrade the bed. It is no accident that

management advice over the history of the oyster fishery has emphasized shell planting.

CONCLUSION

Shell is a finite, but renewable resource, under pristine conditions. Oyster population dynamics, in particular the non-disease mortality rate, appear to be conducive to the maintenance of and maximization of the shell resource on which the population ultimately depends. In fact, the mortality rate of the oyster prior to the advent of disease seems to be gauged specifically to maximize shell supply, thus assuring long-term population survival. The influence of humans is necessarily destructive of that resource, in that interventions normally result in reducing shell input to the bed. This destabilization is minimized, however, over a range of moderate disease-induced mortality rates, particularly if not of permanent duration. Thus the oyster bed is protective of its shell resource in dampening the influence of external factors on the shell content thereon. However, the same dampening effect also minimizes recovery of the shell resource, once debilitated. The perversity of the apparent short-term resiliency of the shell resource and the rapid demise over decadal time periods is the manager's bane and has resulted in the all too often observed loss of oyster reef habitat. It is likely that most such loss is not the proximate result of depositional processes but in fact the direct result of low abundance and taphonomic loss. The former may be partly contributed by the fishing process, certainly in some areas where overfishing has been a time honored tradition, but the influence of disease lowering abundance is significant and persistent periods of recruitment failure are even more so. The burial of oyster beds by siltation, though ultimately the conclusion of the process in many cases, is unlikely the dominant process effecting habitat decline. Siltation and burial are the result of taphonomic loss outweighing the addition rate of carbonate, very likely, rather than the determining agents of habitat decline.

Successful management of the oyster shell resource is obstructed by the simple fact that no additional mortality, whether natural or through fishing, can occur that will not result in habitat loss. The agents mitigating against maintaining equilibrium in the shell resource operate nonlinearly in their proficiency in debilitating the habitat and with disparate trajec-

tories. Thus, the extremes of natural mortality generate disproportionate declines in shell stock whereas small reductions in recruitment rate per adult and the initiation of fishing generate relatively large effects in comparison with their extremes. The shell resource is maximized when the population is at predisease mortality rates and unfished. Thus, if fishing is to be permitted or if disease has increased persistently the natural mortality rate, the only recourse of the manager is the perpetual addition of shell in compensation for the loss or the acceptance of the degradation of the shell bed. Certain management options may reduce the rate of degradation, setting $f \ll m$ being an important example, and these might be pursued, but no management option exists to eliminate degradation without replenishment of the shell debt imposed by the rise in mortality.

The simple model promulgated herein demonstrates that the marriage of the dynamics of the living resource and the shell on which it depends is tractable theoretically and in practice and sufficiently simple to be exposed to the vicissitudes of the management forum. One can evaluate the steady state relationship of abundance and shell stock under population dynamics as influenced by nature and man. One can estimate the likelihood that certain scenarios will lead to a decline in shell stock and ultimately permanent damage to the resource. Whereas we remain uncertain about a number of critical issues, including the influence of shell on the recruitment rate, the explanation for geographic variations in the rate of shell loss, the interaction of the surficial shell layer with the underlying shell bed, and the mechanisms by which taphonomy removes shell, the present state of knowledge is not so limited as to abrogate the inclusion of the shell resource in management decisions, nor should we decry the goal of simultaneously achieving sustainability in the stock and the habitat. The demands of Eqs. (1) and (2) should lead the way.

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