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SITE SELECTION FOR OYSTER HABITAT REHABILITATION IN THE VIRGINIA PORTION OF THE CHESAPEAKE BAY: A COMMENTARY

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ABSTRACT A significant body of knowledge has been generated during the past decade on disease tolerance of the native oyster *Crassostrea virginica*. A major opportunity to move into a large-scale field application phase of that knowledge has been presented by a 10-y commitment by the U.S. Army Corps of Engineers (ACOE) to a partnership in Virginia focused on widespread restoration of oyster resources for ecological purposes. The partnership involves ACOE, the Virginia Institute of Marine Science (VIMS), the Virginia Marine Resources Commission (VMRC), and the Chesapeake Bay Foundation (CBF). This collaboration will effect a sequenced restoration effort involving site selection, site restoration, brood stock addition from known genetic lines, evaluation of the stock in the new location for disease tolerance and/or contribution to cumulative recruitment, and, through adaptive management, will seek to optimize the widespread restoration of the oyster populations in Virginia. This contribution focuses on the importance of site selection in this effort, paying particular attention to the roles of (1) demographics and disease status on fecundity of brood stock, (2) larval feeding and growth rate in high-turbidity conditions typical of low-salinity sanctuaries from disease, (3) ontogenetic changes in larval behavior in such conditions, and (4) the role of estuarine circulation in retaining larvae in regions suitable for subsequent recruitment. We argue that while efforts to develop disease-tolerant brood stock may contribute to restoration efforts, without parallel guiding knowledge of items 1–4 above, efforts at restoration will at best be serendipitous, at worst be doomed to failure, and that site selection in restoration is crucial to success.

KEY WORDS: Chesapeake Bay, *Crassostrea virginica*, restoration

INTRODUCTION

A major opportunity to move into a large-scale field application phase of advances in disease tolerance of the native oyster *Crassaostrea virginica* has been presented by a 10-y commitment by the U.S. Army Corps of Engineers (ACOE) to a partnership in Virginia focused on widespread restoration of oyster resources for ecological purposes. The partnership involves ACOE, the Virginia Institute of Marine Science (VIMS), the Virginia Marine Resources Commission (VMRC), and the Chesapeake Bay Foundation (CBF). This collaboration will effect a sequenced restoration effort involving site selection, site restoration, brood stock addition from known genetic lines, evaluation of the stock in the new location for disease tolerance and/or contribution to cumulative recruitment, and, through adaptive management, will seek to optimize the widespread restoration of the oyster populations in Virginia.

This contribution focuses on site selection, paying particular attention to the role of oyster demographics, fecundity, larval biology, and estuarine circulation in determining the probable success of long-term recruitment. A temporal context is important in developing the rationale for the proposed study. Oysters are a primitive molluscan form with an extensive fossil lineage. They use a primitive planktotrophic larval form. The complex life history of the species, the remarkable physiologic range of tolerance of the adult form and its individual longevity, have served it well in coastal regions that exhibit ephemeral (in geological time) appearance and disappearance of estuaries in dynamic coastal temperate climate regions. Larvae serve as the initial colonizing life stages as estuaries are formed—it is the behavior of these larvae in complex estuarine circulation that facilitates this initial invasion. The adult form establishes long-term residency of the estuary by providing a local larval source, ensuring continued recruitment when conditions allow, and accreting reefs to facilitate recruitment of subsequent generations. These are classic examples of source-sink dynamics (Pulliam 1988, Pulliam et al. 1991, Pulliam et al. 1992, Hanski 1994) during periods of thousands of years. To persist, the adult form must survive the annual temporal variations in a local environment, whereas the larvae survive only a narrow window in that time frame. Oysters are a classic example of the evolution of two distinctly successful evolutionary life stages that are different in their individual environmental tolerances and optima. The complex life history and ancient lineage of oysters argue that the traits of the larval and adult forms are highly conserved [see contributions in McEdwards (1991), Hall & Wake (1999)]. Furthermore, within the conservative limitations of both life history stages, it is realistic to expect limited phenotypic plasticity in response to rapidly (on an evolutionary time scale) changing local environments. Indeed, in a classic evolutionary sense, it is rapid changes in local environments that lead to local extinction.

Consider the situation faced by a collaboration of scientists and managers in restoration of the Chesapeake Bay oyster resource. The watershed has been irretrievably altered in the short period since Colonial settlement with accompanying change in water quality in an absolute sense and in seasonal runoff variability. The estuarine environment has been and continues to be radically altered by fishing, shoreline development, and maintenance of navigable channels. Such rapid change in local conditions would be a stress contributing to local extinction. In addition, two diseases (*Perkinsus* and *Haplosporidium* = MSX) are now endemic in the local populations, one of which (MSX) did not co-evolve with the local oyster populations. Such rapid changes in disease stress could contribute to local extinction. Extant oyster populations are limited to low-salinity sanctuaries. We know that oysters survive over a remarkable salinity range, but we do not know the extent of the low-salinity stress as a suboptimal environment—the abundant oyster literature is remarkably devoid of good data on low-salinity responses because so much literature is devoted to response in optimal environments. The low-salinity sanctuaries are in closer proximity to increasingly turbid regions of the upper estuary that adversely affect optimal feeding in both life-history stages, arguably more so in the larval stage. The exile of reproductive adults

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and larvae to low-salinity, turbid regions would again be a stress contributing to local extinction. Given this litany of stresses, it is indeed surprising that oysters have not become locally extinct.

Placement of three-dimensional reef sanctuaries and enhanced shell plantings (two-dimensional extensive substrate enhancement) cannot have the consistent expectation of stimulating long-term cumulative recruitment when placement is based on geological footprints of reefs that successfully survived for millennia prior to the radical environmental changes that have occurred since Colonial settlement. The environments in which those reefs formed reflect the conservative evolutionary traits of the native oyster—they do not reflect the current, post-Colonial local environment. A recent comprehensive map-based illustration of restoration activity to date in Virginia waters is given by Berman et al. (2002). Though the placement of reefs to date has been guided by a cumulative commonsense approach to data on both long-term disease impact and a much longer term history of oyster productivity (e.g., Baylor 1894, Haven et al. 1981), it has resulted in highly variable temporal (interannual) and spatial success in recruitment [see Bartol & Mann (1997), Luckenbach et al. (1999), Mann (2000), Mann (2001)]. This should not be surprising to us in that the larval and early postlarval stages are challenged by conditions that, we argue, are commensurate with local extinction. If we are to be successful in restoration of oyster populations, we must understand the limitations of the larval forms within this new (to them) suite of adverse environmental variables.

ILLUSTRATING THE CHALLENGE NUMERICALLY, PART 1: COMPONENTS OF THE CALCULATION

The relative importance of brood stock fecundity, larval growth and survival, and larval retention in contributing to the recruitment of a subsequent generation can be illustrated by a numerical approach to life cycle descriptions. Originally and elegantly described by Paulik (1973), this approach was adapted by Mann and Evans (1998) in estimation of oyster, *Crassostrea virginica*, standing stock, larval production, and advective loss in relation to observed recruitment in the James River, Virginia. The current illustration simplifies this approach using a virtual population to examine the effects of three parameters on recruitment in subsequent generations. These parameters are (1) varying egg production by varying age-specific mortality of the parent population as a proxy for disease impacts, (2) varying duration of larval period in response to suboptimal feeding conditions, and (3) varying loss to advection related to estuarine tidal exchange. To summarize and simplify Mann and Evans (1998), recruitment, R, to the 25-mm size class is estimated from larval supply thus:

$$R = (F_{tot} \times F_q \times F_s \times F_d \times F_f) \times (1 - exch)^{2d} \times (1 - L_{mort})^{d} \times P_{sub} \times P_{foul} \times P_{met} \times (1 - J_{mort})^{dp}$$

F_{tot} is total egg production and is estimated from size-specific fecundity. It is a cumulative total for all individuals (F_{ind}) in all size classes and typically estimated from length:dry weight estimators. In the current illustration, all sizes below 40 mm are considered young of the year (spat) and do not contribute to spawning, and fecundity is estimated from relationships given in Thompson et al. (1996) and Mann and Evans (1998). F_q is a sex ratio modifier. Cox and Mann (1992) suggest parity in sex ratio. Given the lack of other data, a single sex ratio modifier, F_q, with a value of 0.5 (50% female in all size classes) is used in this illustration. F_s: F_{ind} and hence F_{tot} can be modified based on salinity (S) effects. Mann and Evans (1998) suggested the following estimators for F_s:

$$\text{if } S > 13.5,\ F_s = 1.0\text{: if } S < 13.5, \text{ then } F_s = [(S - 8.0)/(13.5 - 8.0)] \times 1.0 = (S - 8.0)/5.5$$

F_d modifies fecundity for disease effects with values ranging from 1.0 to 0.0. In the current illustration, it varies from 1.0 to 0.75 (a 25% reduction based on disease impact). F_f describes a density-dependent multiplier for fertilization efficiency with values from 1.0 (100% fertilization) to 0.0 (no fertilization). It is based on Levitan (1991) where:

$$\log \%\ \text{fertilization} = [0.72(\log OD) + 0.49] \text{ or,}$$
$$\%\ \text{fertilization} = [0.49 \times OD^{0.72}]$$

where OD is oyster density in numbers m^{-2}. In the current illustration, it is rewritten thus:

$$F_f = 0.0049 \times OD^{0.72}$$

Production of larvae (strictly speaking embryos or fertilized eggs) m^{-2} is therefore estimated by ($F_{tot} \times F_q \times F_s \times F_d \times F_f$) in units of larvae m^{-2}.

Mann and Evans (1998) estimated retention of the larvae within the James River during planktonic development using the three-dimensional flow model of Hamrick (Hamrick 1992a, Hamrick 1992b) to provide source and sink data at scales within the estuary. For the current illustration, a simple dilution function, $(1 - exch)^{2d}$, is used that assumes uniform dispersal within the estuary and proportional loss on each tidal cycle; that is, larvae are assumed to be neutrally buoyant and exert passive swimming behavior in response to oriented stimuli. Thus, larval numbers decreased with days with the duration of planktonic development by the function where *exch* is proportional volumes exchanged on each tide. The value of *exch* varies in the current study between 0.1 and 0.2 (0.2 equals a 20% exchange per tidal cycle), and d is the duration of the larval development (= planktonic) period. The correction 2d is used with a simple assumption of two tidal exchanges per day. In the current study, d varies from an optimum of 21 days, based on values from Mann et al. (1994), Mann and Evans (1998), Bochenek et al. (2001), and Powell et al. (2002), to a suboptimal value of 25 days based on assumed reduction of feeding and hence growth in low-salinity and/or high-turbidity regions.

The function $(1 - L_{mort})^{d}$ estimates larval mortality in the water column. L_{mort} is the daily larval mortality rate [a proportional value between 1.0 (all died) and 0.0 (no mortality)]. Survival is $(1 - L_{mort})$ for a period of one day or $(1 - L_{mort})^{d}$ for a "d" day planktonic development period. For the current illustration, L_{mort} is set at 0.05, 0.06, 0.07, 0.1, and an extreme value of 0.25. The decreasing exponential relationship ensures a gradual decreasingly sensitive response to increasing values of d. Modification of the original number of larvae to account for dispersal loss and mortality provides an estimate of larvae surviving to immediate premetamorphic size. The transition to an attached benthic form requires successful location of substrate, that the substrate not be occluded by competing organisms, and that the larvae have sufficient energy reserves to complete the metamorphosis to a juvenile feeding form.

P_{sub}, a dimensionless modifier with a value between 1.0 and 0.0, describes the probability of finding suitable substrate. The time scale and availability of shell substrate is crucial to successful recruitment (Morales-Alamo & Mann 1990). Consider that a shell layer 1-cm thick covering 1 m^2 of bottom has a volume of 10 L. For the current illustration, a premise is adopted that a shell layer a minimum of 1-cm thick is required to offer a suitable substrate. P_{sub} is estimated thus:

$$\text{If shell volume} > 10\ \text{L m}^{-2},\quad P_{sub} = 1.0$$
$$\text{If shell volume} < 10\ \text{L m}^{-2},\quad P_{sub} = 0.1 \times \text{shell volume (in L)}$$

P_{foul} describes proportional occupation of the substrate by competing organisms and varies between 1.0 (no fouling) to 0.0 (complete preclusion of settlement). Rheinhardt and Mann (1990) suggest a value of $P_{foul} = 0.33$ based on field studies in the James River. For the current illustration, a constant value of 1.0 is used.

P_{met}, describes the probability of successful completion of metamorphosis to the attached form on a 1.0 (all survive) to 0.0 (no survival) scale. For the current application, the value is set at 0.20.

Recruitment, *R*, to the benthos is therefore estimated from larval supply values by incorporating $(1 - exch)^{2d}$, $(1 - L_{mort})^{d}$, P_{sub}, P_{foul}, and P_{met} thus:

$$R = [(F_{tot} \times F_q \times F_s \times F_d \times F_f) \times (1 - exch)^{2d} \times (1 - L_{mort})^{d} \times P_{sub} \times P_{foul} \times P_{met}]$$

$(1 - J_{mort})^{dp}$ modifies this estimator for postsettlement mortality and growth rates, both of which are known to be size dependent (Roegner & Mann 1995). Mann and Evans (1998) describe daily juvenile mortality rate as J_{mort} (proportional with a value between 0.0 and 1.0). Survival is $(1 - J_{mort})^{dp}$, where dp is the number of days to grow to a defined size. Based on values of J_{mort} in Roegner and Mann (1995), Mann and Evans (1998) suggest a cumulative mortality to 8-mm length of 93% during a 28-day period, a calculated value for J_{mort} of 0.09. Thus, $(1 - J_{mort})^{dp}$ for the current study is set at 0.07 to 8 mm length. Above this, length of J_{mort} is lower and set at 0.05 for another 25 days until a size of 25 mm when the surviving individuals are considered recruits to the subsequent generation (Eggleston 1990). For the current illustration, $(1 - J_{mort})^{dp}$ incorporates two mortality rates with a cumulative mortality value for the premetamorphosis larvae to 25-mm size class, including a P_{met} value of 0.20 is 99.84%, or a proportional survival of 0.0016.

ILLUSTRATING THE CHALLENGE NUMERICALLY, PART 2: DEVELOPING A GROWTH AND AGE VERSUS LENGTH ESTIMATOR

There are surprisingly few studies of oyster growth rate in the field in the Chesapeake Bay that can be directly related to expected growth on the bottom in reef situations. There are no such prior studies in the upper James River. For the current application, we used data from a growth study using two populations of naturally settled oyster spat collected in the James River in 1992. The populations were collected from dredge hauls on separate days and were thus treated as replicates. Spat on shells were placed in plastic mesh cages on the bottom at Horsehead reef in the upper James River [see Haven & Whitcomb (1983), Berman et al. (2002)]. Approximately 200 oysters were contained in each of three cages. Population #1 was collected on 10/15/92 contained in two cages, population #2 was collected on 11/11/92 and contained in one cage. Population #1 was contained in two rather than one tray because of the mass of shell to which the oysters were attached. Measurements of length were made at regular intervals for random samples of oysters from within each cage(s) for the period 10/15/92–7/27/93 for population #1, and for the period 11/11/92–1/28/93 for population #2. After these respective periods, all oysters were measured (Table 1). Data for population #1 was pooled from both cages to avoid pseudoreplication. At sampling events, data were also collected on water temperature and salinity. A description of growth over time is obtained from a plot of time versus the mean length (maximum linear dimension) of the oyster (Fig. 1). The spat on shell were from summer 1992 recruitment but of unknown absolute age, thus time is given in Figure 1 as days after 1/1/92. Oyster growth varies seasonally such that a classic Von Bertalanffy equation describing growth would mask this important seasonal fluctuation. Thus, a modified Von Bertalanffy plot with growth oscillation corresponding to seasonal change in growth rate was used. This takes the following form:

$$Lt = Linf. \times \{1 - e\text{-}k\,[(t - to) + A - B]\}$$
$$\text{where:}\quad A = C. \times \sin[2 \times pi \times (t - ts)]/(2 \times pi),$$
$$\text{and}\quad B = C \times \sin[2 \times pi \times (to - ts)]/(2 \times pi)$$

where Lt is the estimated length at time t, Linf is asymptotic length, set at 120 mm based on field observations, K is the growth constant, to is age at which length is zero, C is the amplitude of the growth oscillation, and ts is the starting point of the oscillation with respect to t = 0 (1/1/1992).

TABLE 1.

Observed growth of oyster populations at horsehead.

		Population #1 mean		Population #2 mean	
Date	Temp (C)	*n*	length (mm)	*n*	length (mm)
10/15/1992	19.8	196	15.8		
11/11/1992	13.8	202	16.7	100	15.4
12/9/1982	7.6	140	16.2	79	16.4
1/28/1993	7	201	16.7	98	15.3
3/31/1993	12.4			175	14.1
4/14/1993		211	16.2		
5/3/1993	18.5	210	16.6	120	17.3
6/2/1993	22	239	16.7	94	17.9
6/28/1993	27.2	212	20.2	77	21.1
7/27/1993	28.8	208	25.3	76	26.6
8/24/1993	28.1	251	28.1	75	30.7
10/25/1993	19	251	33.2	75	36.8
11/16/1993	14.8	251	33.8	72	37.3
12/13/1993	8	243	33.9	72	37.6
4/4/1994	14	243	33.6	72	37.0
5/9/1994	18.5	235	33.2	72	36.7
6/10/1994	24.2	232	33.9	71	37.4
7/11/1994	28.6	234	37.1	70	41.4
8/8/1994	25.8	234	39.3	69	42.8
9/13/1994	24.5	230	41.4	69	43.9
10/18/1994	18	230	44.3	68	47.2
11/15/1994	17	230	45.3	68	49.0
2/20/1995	5	227	45.8	67	49.0
4/18/1995	16.9	229	45.4	65	49.1
5/24/1995	23.1	228	46.2	65	49.7
7/14/1995	28.9	160	47.2	38	50.7
8/29/1995	26.4	131	51	32	52.7
9/27/1995	20.7	135	52.2	30	52.9
10/17/1995	10.5	122	56.5	28	54.7

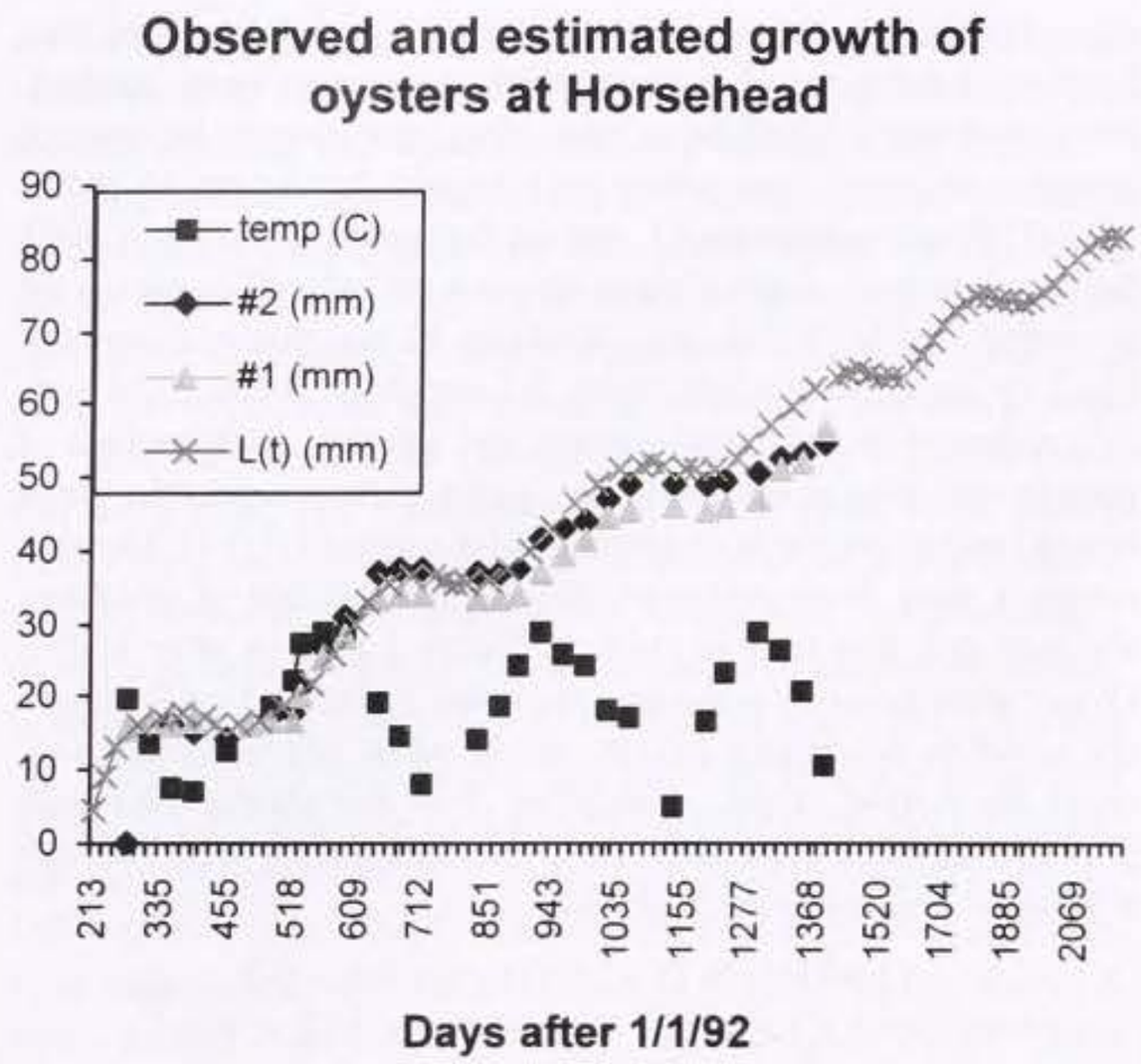


Figure 1. Observed and estimated oyster growth at Horsehead Reef, James River, 1992–1995.

The parameters of this function were estimated by fitting a rearranged function to the size increment data of a data set which records serial increase in length over time so that we have values of L1, L2, and so on. The rearranged function is:

$$L2 = Linf \times \{1 - (1 - L1/Linf) \times e{-}K\,[(t2 - t1) + A' - B']\}$$

$$\text{where } A' = C.\ \sin\,[2 \times pi \times (t1 - ts)]/(2 \times pi),$$

$$\text{and } B' = C.\ \sin\,[2 \times pi \times (t2 - ts)]/(2 \times pi).$$

The parameters were estimated for this data set at the following values: K = 0.204, to = 0.36, and ts = 0.608. From length at age data, a matrix is created of both length and growth rate versus time. Estimated length, L(t), versus time is superimposed on observed data in Figure 1. Estimated growth rate, expressed as mm/month increment, for each year class was calculated and subsequently rearranged as a rate versus temperature matrix. Matrix values were used to generate linear descriptors of monthly growth rate in relation to temperature for each year class. The relationship is in the form: y = mx + c and is expressed as mm/month growth increments. Values are given in Table 2. There is a strong correlation between temperature and growth rate suggesting that the latter can be estimated from the former with a high degree of confidence, despite the obvious influence of seasonally varying factors, such as salinity turbidity and food supply, on growth.

Figure 1 illustrates a limitation of the seasonally oscillating fit equation: the possibility of negative growth rate estimation in the winter months. This is a product of the form of the equation with a positive and a negative component. The values used to generate the equation were means, and if error bars are generated around those means, then the brief period of negative growth inferred in Figure 1 is within the error bars. The negative mean growth rate values are small and are not further adjusted for the current model; however, the question arises of the most suitable form of an oscillating growth estimator, especially in a situation such as the James River where winter temperatures are sufficiently low to cause growth to cease, but the rapid spring rise in temperature results in a similarly rapid transition to a high growth rate. This rapid transition in growth rate may be easily masked in a typical growth study with fixed time intervals. True representation of the transition in growth rate around the time of transition will require increased frequency of sampling.

TABLE 2.

Estimation of size specific growth rate incorporating temperature effects.

Month	Temp (C)	Estimated Monthly Growth Rate (mm/month) = (mx + c) Where x is Mean Temperature		
J	4.8			
F	5.1			
M	7.9			
A	13.7		m	c
M	19.0	year 0	0.27	−2.80
J	24.1	year 1	0.20	−1.74
J	27.0	year 2	0.17	−1.42
A	27.2	year 3	0.14	−1.16
S	24.6	year 4	0.11	−0.94
O	19.2	year 5	0.09	−0.77
N	13.7	year 6	0.07	−0.64
D	8.3			

A point of considerable impact that is illustrated by Figure 1 is the estimated age of James River oysters at 62.5 and 76 mm length, respectively (2.5 and 3.0 inches). Both lengths have been used to discriminate seed from market oysters in the commercial fishery in the decade of the 1990s. Though the popular consensus offered in public discussion of size limits in the James River public oyster fishery is that the difference in age between the two sizes is small, Figure 1 suggests otherwise. Animals may exceed the lower size limit in the age range 3.6–4.2 y, but the inflection of the length versus age curve in the mid–70s-mm range suggest that oysters of greater than 76 mm may be 5.5 or more years old. Thus, the increment from 62.5 to 76 mm length may require as much as two years to attain. The management implications are significant; decreasing the maximum size and subsequently reversing that size limit may require up to two years for stocks to recover to former demographics. Also, decreasing the size limit deprives the population of two extra year classes of spawning adults.

ILLUSTRATING THE PROBLEM NUMERICALLY, PART 3: AN EXAMPLE WITH A VIRTUAL POPULATION

Demographics for a virtual population were generated from a data set describing Horse Head Reef in the upper James River for the period 1994–1998 (R. Mann & J. Wesson, unpublished data shown here as Figs. 2A and 2B). This population was chosen because it was (a) stable over that period with respect to recruitment, total oyster density, and oyster demographics, and (b) suffered essentially no mortality due to disease. The size frequency distribution (in 5-mm size classes) was converted to an age frequency demographic using the age-length estimator described earlier.

The virtual population demography is illustrated in Figure 2C, as a series of populations (A–E inclusive) generated by gradually increasing age-specific mortality (illustrated as cumulative mortality in Fig. 2D) chosen to simulate the effects of increasing disease prevalence and intensity. It is notable that the extreme population, E, represents an approximation of current disease tolerance in the most selected strains under typical disease challenge in medium-

salinity waters. Each virtual population has the 25-mm size class, here considered the young of the year recruits or zero class, set at 100 oyster m^{-2}. This corresponds to the *R* value for recruitment to the benthos in the previously described estimator. In all simulations, performed as a sequential spreadsheet in Microsoft Excel, the barometer for maintenance recruitment of a subsequent generation is attaining a 25-mm size density of 100 oyster m^{-2}. The simulation was run for a single generation time frame with each of A–E as the starting demographic under various scenarios and the end points illustrated in Figures 2E–2L. Although these are just a subset of the many options that can be run with the simulations, they illustrate the following important points:

(a) Under low tidal exchange (*exch* = 0.10) and optimum larval development (d = 21), the recruitment values are very high even with L_{mort} rates (Fig. 2E). With low L_{mort} rates, population A exhibits values of *R* approaching two orders of magnitude above a maintenance recruitment. Consider, however, that the scenario uses many optimal conditions including no reduction in fecundity attributable to salinity, no shell limitation to settlement, and only modest competition for substrate. This is very much an optimal scenario.

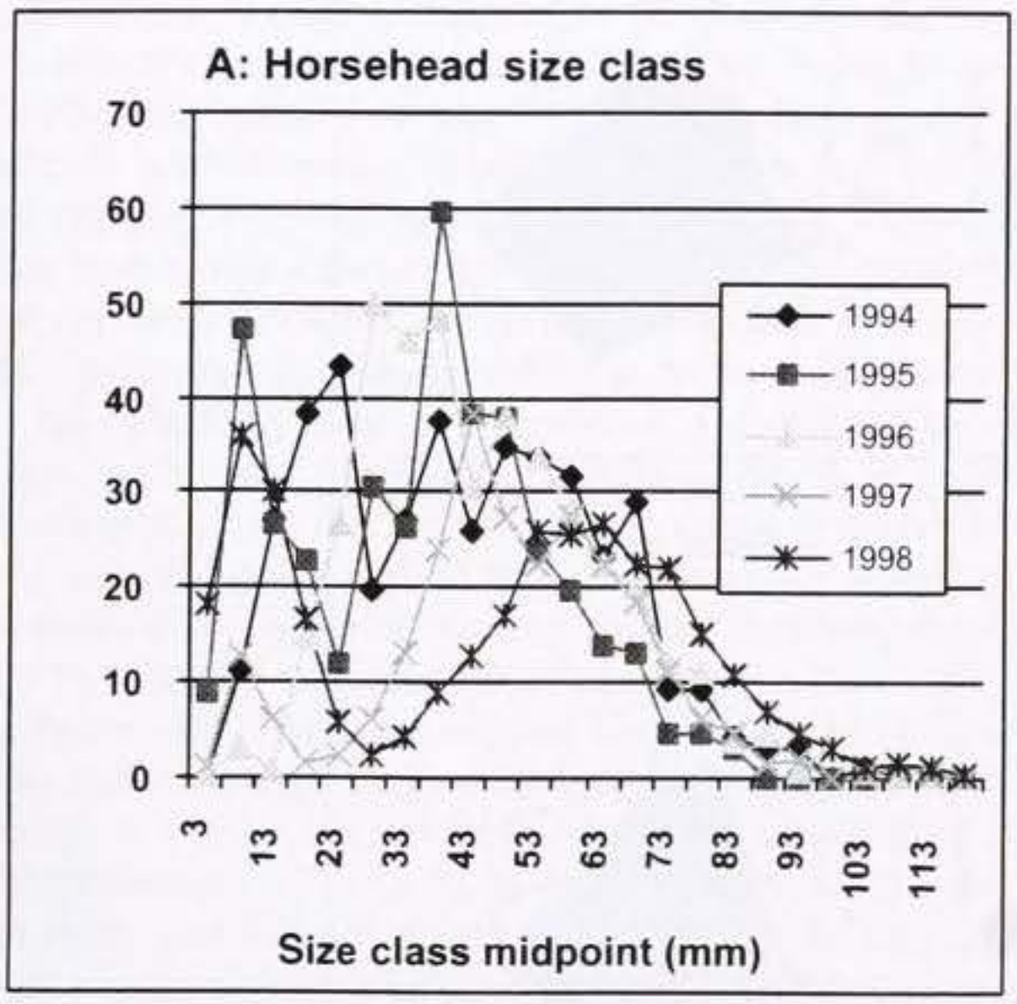
(b) Increasing larval duration by only 4 days (d = 25) reduces recruitment considerably (Fig. 2F), but still at least an order of magnitude above maintenance for optimal demographic profiles.

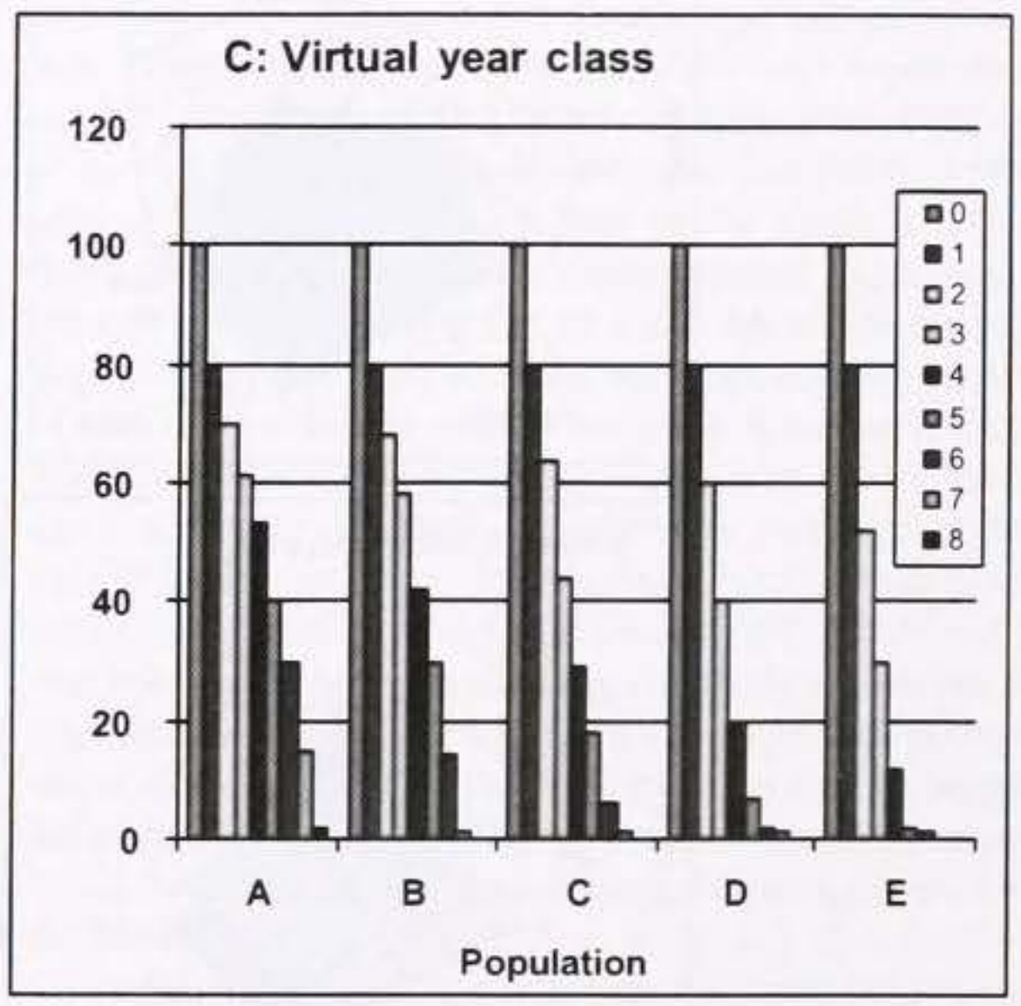
(c) Increasing tidal loss to 20% drives all recruitment values below the critical 100 m^{-2} even with everything else at optimum (Fig. 2E).

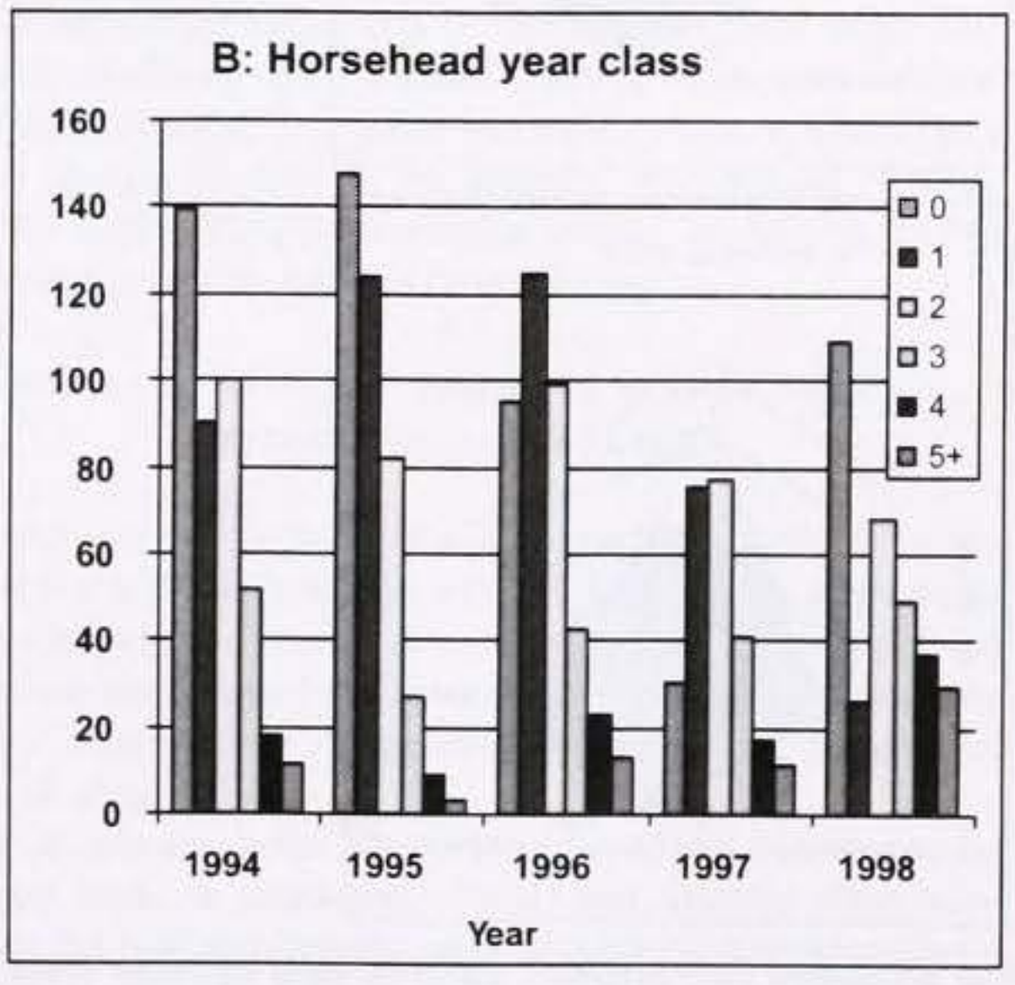
(d) Reducing fecundity by 25% as a proxy for impact of disease and/or salinity has a proportional effect (Fig. 2F).

(e) Reducing fecundity by 25% and increasing tidal loss to 15% provides options for all population structure from A through E to recruit at <100 m^{-2} depending on larval mortality rate—even with all other factors optimized!

The "take home" message from these illustrations is the







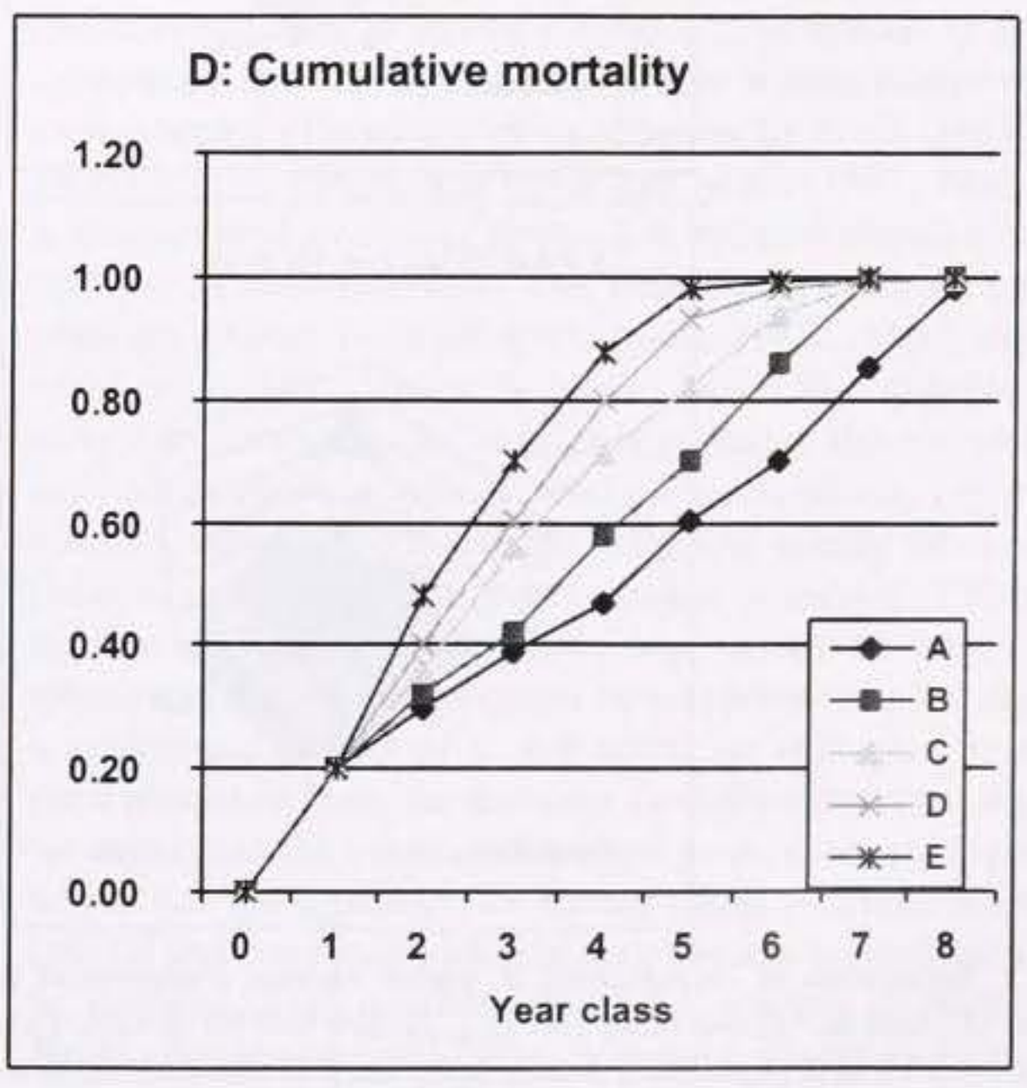


Figure 2. Continued on next page.

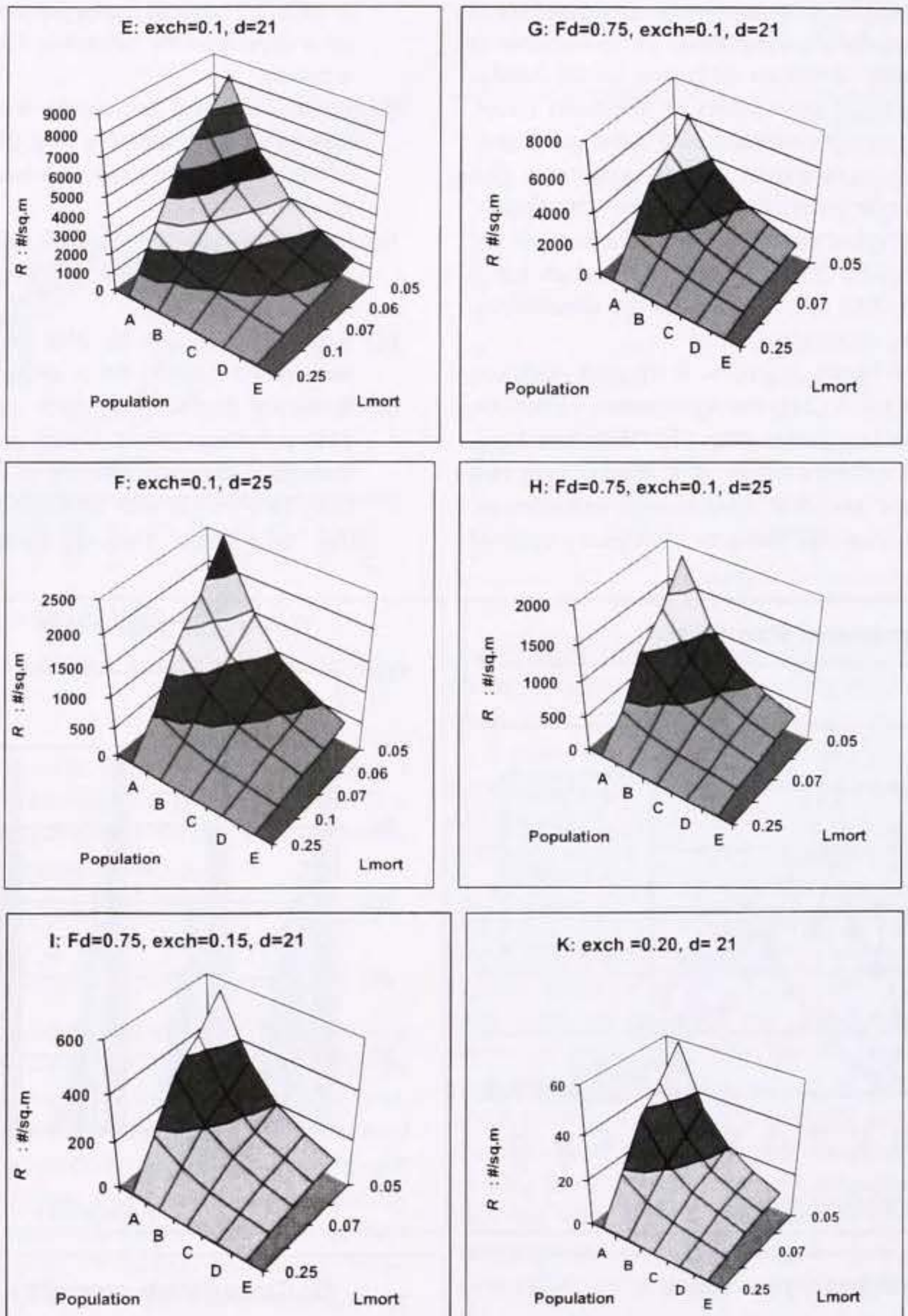


Figure 2. Estimation of recruitment, R, under various scenarios of initial population demographics, estuarine tidal exchange (exch), larval duration (d), and larval mortality rate (L_{mort}). See text for details. (A) Demographic data from Horsehead Reef 1994–1998. (B) Data recast as age class. (C) Virtual population demography used in simulations as a series of populations (A–E inclusive) generated by gradually increasing age-specific mortality (illustrated in D). (E–L) End points of simulations with varying values of exch, d, and L_{mort}.

very nonlinear response to various combinations of tidal exchange, reduced fecundity, and larval duration as we move away from an optimal combination. Even the most stable population structure, A in Figure 2C, may produce marginal recruitment scenarios despite the optimization of shell and substrate competition (P_{sub} and P_{foul}) and with no consideration of greater impact of postsettlement mortality. In a large number of slightly less than optimal scenarios, a population approaching current "disease tolerant" strains under sustained disease pressure—E in Figure 2C—is prone to inadequate recruitment. In other words, disease tolerance alone will not get us to where we want to be in current restoration work. In practical terms, failure to effect restoration in the optimal location will result in failure in recruitment. Optimal location is a product of species traits that are arguably very conservative because of the evolution of the species [again see McEdwards (1991), Hall & Wake (1999)] in combination with circulation patterns of the host estuary—a unique feature. Critical oyster traits in this mix include, but are not limited to, adult egg production, a trait for which we have not actively selected in breeding programs to date, and larval feeding ability and swimming behavior in turbid conditions. Fecundity is critical to driving the simulation as shown, yet we know essentially nothing of size–fecundity relationships under challenging conditions in which we are attempting restoration. Both larval traits are arguably very highly conserved because of structural limitations in the velar structure and the clear selective pressure over time for larval forms that recruit in optimal rather than suboptimal environments. Turbid conditions can be viewed as transitions in the ephemeral lives of estuaries on a geological time frame, signals for oyster populations to move as they have done over periods of sea level rise. Larvae have no reason to evolve to survive in regions doomed to local extinction by rapidly changing environments—their conserved feeding abilities and behavioral strategies have served them more than adequately without such abilities. Restoration efforts thus match a suite of larval traits with conditions that we strongly suspect are very far from optimal, yet we often proceed in the absence of knowledge as to how debilitating this mismatch may be to the desired end point. These troubling scenarios, well founded in both our current understanding of the evolution of complex life history and simple numerical simulations of recruitment processes in virtual populations under near optimized conditions, are cause for concern. Without quantification of the individual data needs and their holistic synthesis in a practical model, the options for adaptive management of long-term, very high dollar cost restoration efforts, are limited, indeed sobering and probably doomed to mediocrity.

ARE DATA NEEDS FOR HOLISTIC SYSTEM LEVEL RESTORATION ACHIEVABLE?

The pressing need is to build a comprehensive model of oyster reproductive biology, larval growth and behavior, in response to estuarine circulation as a holistic adaptive management tool to guide restoration efforts for *Crassostrea virginica* in "low-salinity sanctuary" zones of the Chesapeake Bay. Fortunately, the tools for this are in place.

Disease-tolerant oyster strains have been, and continue to be developed under a multi-institutional, mid-Atlantic effort supported by the National Oceanic and Atmospheric Administration's Oyster Disease Research Program in a program whose heritage can be traced back to the pioneering efforts of Harold Haskin in Delaware Bay following the early impacts of MSX. Current hatchery protocols allow for the description of the quantitative relationship between oyster size and fecundity at varying salinities typical of restoration sites. Whereas optimal salinity from literature studies may target a 15–25 ppt range, values in the 6–12 ppt range better reflect the upriver sanctuary regions of much of the Virginia subestuaries where extant oyster populations survive at the edge of endemic disease challenge. Culture of larvae from these fecundity studies at prevailing salinity under optimal and suboptimal (increased turbidity) conditions would greatly increase the confidence in growth and mortality rates as applied in the earlier simulation exercise.

The description of feeding under the combined stresses of low salinity and high turbidity remain poorly examined, although are eminently tractable in experimental systems. Mann, Kingsley-Smith, and Southworth (unpublished data) have used monocultured phytoplankton food and parallel cultures from the same source with additions of montmorillonite clay to simulate turbidity from upstream locations approaching the turbidity maximum; however, the challenge remains to use a complete characterization of low-salinity turbidity zones in terms of light penetration, particle concentration, and particle size in such experiments. The turbidity component of such data is emerging from separate studies of water quality on temporal and spatial variability in water column conditions in selected regions in the Virginia tributaries as these promote or limit submerged aquatic vegetation growth (Moore et al. 1996, Moore et al. 1997, Moore & Wetzel 2000). Sophisticated instrumentation for real-time, continuous generation of such data in transect mode is available. A critical issue yet to be examined is the changing quality of available food in these drainage conduits for disturbed watersheds. In such regions, increased run-off in conjunction with agricultural- and sewage-based nutrient enrichment serve to alter the balance of C:N:P:Si and thus the composition of the phytoplankton community. Concern over eutrophication typically focuses on mass rather than compositional issues, but it is inevitable that food quality will also change. Given the evolutionary history of larval forms, such changes can only be viewed as negative with concomitant prospects for recruitment to the benthos.

The contribution of oyster larval swimming behavior to larval retention has been extensively debated. Discussions of the additive, compounded, or antagonistic effects of these stimuli on larval swimming are offered in a series of papers by Mann (1985, 1986a, 1986b, 1988a, 1988b) and Baker and Mann (1997, 1998, 2003). Examination of swimming response to oriented stimuli are equally tractable in both laboratory and field settings using established protocols (Mann & Wolf 1983, Mann 1988a, McCarthy 1990, Mann et al. 1991, Baker & Mann 2003). The question in the current context is which (singular or plural) of these stimuli [light as intensity and/or wavelength, temperature, salinity (= density), pressure, and gravity] is relevant to the low-salinity location and is liable to modification by local increases in turbidity? Remember that we are seeking modification of a conserved behavioral response that has served the oyster larval form during the millennia, a modification particular to this recent (in geological time) temporal aberration from the optimum. In shallow upstream situations, we argue that the oriented responses to pressure are highly conserved [see the arguments for *Ostrea edulis* by Cragg & Gruffydd (1975)] and that stratification in both temperature and salinity will be minimal. This is substantiated for shallow locations in the James, Piankatank, and Great Wicomico Rivers from extensive summer survey data for the period 1985–2003 (reports available

on the VIMS Molluscan Ecology website at www.vims.edu/mollusc). We present the opinion that response to light in terms of both intensity and spectral composition as that most liable to modification, with resultant changes in larval depth stratification, and hence passive lateral dispersal; however, experimental verification of this stance must await future work.

The advancement of computer central processing power and code have fueled the development of three-dimensional transport models with biologically relevant cell sizes (with respect to known habitat heterogeneity) and time steps that have particle tracking capability in specific locations in the Chesapeake Bay. These models have been used in applications varying from water quality and sediment transport simulations to modeling circulation impacts of channel or shoreline alteration (such as in maintenance dredging or port construction), to modeling dispersal patterns of crab species with contrasting larval development (Garrison 1997), and critical placement of hard clam sanctuaries in the York River (see simulations at http://www.vims.edu/physical/WEB/York1.htm). All major restoration programs should have within their goals the development of such models as guidance tools.

Exploratory simulations can be run for virtual restoration scenarios driven by initial egg production estimates based on the modifications to the function ($F_{tot} \times F_q \times F_s \times F_d \times F_f$) as dictated by the projected additions of disease-tolerant broodstock. In a practical sense, we need realistic values for the function $(1 - exch)^{2d}$ in various locations targeted for restoration in the Chesapeake Bay by the communal efforts of ACOE, VIMS, VMRC, and others. Historical observations on the role of the Piankatank and Great Wicomico Rivers as trap-type estuaries (Andrews 1979) suggest this function to be small in both rivers. Indeed, both the Piankatank and Great Wicomico Rivers have successful histories of restoration activity (Southworth & Mann 1998, Luckenbach et al. 1999). The James River, the site of the only extant oyster fishery of any consequence in Virginia, is of historical context in terms of circulation (Pritchard 1953, Wood & Hargis 1971, Mann 1988a, Ruzecki & Hargis 1989) in that depth-related counter flows, gyre-like circulation in Hampton Roads, and tidally driven frontal systems all contribute to larval retention. These locations provide extensive historical data sets to blind test our simulations through hind casting. Iterative improvement of such simulations in turn provide for robust capability in forecasting mode and, ultimately, successful restoration of populations in the field. The challenge is simply to use this vast array of exciting tools in the task before us.

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